PLOS | BIOLOGY

PERSPECTIVE

The paradoxical extinction of the most charismatic animals

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Citation: Courchamp F, Jaric I, Albert C, Meinard Y, Ripple WJ, Chapron G (2018) The paradoxical extinction of the most charismatic animals. PLoS Biol 16(4): e2003997. https://doi.org/10.1371/journal.pbio.2003997

Published: April 12, 2018

Funding: The authors received no specific funding for this work.

Competing interests: The authors have declared that no competing interests exist.

Abbreviations: #patch, number of patches; CBD, Convention on Biological Diversity; Dyn, dynamical; IUCN, International Union for the Conservation of Nature; LC, Least Concern; MVP, minimum viable population; NGO, nongovernmental organization.

Provenance: Not commissioned; externally peer reviewed.

Abstract

A widespread opinion is that conservation efforts disproportionately benefit charismatic species. However, this doesn't mean that they are not threatened, and which species are "charismatic" remains unclear. Here, we identify the 10 most charismatic animals and show that they are at high risk of imminent extinction in the wild. We also find that the public ignores these animals' predicament and we suggest it could be due to the observed biased perception of their abundance, based more on their profusion in our culture than on their natural populations. We hypothesize that this biased perception impairs conservation efforts because people are unaware that the animals they cherish face imminent extinction and do not perceive their urgent need for conservation. By freely using the image of rare and threatened species in their product marketing, many companies may participate in creating this biased perception, with unintended detrimental effects on conservation efforts, which should be compensated by channeling part of the associated profits to conservation. According to our hypothesis, this biased perception would be likely to last as long as the massive cultural and commercial presence of charismatic species is not accompanied by adequate information campaigns about the imminent threats they face.

One of the difficulties faced by endangered species conservation efforts is the lack of a strong public support and mobilization. Whereas the biodiversity decline shows no sign of abatement, public mobilization has not scaled up with the severity of this crisis. For example, 20 million Americans took to the streets to demonstrate on the first Earth Day in 1970, but similar levels of mobilization have not been seen in the 21st century. This surprising discrepancy between the need for global mobilization to avert species extinction and the lack thereof might be due in part to the disconnection of the general public from nature [1], because many endangered species and ecosystems are of limited appeal for the broad public. Here, we argue that the problem stems from deeper roots, because even the most charismatic wild animals suffer from the same predicament. We show that, paradoxically, the most charismatic species remain severely endangered, and rather unknowingly so by the general public, a situation that has dramatically worsened over the last decades despite massive cultural and commercial presence.

The concept of charismatic species is pervasive in the conservation literature and refers to species attracting the largest interest and empathy from the public [2]. As a consequence, charismatic species are often considered as privileged by having enjoyed the bulk of conservation efforts [3]. Therefore, the conservation of charismatic species is often taken for granted, and accordingly the literature emphasizes the need to go beyond charismatic species to conserve more discrete ones [4] and even to shift the conservation focus towards units that are more integrative and less visible to the broad public, such as ecosystems or ecosystem functions [5]. Using four different methods, we established the ranking of the 10 most charismatic species for the public and reviewed their conservation status and the public knowledge of it. We unveil that the conservation status of the ten most charismatic species is grave, while the public ignores it. We surmise that this "beloved but ignored" paradox may stem from a mismatch between the virtual presence and natural presence of these particular species. We argue that the representations of charismatic species in commercial, artistic, and cultural outlets act as virtual, abundant populations competing for public attention against real threatened populations. The competitive advantage of virtual populations reinforces the perception that natural populations are not threatened and may paradoxically lessen the necessary conservation efforts and consequently accentuate the risk of extinction of these species most cherished by the general public. We propose a mechanism whereby these virtual populations would not compete against threatened species but instead benefit them through a payment mechanism represented by fees for rights of use for commercial purposes.

Identifying the 10 most charismatic animals

Although species charisma is increasingly used in conservation biology [2], this concept has never been operationalized, and which species the public considers the most charismatic has not been established. We collected data from four complementary sources to quantify the charisma of species for the Western public (see S1 Text for details): (i) an online large-scale survey ($n = 4{,}522$); (ii) a questionnaire given to primary schoolchildren of France, Spain, and England ($n = 224$); (iii) a survey of the animals displayed on the websites from zoos in the 100 largest cities in the world; and (iv) a survey of the animals featured on the covers of animated movies produced by Disney and Pixar (see S1 Text). The first two sources represented direct questions to the public about which species they perceived as charismatic, while for the other two, we worked under the assumption that the species displayed on zoo websites and movies would be selected by communication experts based on their appeal to the public. The survey on pupils was intended to complement the internet survey for which children below 15 years old represented only 0.9% of the 4,522 respondents. Collectively, these data provided a coherent list that can be considered representative of animals regarded by the Western public as being the most charismatic. We call them animals instead of species, because taxonomic precision to the species level for public knowledge was possible for none of the four sources and, among the top 10 animals cited, 2 represent more than one species. Indeed, elephants represent three species, while gorillas represent two species; we will thus hereafter mention 10 animals or 13 species. The compiled list of the 10 animals considered the most charismatic by the public was in this order (S1 Fig): the tiger (*Panthera tigris*), the lion (*P. leo*), the elephant (*Loxodonta africana*, *L.*

cyclotis, and *Elephas maximus*), the giraffe (*Giraffa camelopardalis*), the leopard (*P. pardus*), the panda (*Ailuropoda melanoleuca*), the cheetah (*Acinonyx jubatus*), the polar bear (*Ursus maritimus*), the gray wolf (*Canis lupus*), and the gorilla (*Gorilla beringei* and *G. gorilla*).

Severe endangerment of the most charismatic species

Although conservation efforts are indeed probably disproportionately focused on them, these 13 species are nevertheless in a dire conservation status (Box 1, Tables 1 and S1). Except for the gray wolf, all the species are either Vulnerable, Endangered, or Critically Endangered [6]. Furthermore, most of the species that are classified within lower threat categories, such as Vulnerable, are considered as such based on global and outdated assessments, masking important discrepancies between more threatened populations or subspecies. Although conservation biology has been particularly active the last three decades, dramatic declines have taken place over the same period, with losses often exceeding half of the entire species' population in an extremely short time (Fig 1A). One interesting observation is that direct killing constitutes one of the principal causes of endangerment, a surprising finding for the 10 most charismatic animals (see S2 Text). Moreover, population estimates are generally provided as global numbers, masking the fact that the number of breeding animals is often much lower and that the global population corresponds to many disconnected populations, many of which are too small to be viable (see S2 Text). Demographic studies of minimum viable population (MVP) show insufficient population sizes to expect high survival probabilities in the short term if strong conservation measures are not taken rapidly (Table 1).

The severe decline of species ranges is even more of a problem because all these species are large mammals requiring extended individual home ranges and correspondingly wide population distributions (S1 Table). As a result, most species suffer simultaneously from the declining and the small population paradigms (Fig 2). In the few remaining habitats of those 10 charismatic animals, the percentage of range in protected area is insufficient (41 ± 20, mean ± SD, Table 1) and the percentage of land under human pressure remains substantial (33 ± 28, Table 1). An aggravating factor for all populations is the severe fragmentation, by both the number of patches (71.3 ± 81.1, Table 1) and the surface/edge ratio (0.069 ± 0.12, S1 Table).

Public ignorance of threatened status

Perhaps even more noteworthy than the poor conservation status of the animals that people cherish the most is our finding of the lack of awareness of the public on this matter. First, with two of our approaches to identify the most charismatic species (internet survey and pupil poll), we asked respondents whether they would associate each species with being "Endangered." This attribute was selected less often than randomly, and less often than expected if the conservation status was known, suggesting that the public is often unaware that the animals they deem charismatic are threatened with extinction. Second, we conducted a targeted survey among students of the University of California, Los Angeles campus, in 2015. Ninety-six students were asked during individual interviews whether or not the 10 animals listed by the 4 sources were threatened; results (Fig 1B) show similarly that the public, even when represented by scientifically educated respondents, is often unaware of the dire conservation status of most of these species. On average, one in two persons was incorrectly assessing the endangerment of these animals, be it the general public or the supposedly more educated students of a world-class university. Exceptions are pandas, tigers, and polar bears, for which communication efforts may have borne their fruits in this regard—the first one being widely recognized as a global conservation icon and the two others as flagship species for traditional medicine and climate change impacts. Overall, these two lines of evidence suggest that these ten animals are

Box 1. The jeopardized future of the 10 most charismatic species.

- Tiger—total abundance estimated at less than 7% of their historic numbers [7]. Three subspecies (Bali tiger, *P. tigris balica*; Javan tiger, *P. t. sondaica*; and Caspian tiger, *P. t. virgata*) are now extinct, and another one (the South China tiger, *P. t. amoyensis*) is considered as possibly extinct [8,9].
- Lion—declining almost everywhere in Africa, with populations estimated to be at less than 8% of historic levels [10,11]. In Eurasia, with the exception of the only remaining population of about 175 individuals of *P. leo persica* in India, all lions are now extinct [12].
- Elephant—the African savannah elephant never recovered from the 20th century massive poaching levels and are believed to remain at less than 10% of their historic numbers [13]; the African forest elephant declined in a mere 9 years (2002–2011) by 62%, with about 30% corresponding range contraction [14]; the Asian elephant lost 85% of historic range, and almost half of the remaining 15% is both fragmented and heavily impacted by an ever increasing human population [15,16].
- Giraffe—previously classified as Vulnerable because it was assessed as a single species [17]. Three of the four newly identified species [18] have declined by 52%–97% in the last 35 years and are likely to be uplisted by IUCN [17].
- Leopard—classified as a Vulnerable species because the 9 subspecies are altogether abundant and widely distributed [19]; however, 3 are Critically Endangered, 2 are Endangered, 2 are recommended for uplisting to Critically Endangered and Endangered, and 2 are Near Threatened [20]. Leopards have already lost as much as 75% of their habitat range, and 6 out of the 9 subspecies occupy a mere 3% of the remaining range [20].
- Panda—with fewer than 2,000 remaining individuals, distributed within 33 subpopulations and scattered on less than 1% of its historic range, its future remains particularly uncertain [21], especially in light of climate change, predicted to reduce most of its bamboo habitat [22,23].
- Cheetah—occupies only 9% of its historic range in Africa, being extirpated from 29 countries on the continent [24], while the Asiatic subspecies *Acinonyx jubatus venaticus*, numbering fewer than 100 individuals, is listed as Critically Endangered [25].
- Polar bear—lack of population abundance and trend estimates; 9 out of the 19 known populations are of unknown status. It is considered severely impacted by climate change and related sea ice decline [6]. The few populations with available data show drastic population declines (see Fig 1).
- Wolf—once the world's most widely distributed large predator, it has now lost about one third of its original range, becoming extinct in much of Western Europe and the United States and being endangered in several other regions [26].
- Gorilla—of the 4 gorilla subspecies, 2 are limited to a few hundred individuals in small and highly fragmented populations [27,28], while the 2 others have lost most of their numbers in about 20 years [29,30].

Table 1. Status and trends of the 10 most charismatic animals. See S1 Text for the calculus of variables. African forest elephants have been distinguished from savannah elephants when information was available.

Species			IUCN	Demography			Habitat			
Species		**Taxonomic fractionation**	**Status**	**Estimated population size**	**Current trend**	**Percent MVP (pop/#patch)/ MVP**	**Percent historical range**	**Percent range protected**	**Percent "viable" habitat**	**Fragmentation (#patch)**
Tiger	*Panthera tigris*	9 subspecies	EN	3,159	↓ Decr.	30	<6[h]	36	76	>54[p]
Lion	*P. leo*	2 subspecies	VU	20,000[a]	↓ Decr.	155	17[i]	82	84	67[q]
Elephant	*Loxodonta Africana*	3 species	VU	500,000[b]	↑ Incr.[*]	1,431	19.9[b]	57	83	70[r]
	L. cyclotis		/	<100,000[c]	↓ Decr.	231	<25[c]	57	83	70[r]
	Elephas maximus		EN	47,000[b]	↓ Decr.	93	15[j,k]	30	67	>138[s]
Giraffe	*Giraffa camelopardalis*	4 species, 9 subspecies	VU	80,000[b]	↓ Decr.	714	11.3[b]	57	77	>66[t]
Leopard	*P. pardus*	9 subspecies	VU	Unkn.	↓ Decr.	/	25[l]	34	7	289[l]
Panda	*Ailuropoda melanoleuca*	/	VU	1,864[d]	↑ Incr.	23	<1[m]	62	94	33[m]
Cheetah	*Acinonyx jubatus*	9 subspecies	VU	7,000[e]	↓ Decr.	45	9[n]	40	51	29[e]
Polar bear	*Ursus maritimus*	/	VU	Unkn.	Unkn.	/	Dyn	12	24	19[u]
Wolf	*Canis lupus*	12 subspecies	LC	Unkn.	→ Stable	/	About 66[o]	14	58	/
Gorilla	*Gorilla beringei*	2 species, 4 subspecies	CR	3,800+880[f]	↓ Decr.	388	/	51	93	2[f]; 4[f]
	G. gorilla		CR	300+150,000[g]	↓ Decr.	5,330	/	24	89	13[v,w]; /

References:

[a] [31]
[b] [32]
[c] [14]
[d] [33]
[e] [25]
[f] [29]
[g] [30]
[h] [34]
[i] [35]
[j] [32]
[k] [16]
[l] [20]
[m] [21]
[n] [24]
[o] [26]
[p] [9]
[q] [12]
[r] [36]
[s] [37]
[t] [17]
[u] [38]
[v] [27]
[w] [39]

"/" means "no data available."

[*] IUCN assessment of 2008; shown to be decreasing since

Abbreviations: #patch, number of patches; CR, Critically Endangered; Decr., decreasing; Dyn, dynamical; EN, Endangered; Incr., increasing; IUCN, International Union for the Conservation of Nature; LC, Least Concern; MVP, minimum viable population; Unkn., unknown; VU, Vulnerable.

https://doi.org/10.1371/journal.pbio.2003997.t001

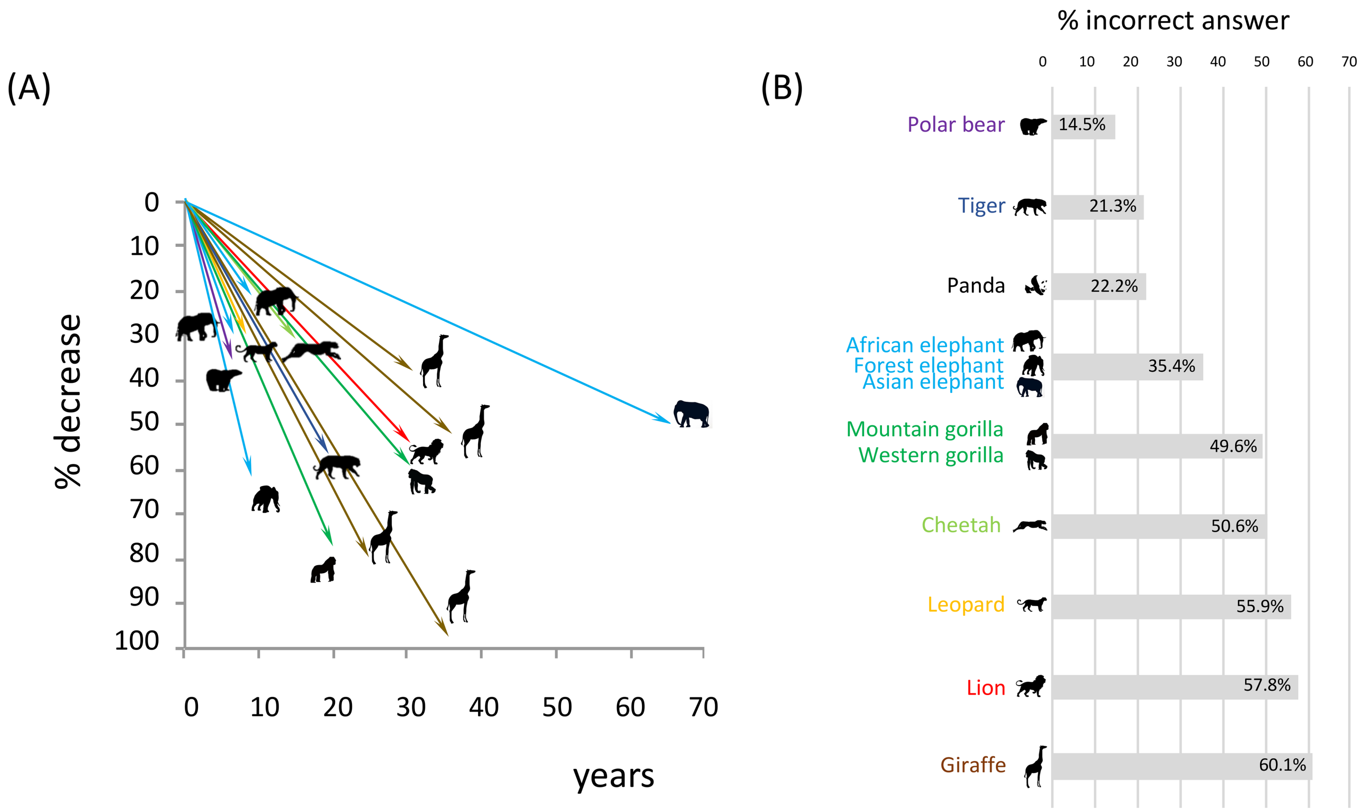

Fig 1. (A) Recent, dramatic declines of the most charismatic animals. Time, but not date, is taken into account, explaining why all trajectories have the same origin. Long, steep lines indicate a large decline at a high rate. Icons represent populations. Wolf is not represented and 4 subspecies of giraffes are represented. The declines are tigers: over 55% in the last 20 years [7]; African lions: 54% over the last three decades [40]; African elephants: over 20% over less than 10 years [41]; savannah elephants: over 30% between 2007 and 2014 [42]; Central African forest elephants: 62% between 2002–2011 [14]; Asian elephant: over 50% in 65 years [15,16]; giraffes: 38% in the last 30 years [17]; Masai giraffes (*Giraffa camelopardalis tippelskirchi*): 52% in 35 years [17]; reticulated giraffes (*G. c. reticulata*): 80% in 25 years [17]; Nubian giraffes (*G. c. camelopardalis*): 97% in 35 years [17]; leopards: over 30% in 8 years [19]; cheetahs: over 30% in the last 15 years [24,25]; southern Beaufort Sea polar bears: 63% between 2004 and 2010 [43,44]; Grauer's gorillas: 77% in less than 20 years [45]; Western lowland gorillas: nearly 60% in 30 years [30]. (B) Percentage of incorrect answers to the question, "Is this species endangered," reflecting biased knowledge of conservation status of the most charismatic species. See text for details.

https://doi.org/10.1371/journal.pbio.2003997.g001

not perceived as charismatic because of their conservation status, which is often not known. Conversely, these animals may be assumed to be abundant because of their omnipresence in our culture, as they are seen everywhere—in zoos and toys, on small and large screens, on advertisements and books alike. We emphasize that the gap between conservation status awareness and actual status should be especially unlikely in the most charismatic species, due to the high level of public attention they receive.

Competition between real and virtual populations

Despite their poor conservation status, these species are omnipresent in our modern societies. A good illustration is in the advertising realm. Charismatic animals are often prime candidates for product marketing purposes or general cultural consumption. For example, 48.6% of all non-teddy bear plush animal toys sold on Amazon (US) were one of the ten animals, suggesting high likelihood that a majority of children has/had at least one of them as a stuffed companion during their childhood. Similarly, the number of "Sophie la girafe" baby toys sold in France (800,000 in 2010) exceeds the number of babies born [49] and is over 8 times more than the number of actual, living giraffes in Africa [17].To further support our idea, we asked 42 volunteers to document every encounter with one of the 10 species in "virtual" populations

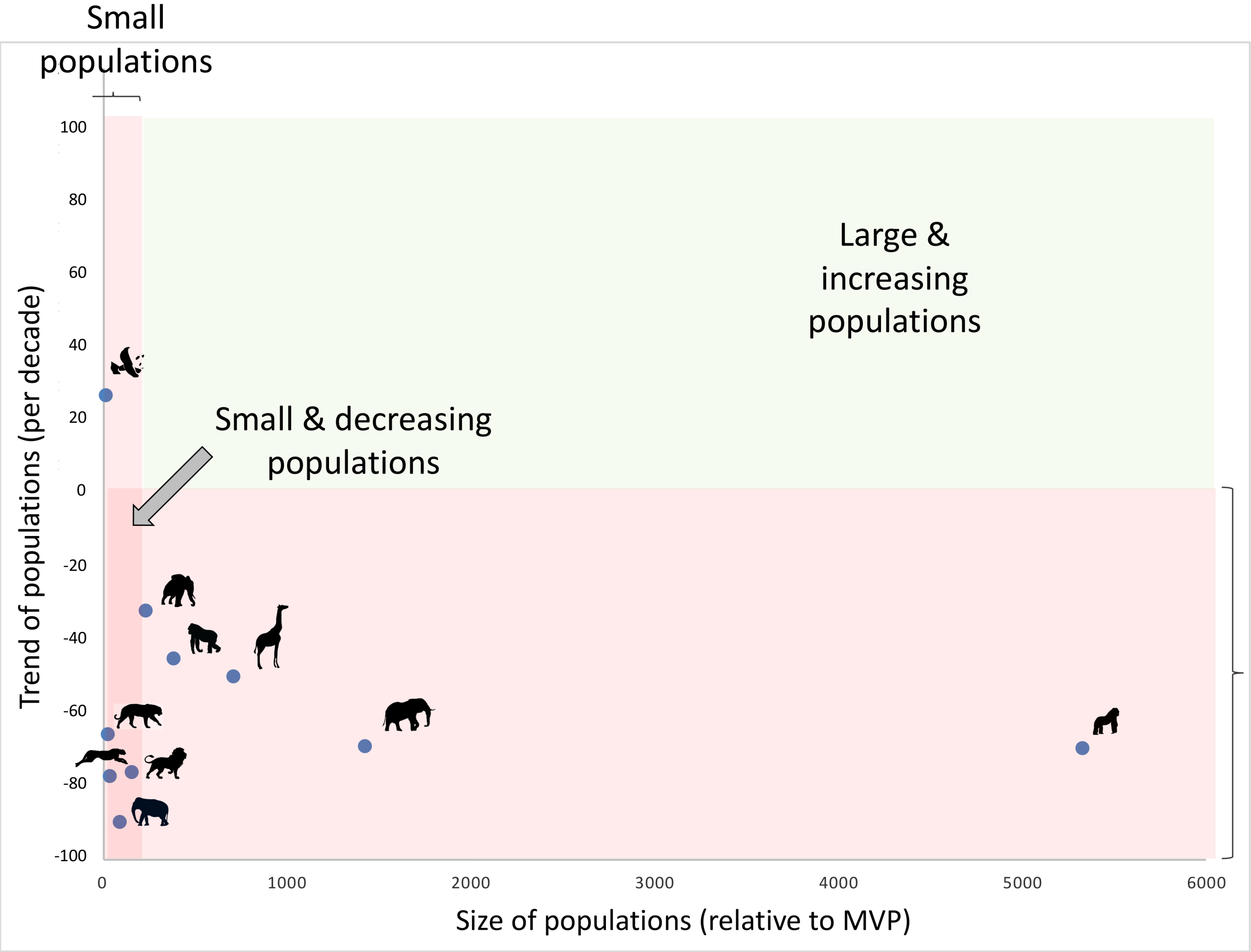

Fig 2. Population sizes and trends of the 10 animals. Trends are calculated per decade, based on the data presented in Fig 1 (and on the latest IUCN assessment for the panda [33]). Average population size is calculated conservatively as the overall population size divided by the number of isolated patches (see Table 1 for data and references). Resulting size is shown relative to the MVP size, as calculated for these species in recent syntheses [46]. Note that previous syntheses provide more pessimistic data, with MVPs one order of magnitude higher [47,48]. Icons correspond to names in Fig 1. Note that no overall population sizes are available for polar bears, wolves, and leopards, and no trends are available for wolves, while data were available for forest elephants, which we have here distinguished from savannah elephants. IUCN, International Union for the Conservation of Nature; MVP, minimum viable population.

https://doi.org/10.1371/journal.pbio.2003997.g002

(commercial, artistic, cultural, in zoos, books, magazines, on objects, on logos, on television, etc.) during 7 consecutive days. All volunteers lived in France, with a combination of rural and urban environments, living with or without television, with or without interest in animals, etc. On average, they encountered up to 31 individuals of each of the 10 species, which corresponds for each person to several hundred total encounters per month (S2 Fig). For example, the volunteers saw an average of 4.4 lions a day, meaning that people see on average two to three times as many "virtual" lions in a single year than the total population of wild lions currently living in the whole of West Africa. This reinforces our idea that the ubiquity of "virtual" species may be hindering the perception of rarity of these animals.

These species are therefore ubiquitous in our culture through what could be called virtual populations. The public perception of the conservation status of these species appears to reflect virtual populations rather than real ones. This is not surprising, because most people will only see wild animals in virtual populations. We suggest that the abovementioned mismatch between perceived and real conservation status may be due to the fact that people base their perception of these species on their virtual rather than real populations. It is unfortunately difficult to unambiguously demonstrate a causal relationship between the overabundance of virtual species and the biased perception of their actual endangerment, mostly because causes of ignorance are always multiple and difficult to isolate and unconditionally tie in.

This mechanism amounts to an intraspecific competition mediated by human perception, in which abundant but virtual populations outcompete for human attention the real but threatened populations (Fig 3). The perceived extinction risk, which is low, as it is influenced by highly abundant, virtual populations, masks the real, high extinction risk. As humans would expectedly strive to prevent extinction of, at the very least, the 10 animals they cherish the most, the fact that they make decisions (or refrain from making any) based on perceived risk rather than the real one [50] would likely prevent conservation efforts from getting the necessary support.

Turning competition into cooperation for conservation

One challenge for the success of conservation biology may therefore be how to transform these omnipresent but virtual populations from a liability to an asset for real populations. By using animals in their marketing, some products and brands gain a competitive market advantage, but the induced damages of contributing to the creation of competing, virtual populations are never taken into account and never compensated for. According to economic theory, such damages are "externalities," and they must be "internalized" through institutional

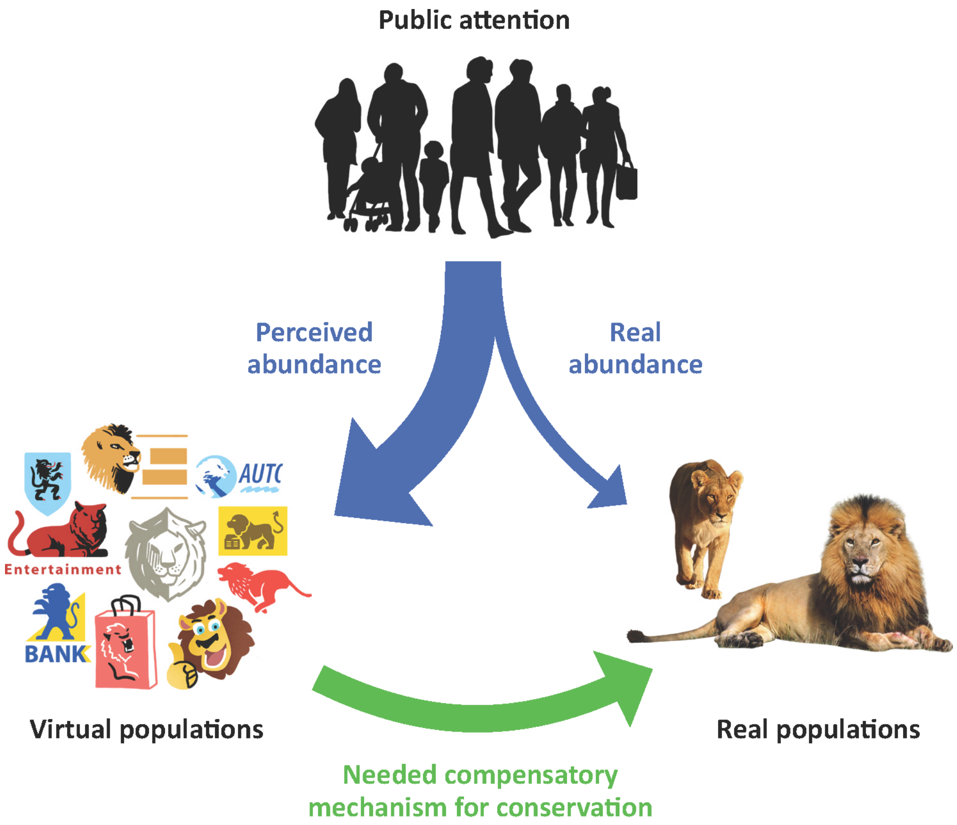

Fig 3. Illustration of the competition hypothesis between virtual populations (here represented by iconic logos of commercial companies) and natural populations (here represented by clip art of real animals), whereby abundance of virtual animals in culture alters the perception of actual rarity in real animals and, therefore, the perceived need for their conservation. A compensatory mechanism is needed to restore adequate conservation funding. *Credit for logo illustration and human silhouettes*: *Mathieu Ughetti*.

https://doi.org/10.1371/journal.pbio.2003997.g003

arrangements and/or payment mechanisms compelling companies to take responsibility for the damages they cause—albeit inadvertently [51]. Currently, companies do not pay a fee to use lions for their branding but, as we hypothesize, may unknowingly and indirectly weaken conservation support by contributing to a mistaken perception that lions are abundant, akin to a competition for attention from the public. Linking the use of threatened animal representations for commercial use to payment to conservation efforts could contribute to turning competition into cooperation between virtual and real populations. This logic of payment for rights to use is not different to, e.g., merchandising of derivative products: a clothes company needs to pay a fee to display the photo of a celebrity, of the illuminated Eiffel tower, or of the English Premier League logo on its products. That fee is paid to the brand copyright holder, in that latter case, the Football Association Premier League Ltd. Our proposed mechanism would scale up an idea that was once suggested for media firms [52] and applies it in areas where its benefits for biodiversity promise to be vastly superior. Assuming that biodiversity is a public good and that the above payment scheme should not be captured by private or sectoral interests, we propose that a scheme is established whereby companies would pay a fee to an existing or ad hoc institution representing the global public interest in preserving biodiversity, for using threatened animal representations in their branding. A voluntary program called "Save your logos" (http://www.saveyourlogo.org/) has been attempted, but we believe scaling up the idea requires grounding it in a formal compulsory mechanism. Global agreements such as the Convention on Biological Diversity (CBD) are often criticized for being ineffective due to their being non-compulsory and sometimes inexplicit [53]. The implementation of such payment mechanisms would be a major step towards improving their effectiveness to protect biodiversity.

The limits of so-called "standard economic" approaches to solve biodiversity conservation problems have been largely discussed in the literature [54,55]. The proposed mechanism should therefore not be seen as a panacea but rather as practical means to secure funding for conservation biology. The above critical analysis should also be used to identify and implement the important safeguards required to ensure proper implementation. These would include avoiding lobbying attempts to influence endangerment classification either way (from conservationists as well as from companies) and would address fairness as well as equity issues from the companies' standpoints. Other perverse effects, such as attempts by companies to marginally modify representations to argue that they refer to fictitious rather than to real species, should also be listed and addressed. It would also probably be beneficial if the compensatory mechanism could be coupled with information campaigns from the companies about the reason for such funding, i.e., about the conservation status of their icons. This option would further benefit their conservation while possibly being better perceived by the company and their customers. Being perceived as acting at the forefront of the conservation of the imperiled charismatic animal that represents them could even create a very positive response from previous and new customers of such companies. Indeed, these firms may improve their corporate social responsibility by helping to save their icons, providing them with additional incentives to adhere to this scheme. Another critical element will be the choice of the institution(s) entrusted to receive the money and allot it to conservation initiatives. Global institutions devoted to biodiversity are prominent candidates, but other smaller-scale nonprofit local nongovernmental organizations (NGOs) might prove more resilient to interest groups and more knowledgeable about relevant local conservation issues in some situations. Elaborating an adequate institutional design and quantitatively calibrating the fees falls beyond the scope of the present paper and should be covered by interdisciplinary collaborations between conservation scientists and experts in the economic theory of incentives, institutional economics, and property right laws [55].

Conclusion

Our study highlights that the 10 most charismatic animals for the public are in a dire conservation state but that the public is generally ignorant of this. Unless a radical change is operated, it is highly likely that most of these most-cherished species will go extinct in the wild within the next few decades. This situation is hidden by the large cultural abundance of these animals, which hinders conservation communication efforts and therefore acts as an additional, pernicious threat.

Beyond being a conservation tragedy in its own right, the likely extinction of these species can also turn into a double penalty for conservation biology. Indeed, charismatic species remain one of the most efficient vehicles to motivate the general public to support conservation action [56–58]. If these species go extinct in the wild, the whole conservation movement might suffer by losing its point in the eye of a large part of the general public.

We therefore claim that conservation studies, actions, and policies should stop seeing charismatic species as overprivileged conservation targets and face the fact that they are badly threatened species that urgently need an intensification of conservation effort. Such an intensification would not amount to demeaning the importance of conserving other elements of biodiversity, poorly known species, and whole ecosystems. For one thing, increasing the protection on the charismatic species does not mean zeroing on other conservation targets, especially if involved funding mechanisms are additive to already existing resources [53], as we propose here. Besides, because most charismatic species are keystone species with large habitat requirements, preserving them can have cascading co-benefits on the conservation status of numerous other species and ecosystem properties [59]. Similarly, communicating more about the endangerment of the most beloved species could raise public awareness of wider conservation issues.

Despite the fact that the increase needed in conservation revenue has been estimated to be more modest than other domains of public expenditure by at least one order of magnitude [60], in a world in which budget constraints are everywhere, our call for conservation intensification can look like wishful thinking. That is why we suggest, as a concrete mechanism to ensure its feasibility, a support from companies that use charismatic, endangered species for their branding. Setting up such a fund-raising scheme will require innovative interdisciplinary works involving conservation scientists, environmental economists, and legal scholars, but the relevant expertise is available, and action is required urgently.

Supporting information

S1 Text.
(DOCX)

S2 Text.
(DOCX)

S1 Table. Range size, proportion that is both suitable and protected (see S1 Text), and fragmentation (ratio of range size over perimeter of the range size) for the 10 most charismatic animals.
(DOCX)

S1 Fig. Ranking of the 10 most charismatic animals, according to the general public. These correspond to 13 species, as elephants and gorillas are represented by three and two species, respectively.
(TIF)

S2 Fig. Number of sightings of each of the 10 animals in "virtual" populations (commercial, artistic, cultural, in zoos, books, magazines, on objects, on television, etc.) during 7

consecutive days by 42 volunteers living in France. Dark blue is the number of sightings and light blue is the total cumulative number of individuals seen (e.g., a chocolate bar with 1 elephant counts as 1 in dark blue and 1 in light blue, while a bar with 2 elephants counts as 1 in dark and 2 in light blue). Volunteers all lived in France but in various settings (from staying always indoors with no television in a rural house, to regular use of the internet and television and going out every day to work and shop in a large city). Volunteers were asked to pay attention to representation of those 10 animals in order to record them but not to seek them. After an information meeting, a one-day trial was used to homogenize observation behaviors and information recording.
(TIF)

S3 Fig. Distribution of different drivers of threat for each of the 13 species, according to whether they are directly or indirectly human caused. Colors indicate whether a threat is primary (red) or secondary (yellow).
(TIF)

Acknowledgments

The authors wish to thank Morgane Barbet-Massin, Alice Fournier, Camille Leclerc, and François de Guibert for their help with modelling analyses of Table 1 and Céline Bellard, Muriel Perron, Luca Börger, and Duan Biggs for helpful comments on the manuscript. We are also grateful to the 42 volunteers who recorded sightings of virtual animals for a week.

References

1. Soga M, Gaston KJ. Extinction of experience: The loss of human-nature interactions. Front Ecol Environ. 2016; 14: 94–101. https://doi.org/10.1002/fee.1225
2. Ducarme F, Luque GM, Courchamp F. What are "charismatic species" for conservation biologists? Biosci Master Rev. 2013;July: 1–8.
3. Brambilla M, Gustin M, Celada C. Species appeal predicts conservation status. Biol Conserv. 2013; 160: 209–213. https://doi.org/10.1016/j.biocon.2013.02.006
4. Ford AT, Cooke SJ, Goheen JR, Young TP. Conserving Megafauna or Sacrificing Biodiversity? Bioscience. 2017; 67: 193–196. https://doi.org/10.1093/biosci/biw092 PMID: 28533560
5. Keith DA, Rodriguez JP, Brooks TM, Burgman MA, Barrow EG, Bland L, et al. The IUCN red list of ecosystems: Motivations, challenges, and applications. Conserv Lett. 2015; 8: 214–226. https://doi.org/10.1111/conl.12167
6. IUCN. The IUCN Red List of Threatened Species. In: 2017 [Internet]. [cited 4 Feb 2017]. Available: http://www.iucnredlist.org
7. Sanderson EW, Forrest J, Loucks C, Ginsberg J, Dinerstein E, Seidensticker J, et al. Setting Priorities for Tiger Conservation [Internet]. Second Edi. Tigers of the World. Elsevier Inc.; 2015. https://doi.org/10.1016/B978-0-8155-1570-8.00009–8
8. Goodrich J, Lynam A, Miquelle D, Wibisono H, Kawanishi K, Pattanavibool A, et al. Panthera tigris. IUCN Red List Threat Species 2015. 2015; doi:e.T15955A50659951
9. Dinerstein E, Loucks C, Wikramanayake E, Ginsberg J, Sanderson E, Seidensticker J, et al. The Fate of Wild Tigers. Bioscience. 2007; 57: 508. https://doi.org/10.1641/B570608
10. Riggio J, Caro T, Dollar L, Durant SM, Jacobson AP, Kiffner C, et al. Lion populations may be declining in Africa but not as Bauer et al. suggest. Proc Natl Acad Sci. 2015; 113: 201521506. https://doi.org/10.1073/pnas.1521506113 PMID: 26719424
11. Bauer H, Chapron G, Nowell K, Henschel P, Funston P, Hunter LTB, et al. Reply to Riggio et al.: Ongoing lion declines across most of Africa warrant urgent action. Proc Natl Acad Sci. 2015; 113: 201522741. https://doi.org/10.1073/pnas.1522741113 PMID: 26719423
12. Riggio J, Jacobson A, Dollar L, Bauer H, Becker M, Dickman A, et al. The size of savannah Africa: A lion's (Panthera leo) view. Biodivers Conserv. 2013; 22: 17–35. https://doi.org/10.1007/s10531-012-0381-4
13. Lee PC, Graham MD. African elephants and human-elephant interactions: implications for conservation. Int Zoo Yearb. 2006; 40: 9–19. https://doi.org/10.1111/j.1748-1090.2006.00009.x

14. Maisels F, Strindberg S, Blake S, Wittemyer G, Hart J, Williamson EA, et al. Devastating Decline of Forest Elephants in Central Africa. PLoS ONE. 2013; 8(3): https://doi.org/10.1371/journal.pone.0059469 PMID: 23469289
15. Leimgruber P, Gagnon JB, Wemmer C, Kelly DS, Songer MA, Selig ER. Fragmentation of Asia's remaining wildlands: implications for Asian elephant conservation. Anim Conserv. 2003; 6: 347–359. https://doi.org/10.1017/S1367943003003421
16. Goswami VR, Vasudev D, Oli MK. The importance of conflict-induced mortality for conservation planning in areas of human-elephant co-occurrence. Biol Conserv. Elsevier Ltd; 2014; 176: 191–198. https://doi.org/10.1016/j.biocon.2014.05.026
17. Muller Z, Bercovitch F, Brand R, Brown D, Brown M, Bolger D, et al. Giraffa camelopardalis. IUCN Red List Threat Species 2016. 2016; 1–8. https://doi.org/10.1126/science.194.4268.933 PMID: 17748550
18. Fennessy J, Bidon T, Reuss F, Kumar V, Elkan P, Nilsson MA, et al. Multi-locus Analyses Reveal Four Giraffe Species Instead of One. Curr Biol. Elsevier Ltd; 2016; 26: 2543–2549. https://doi.org/10.1016/j.cub.2016.07.036 PMID: 27618261
19. Henschel P, Hunter L, Breitenmoser U, Purchase N, Packer C, Khorozyan I, et al. Panthera pardus. IUCN Red List Threat Species 2008. 2008;
20. Jacobson AP, Gerngross P, Lemeris Jr. JR, Schoonover RF, Anco C, Breitenmoser-Würsten C, et al. Leopard (Panthera pardus) status, distribution, and the research efforts across its range. PeerJ. 2016;4: e1974. doi:10.7717/peerj.1974
21. Kang D, Li J. Premature downgrade of panda's status. Science (80-). 2016; 354: 295–295. https://doi.org/10.1126/science.aaj1963 PMID: 27846523
22. Li R, Xu M, Wong MHG, Qiu S, Li X, Ehrenfeld D, et al. Climate change threatens giant panda protection in the 21st century. Biol Conserv. Elsevier Ltd; 2015; 182: 93–101. https://doi.org/10.1016/j.biocon.2014.11.037
23. Tuanmu M-N, Viña A, Winkler J a., Li Y, Xu W, Ouyang Z, et al. Climate-change impacts on understorey bamboo species and giant pandas in China's Qinling Mountains. Nat Clim Chang. Nature Publishing Group; 2013; 3: 249–253. https://doi.org/10.1038/nclimate1727
24. Durant SM, Mitchell N, Groom R, Pettorelli N, Ipavec A, Jacobson AP, et al. The global decline of cheetah Acinonyx jubatus and what it means for conservation. Proc Natl Acad Sci. 2016; 114: 201611122. https://doi.org/10.1073/pnas.1611122114 PMID: 28028225
25. Durant S, Mitchell N, Ipavec A, Groom R. Acinonyx jubatus, cheetah. IUCN Red List Threat Species 2015. 2015; doi:10.1644/1545-1410(2005)771[0001:AJ]2.0.CO;2
26. Mech LD, Boitani L. Canis lupus. IUCN Red List Threat Species 2010. 2010; 10. https://doi.org/10.2305/IUCN.UK.2010-4.RLTS.T3746A10049204.en
27. Dunn A, Bergl R, Byler D, Eben-Ebai S, Etiendem DN, Fotso R, et al. Revised Regional Action Plan for the Conservation of the Cross River Gorilla (Gorilla gorilla diehli) 2014–2019. 2014.
28. Xue Y, Prado-martinez J, Sudmant PH, Narasimhan V, Ayub Q, Szpak M, et al. Decline and Inbreeding. Science (80-). 2015; 348: 242–245.
29. Plumptre A, Robbins M, Williamson EA. Gorilla beringei. IUCN Red List Threat Species 2016. 2016;
30. Maisels F, Bergl RA, Williamson EA. Gorilla gorilla. IUCN Red List Threat Species 2016. 2016;
31. Bauer H, Packer C, Funston PF, Henschel P, Nowell K. Panthera leo. IUCN Red List Threat Species 2016. 2016; 2–12. Available: https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en
32. Ripple WJ, Newsome TM, Wolf C, Dirzo R, Everatt KT, Galetti M, et al. Collapse of the world's largest herbivores. Sci Adv. 2015; 1: e1400103–e1400103. https://doi.org/10.1126/sciadv.1400103 PMID: 26601172
33. Swaisgood R, Wang D, Wei F. Ailuropoda melanoleuca. IUCN Red List Threat Species 2016. 2016; https://doi.org/10.2307/3503982
34. Walston J, Robinson JG, Bennett EL, Breitenmoser U, da Fonseca G a B, Goodrich J, et al. Bringing the tiger back from the brink-the six percent solution. PLoS Biol. 2010; 8(9): https://doi.org/10.1371/journal.pbio.1000485 PMID: 20856904
35. Morrison JC, Sechrest W, Dinerstein E, Wilcove DS, Lamoreux JF. Persistence of Large Mammal Faunas as Indicators of Global Human Impacts. J Mammal. 2007; 88: 1363–1380. https://doi.org/10.1644/06-MAMM-A-124R2.1
36. Barnes RFW. Is there a future for elephants in West Africa? Mamm Rev. 1999; 29: 175–199. https://doi.org/10.1046/j.1365-2907.1999.00044.x
37. Choudhury A, Lahiri Choudhury DK, Desai A, Duckworth JW, Easa PS, Johnsingh AJT, et al. Elephas maximus. IUCN Red List Threat Species 2010. 2008; doi:e.T7140A12828813

38. Peacock E, Sonsthagen SA, Obbard ME, Boltunov A, Regehr E V., Ovsyanikov N, et al. Implications of the circumpolar genetic structure of polar bears for their conservation in a rapidly warming Arctic. PLoS ONE. 2015; 10(1): https://doi.org/10.1371/journal.pone.0112021 PMID: 25562525

39. Bergl RA, Vigilant L. Genetic analysis reveals population structure and recent migration within the highly fragmented range of the Cross River gorilla (Gorilla gorilla diehli). Mol Ecol. 2007; 16: 501–516. https://doi.org/10.1111/j.1365-294X.2006.03159.x PMID: 17257109

40. Bauer H, Chapron G, Nowell K, Henschel P, Funston P, Hunter LTB, et al. Lion (Panthera leo) populations are declining rapidly across Africa, except in intensively managed areas. Proc Natl Acad Sci U S A. 2015; 112: 14894–9. https://doi.org/10.1073/pnas.1500664112 PMID: 26504235

41. Thouless CR, Dublin HT, Blanc JJ, Skinner DP, Daniel TE, Taylor RD, et al. African Elephant Status Report 2016. An update from the African Elephant Database. 2016.

42. Chase MJ, Schlossberg S, Griffin CR, Bouché PJC, Djene SW, Elkan PW, et al. Continent-wide survey reveals massive decline in African savannah elephants. PeerJ. 2016; 4: e2354. https://doi.org/10.7717/peerj.2354 PMID: 27635327

43. Bromaghin JF, McDonald TL, Stirling I, Derocher AE, Richardson ES, Regehr EV, et al. Polar bear population dynamics in the southern Beaufort Sea during a period of sea ice decline. Ecol Appl. 2015; 25: 634–651. https://doi.org/10.1890/14-1129.1 PMID: 26214910

44. Regehr EV, Amstrup SC, Stirling I. Polar Bear Population Status in the southern Beaufort Sea; U.S. Geological Survey. Reston, Virginia, USA.; 2006.

45. Plumptre AJ, Nixon S, Kujirakwinja DK, Vieilledent G, Critchlow R, Williamson EA, et al. Catastrophic decline of world's largest primate: 80% loss of grauer's gorilla (Gorilla beringei graueri) population justifies critically endangered status. PLoS ONE. 2016; 11(10): https://doi.org/10.1371/journal.pone.0162697 PMID: 27760201

46. Hilbers JP, Santini L, Visconti P, Schipper AM, Pinto C, Rondinini C, et al. Setting population targets for mammals using body mass as a predictor of population persistence. Conserv Biol. 2016; 31: 1–24. https://doi.org/10.1111/cobi.12846.This

47. Traill LW, Bradshaw CJA, Brook BW. Minimum viable population size: A meta-analysis of 30 years of published estimates. Biol Conserv. 2007; 139: 159–166. https://doi.org/10.1016/j.biocon.2007.06.011

48. Reed DH, O'Grady JJ, Brook BW, Ballou JD, Frankham R. Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. Biol Conserv. 2003; 113: 23–34. https://doi.org/10.1016/S0006-3207(02)00346-4

49. Levin J. Sophie the Giraffe, the European teething toy that's sweeping America. In: Slate [Internet]. 2011 [cited 11 Jan 2018]. Available: http://www.slate.com/articles/arts/number_1/2011/03/im_french_chew_on_me.html

50. Slovic P. The Feeling of Risk: New Perspectives on Risk Perception (Earthscan Risk in Society). EarthScan. London, Washington DC; 2010.

51. Ninan KN. Conserving and Valuing Ecosystem Services and Biodiversity: Economic, Institutional and Social Challenges. London, UK: EarthScan; 2009.

52. Jepson P, Jennings S, Jones KE, Hodgetts T. Entertainment Value: Should the Media Pay for Nature Conservation? Science (80-). 2011; 334: 1351–1352. https://doi.org/10.1126/science.1213189 PMID: 22158806

53. Butchart SHM, Di Marco M, Watson JEM. Formulating Smart Commitments on Biodiversity: Lessons from the Aichi Targets. Conserv Lett. 2016; 9: 457–468. https://doi.org/10.1111/conl.12278

54. Sagoff M. The Economy of the Earth: Philosophy, Law, and the Environment. Second Edi. University C, editor. Cambridge, U.K.; 2008.

55. Vatn A. Environmental Governance. Institutions, Policies and Actions. Edward Elg. Cheltenham; 2016.

56. Macdonald EA, Burnham D, Hinks AE, Dickman AJ, Malhi Y, Macdonald DW. Conservation inequality and the charismatic cat: Felis felicis. Glob Ecol Conserv. Elsevier B.V.; 2015; 3: 851–866. https://doi.org/10.1016/j.gecco.2015.04.006

57. Colléony A, Clayton S, Couvet D, Saint Jalme M, Prévot A-C. Human preferences for species conservation: Animal charisma trumps endangered status. Biol Conserv. Elsevier Ltd; 2016; https://doi.org/10.1016/j.biocon.2016.11.035

58. Caro T. Conservation by proxy. Washington, Covelo, London: Island Press; 2010.

59. Ripple WJ, Chapron G, López-bao JV, Durant SM, Macdonald DW, Corlett RT, et al. Saving the World ' s Terrestrial Megafauna. Bioscience. 2016; 66: 807–812. https://doi.org/10.1093/biosci/biw092 PMID: 28533560

Isolation Management with Artificial Barriers as a Conservation Strategy for Cutthroat Trout in Headwater Streams

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Abstract: *We evaluated the effectiveness of isolation management and stocking to meet protection and enhancement goals for native Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in Wyoming (U.S.A.). As a management strategy of the Wyoming Game and Fish Department, cutthroat trout were isolated upstream of artificial barriers in small headwater streams. Non-native trout that might have hybridized, competed with, or preyed upon cutthroat trout were removed from the isolated reaches, and then cutthroat trout of hatchery origin were stocked to augment populations. We monitored the abundance and body condition of cutthroat trout for 4–7 years following isolation in four streams with barriers and in two reference streams without barriers. Barriers limited new invasions by non-native trout, and removals of non-native trout greatly reduced their abundance but did not eliminate them (mainly brook trout [*Salvelinus fontinalis*]). Wild cutthroat trout persisted in low numbers upstream of barriers, but there was no evidence of enhancement of populations. Stocked cutthroat trout did not persist upstream of barriers, and many moved downstream over barriers. The body condition of wild cutthroat trout was comparable among populations upstream and downstream of barriers and in reference streams. Isolation management provided only short-term benefits by minimizing the risks of hybridization and allowed populations to persist during the study. Removal of non-native trout and stocking did not enhance wild cutthroat trout populations, however, likely because the isolated reaches lacked critical habitat such as the deep pools necessary to sustain large fish. Also, barriers disrupt migratory patterns and prevent seasonal use of headwater reaches by adult cutthroat trout. Longer-term consequences of isolation include vulnerability to stochastic processes and loss of genetic diversity. Where non-native species pose an immediate threat to the survival of native fishes, isolation in headwater streams may be the only conservation alternative. In such situations, isolated reaches should be as large and diverse as possible, and improvements should be implemented to ensure that habitat requirements are met.*

El Aislamiento con Barreras Artificiales como una Estrategia de Conservación para la Trucha (*Oncorhynchus clarki pleuriticus*) en Arroyos de Cabecera

Resumen: *Evaluamos la efectividad del aislamiento y de la repoblación para alcanzar las metas de protección y mejoramiento de la trucha nativa del río Colorado,* Oncorhynchus clarki pleuriticus, *en Wyoming (EE.UU.). Como una estrategia de manejo del Departamento de Caza y Pesca de Wyoming, se aislaron las truchas nativas aguas arriba de barreras artificiales, en arroyos de cabecera. Se removieron de estas zonas aisladas las truchas no nativas que pueden hibridizar, competir o depredar a la trucha nativa y se sembraron estas zonas con truchas de criadero para aumentar las poblaciones. Hicimos un seguimiento de la abundancia y la condición corporal de las truchas por 4 a 7 años después del aislamiento en cuatro arroyos con barreras y en dos arroyos sin barreras como referencia. Las barreras limitaron nuevas invasiones de truchas no nativas, y las remociones de truchas no nativas redujeron su abundancia pero no las eliminaron (*principalmente Salvelinus fontinalis*). Las truchas nativas silvestres persistieron en pequeño número aguas arriba de las barreras; sin embargo, no hubo evidencia de incrementos de sus poblaciones. Las truchas sembradas no persisti-*

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Paper submitted November 3, 2000; revised manuscript accepted November 20, 2002.

Conservation Biology, Pages 772–781
Volume 17, No. 3, June 2003

eron aguas arriba de las barreras y muchas se desplazaron aguas abajo cruzando las barreras. La condición corporal de las truchas nativas era similar entre las poblaciones aguas arriba y aguas abajo de las barreras y en los arroyos sin barreras. El aislamiento como herramienta de manejo solo proporcionó un beneficio a corto plazo al minimizar los riesgos de la hibridación y permitió que las poblaciones persistieran durante el estudio. Sin embargo, la remoción de truchas no nativas y la siembra no mejoró las poblaciones de truchas nativas silvestres, debido probablemente a que las áreas aisladas carecían del hábitat crucial tal como pozos profundos necesarios para proveer sustento a los peces de mayor tamaño. Además, las barreras desestabilizan los patrones migratorios e impiden que las truchas adultas hagan un uso estacional de los arroyos de cabecera. Las consecuencias a largo plazo del aislamiento incluyen la vulnerabilidad a procesos estocásticos y la pérdida de diversidad genética. El aislamiento de arroyos de cabecera puede ser la única alternativa de conservación en la que las especies no nativas son una amenaza inmediata para la supervivencia de peces nativos. En tales situaciones, las áreas aisladas deben ser tan extensas y diversas como sea posible, y se deben implementar mejoras para asegurar que se cumplan los requerimientos de hábitat.

Introduction

The intentional isolation of populations of threatened native species is an extreme measure to protect them from the negative effects of non-native species (Moyle & Sato 1991; Melvin et al. 1992; Shafer 1995). Isolation approaches to conservation management have been utilized most frequently in aquatic systems where movement corridors are well defined and the passage of animals is easier to control (Moyle & Sato 1991; Rinne & Turner 1991; Thompson & Rahel 1998). For example, cyprinodontid fishes in the southwestern United States (e.g., desert pupfishes [*Cyprinodon macularius*]) persist only in isolation from non-native mosquitofish (*Gambusia affinis*) and largemouth bass (*Micropterus salmoides*) (Minckley et al. 1991). Although isolation may confer short-term benefits by minimizing external threats, longer-term conservation success requires sufficient ecological and genetic resources to sustain or enhance populations in the isolated habitat fragments (Saunders et al. 1991; Wiens 1997). Undesirable consequences of isolation may include increased intraspecific competition, high levels of inbreeding, and susceptibility to chance catastrophes that can lead to population bottlenecks or local extirpation (Wilcox & Murphy 1985; Simberloff et al. 1992).

Isolation management is being employed by resource managers to protect threatened populations of cutthroat trout (*Oncorhynchus clarki*) in Rocky Mountain streams (Stuber et al. 1988; Propst et al. 1992; Young et al. 1996). Various subspecies of cutthroat trout have declined dramatically throughout the western United States following degradation of critical habitat, exploitation, and invasions of non-native trout species (Griffith 1988). Introduced rainbow trout (*Oncorhynchus mykiss*) and other subspecies of introduced cutthroat trout may hybridize with and threaten the genetic integrity of native cutthroat trout (Behnke 1992). Introduced brook trout (*Salvelinus fontinalis*) are hypothesized to compete with and prey upon cutthroat trout (Fausch 1989; Young 1995; Dunham et al. 1997; Harig et al. 2000). The mechanisms underlying these species interactions in natural populations are not clear. However, empirical studies suggest that brook trout could limit the downstream distribution of cutthroat trout through temperature-mediated competition, where brook trout have increased competitive abilities at warmer temperatures associated with lower elevations (De Staso & Rahel 1994; Novinger 2000), and via demographic effects in which brook trout tolerate higher population densities and may thereby exclude cutthroat trout from complex habitat (Schroeter 1998). Size-selective predation on age-0 cutthroat trout may also be a significant source of mortality (Gregory & Griffith 2000; Novinger 2000).

Conservation goals for cutthroat trout include protection and enhancement of genetically pure populations of the Colorado River subspecies of cutthroat trout (*O. c. pleuriticus*) that have declined and disappeared in many Wyoming streams. To eliminate immediate threats believed to be posed by non-native trout, the Wyoming Game and Fish Department initiated isolation management, beginning with installation of migration barriers on several high-elevation headwater streams in western Wyoming. Following completion of the barriers, they used intensive electrofishing to remove non-native fishes, mainly brook trout, and stocked the isolated stream reaches with cutthroat trout of hatchery origin in an attempt to augment populations. It was hoped that these activities would protect cutthroat trout from the negative effects of hybridization and competition and allow populations to increase (Wyoming Game and Fish Department 1987). Initial surveys showed that removal efforts greatly reduced the abundance of brook trout upstream of barriers and achieved the short-term benefit of protecting cutthroat trout from threats posed by non-native species (Thompson & Rahel 1996). Subsequent annual surveys were implemented to gauge the continued effectiveness of the barriers and monitor the success of isolation management and stocking in protecting and enhancing cutthroat trout populations.

Our purpose was to evaluate the effectiveness of this isolation-management approach for protecting and enhancing cutthroat trout following isolation for periods of 4 to 7 years. By definition, the process of isolation should exclude non-native trout that might hybridize or compete with native populations, but it also should not impede the potential recovery of populations. Elimination of brook trout, a potential competitor and predator, should enhance cutthroat trout populations by promoting increased growth and survival. Augmentation of wild populations of cutthroat trout by stocking should enhance spawning and facilitate population growth. We assessed the success of isolation management in achieving these aims by comparing the characteristics of cutthroat trout populations located upstream of barriers, where non-native trout were removed and hatchery cutthroat trout were stocked, with populations located downstream of barriers, where no such manipulations occurred. We also examined cutthroat trout populations in reference streams that lacked barriers and had sympatric populations of brook trout. Our assessment provided insight into the long-term potential for successful isolation management of cutthroat trout in Rocky Mountain headwater streams.

Methods

We performed annual monitoring surveys to assess temporal changes in cutthroat trout populations in response to isolation upstream of barriers, removal of non-native trout, and enhancement through stocking. We sampled four streams with barriers ("treatment" streams): Irene and Nylander creeks in the North Cottonwood Creek watershed (Sublette County, Wyoming) and Clear and Nameless creeks in the LaBarge Creek watershed (Lincoln County, Wyoming) (Table 1; Fig. 1). Two to four monitoring sites were established upstream of each barrier to the farthest extent of fish occurrence (Thompson & Rahel 1996). One monitoring site was established immediately downstream from each barrier. We also sampled sites on two reference streams in the LaBarge Creek watershed that lacked barriers: Spring Creek and Trail Creek. Two monitoring sites were on Spring Creek, one downstream near the stream's mouth and the other upstream near the spring source. Only one site near the mouth of Trail Creek was sampled because upstream reaches were intermittent (Table 1; Fig. 1). Monitoring surveys on treatment streams were performed for periods of 4 to 7 years between 1992 and 1999. The first year of data for each treatment stream represented fish abundances prior to removal of non-native trout. Sampling on the reference streams commenced in 1994. The streams we studied were typical of first-order, headwater streams in the Rocky Mountains of western Wyoming, with significant spring inputs and wetted widths of 1–3 m. All the streams were within the boundaries of Bridger National Forest and the Green River watershed.

With the purpose of directly augmenting isolated cutthroat trout populations, the Wyoming Game and Fish Department stocked each of the four treatment streams three times during 1990–1998. Stocking efforts involved the release upstream of barriers of approximately 500–2000 juvenile fish 120 mm in length. Each stocking was marked with a distinctive fin clip.

To sample fish populations, we used a single backpack unit and methods described by Thompson and Rahel (1996) to conduct three-pass, depletion-removal electrofishing. We sampled in August when streams were at base flow. Block nets (1-cm mesh) were set at upstream and downstream extents of each 100-m site to ensure closure of the sample reach. Following each electrofishing pass, all trout captured were counted, measured for total length to the nearest 1 mm, weighed to the nearest 1 g, and placed in a holding cage outside of the site. Age-0 cutthroat trout (young-of-year; length < 50 mm) were rarely observed because sampling dates occurred just prior to emergence. Hence, our samples reflect only the abundance of one-year-old and older ($\geq$age 1) cutthroat trout. We counted stocked cutthroat

Table 1. Characteristics of streams in western Wyoming, where isolation management of cutthroat trout populations was monitored, including stream length (upstream of barriers or from mouth for reference streams), number of 100-m sampling sites, range in elevation from most downstream to most upstream site, and years sites were sampled.*

Stream	*Stream length (km)*	*Number of sites*	*Elevation range (m)*	*Years sampled*
Treatment streams (migration barriers)				
Clear Creek	1.5	3	2540–2550	1994–1998
Irene Creek	3.6	5	2425–2500	1993–1999
Nameless Creek	2.9	5	2455–2510	1992–1998
Nylander Creek	1.2	3	2470–2485	1992–1999
Reference streams (no barriers)				
Spring Creek	6.0	2	2495–2585	1994–1998
Trail Creek	4.5	1	2550	1994–1998

**On the four streams with a barrier (treatment streams), one site was immediately downstream of the barrier, whereas the remainder of sites were distributed upstream (Fig. 1). For comparison, upstream and downstream sites on two streams without barriers (reference streams) were sampled.*

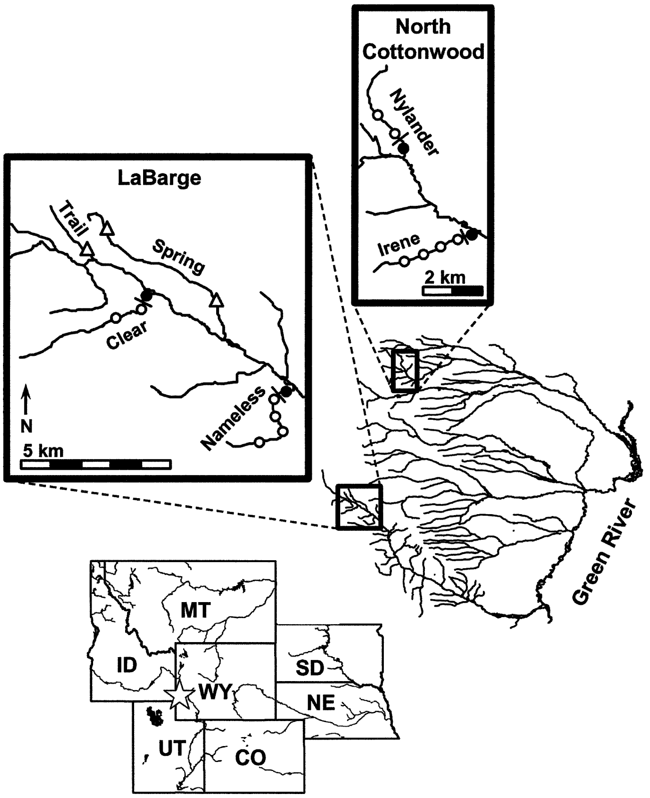


Figure 1. Study sites on headwater streams in the Green River watershed of western Wyoming. Sites were located both upstream (open circles) and downstream (closed circles) of fish migration barriers on Clear and Nameless creeks in the LaBarge Creek watershed and Nylander and Irene creeks in the North Cottonwood Creek watershed. Reference sites (triangles) were located on two streams without fish migration barriers in the LaBarge Creek watershed: Spring and Trail creeks.

trout separately. Age-0 brook trout (length 50–90 mm) had emerged the previous spring and were distinguished from older, larger brook trout (≥age 1). Following processing, brook trout collected upstream of barriers were either euthanized or marked with a visual implant tag and released downstream of the barrier to aid in documenting upstream movement past barriers (Thompson & Rahel 1998). We used Zippen model M_b in the program Capture (White et al. 1982) to calculate probabilities of capture, population estimates, and upper 95% confidence intervals when a descending pattern of removal was achieved. When a descending pattern of removal was not achieved, we used the total number of fish caught during the three electrofishing passes as the population estimate. This occurred at only a few sites with low trout abundance, where few or no trout were captured on each electrofishing pass.

We also assessed the body condition of cutthroat trout to test for the effects of brook trout removal on factors related to the length-weight relationship of individual fish. To describe body condition, we calculated relative weight (W_r; Kruse & Hubert 1997), an index widely used to assess the body form or plumpness of fishes relative to an average length-weight relationship for the species. Values of W_r close to 100 are assumed to reflect good body condition.

We evaluated the effectiveness of isolation management to enhance cutthroat trout populations by testing for evidence of temporal trends in abundance and body condition attributable to non-native trout removal and supplemental stocking. We assessed changes in the longitudinal difference in trout abundance (estimated population size per 100 m) in upstream and downstream sites by calculating the following metric: longitudinal difference = (mean number of trout/100 m in upstream sites) − (number of trout/100 m in downstream site).

We expected to see an increase in the longitudinal difference over time if removal of non-native trout and supplemental stocking were effective at increasing the abundance of wild cutthroat trout above the isolation barriers. Using Kendall's τ (tau), a nonparametric rank correlation procedure robust to small sample sizes (Sokal & Rohlf 1981), we performed separate tests on data from each stream for an association between the longitudinal difference in abundance and the number of years after removal of non-native fishes. This test is appropriate given our limited time series and lack of evidence for serial correlations in residuals from regression of the longitudinal difference on time. We assessed temporal trends in trout abundance in each site on reference streams (two sites on Spring Creek, one site on Trail Creek) by submitting the actual population estimates to the same test for correlation. Comparisons between treatment and reference streams were done visually. We used similar procedures to assess temporal patterns in the body condition of cutthroat trout by utilizing longitudinal differences in relative weight and calculating Kendall's correlation coefficient. We performed all analyses using SAS (SAS Institute 1999) and $\alpha = 0.05$ to judge statistical significance.

Results

Depletion-removal electrofishing was an effective census method, and reliable population estimates with 95% confidence intervals were possible for 135 of 152 samples (89%). Nondescending removal patterns occurred when the total number of fish captured was low (<6) and more individuals were collected during the second or third pass. Mean probabilities of capture (±1 SD) were highest for cutthroat trout (0.82 ± 0.18) and brook trout at ≥age 1 (0.77 ± 0.19), whereas brook trout at age 0 were only slightly more difficult to collect (0.74 ± 0.20). Of 268 brook trout tagged and released downstream of barriers between 1992 and 1994, 19 (7%)

were subsequently recaptured upstream of barriers; however, we did not recapture additional tagged brook trout upstream of barriers during the remainder of the study (1995–1999). One rainbow trout (length = 171 mm) was removed from upstream of the barrier on Nameless Creek during the first year of sampling on that stream (1992).

Initial removal efforts greatly reduced brook trout abundance upstream of barriers, although the species was not eliminated. Abundances of brook trout at ≥age 1 upstream of barriers declined by 75–96% following the first year of removal and remained depressed relative to downstream sites in subsequent years (Fig. 2). The brook trout population downstream of the barrier on Nylander Creek was especially dense and increased markedly across 8 years of sampling. Abundances of age-0 brook trout declined by similar amounts upstream of barriers following initial removals and remained low (<1 fish/100 m; Fig. 3). In Clear and Nameless creeks, brook trout at age 0 were not observed in upstream sites after 1995 and disappeared from both upstream and downstream sites by 1997 and 1998. Trends in abundance of brook trout in the reference streams appeared stable during the study and were comparable to trends in most sites downstream of barriers. We consistently observed higher fish densities in the downstream sites on Spring Creek and Trail Creek (also at a site downstream) relative to the upstream site on Spring Creek. Brook trout at age 0 were never observed in this latter site.

Sustained reductions in brook trout abundance, com-

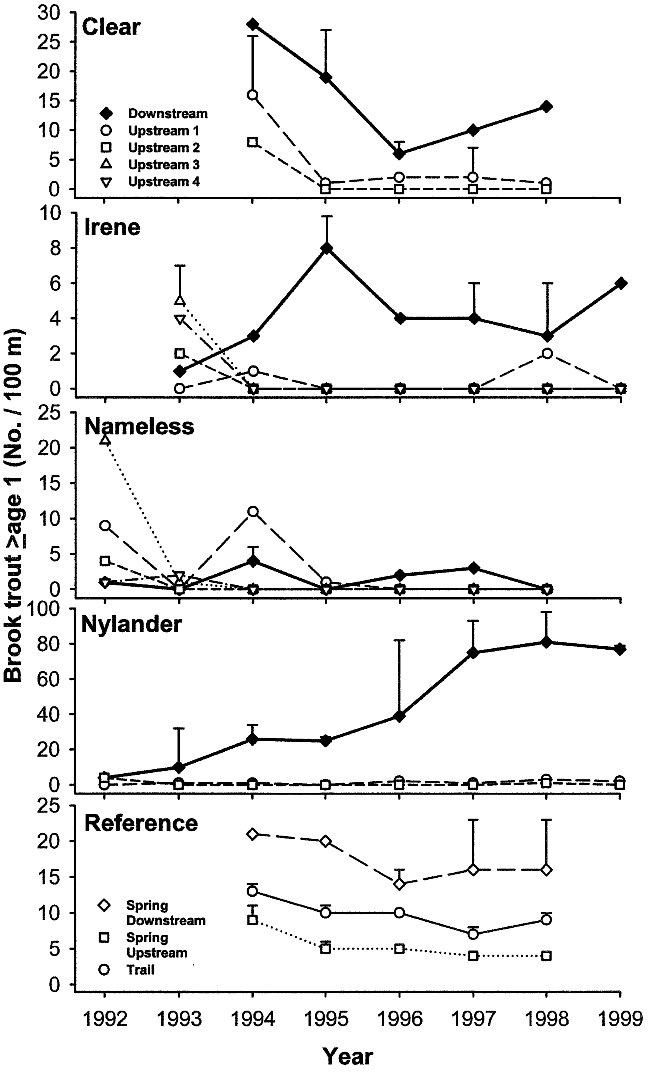


Figure 2. Population estimates (+95% C.I.) for brook trout aged 1 year and older (≥age 1) in sites upstream and downstream of barriers in treatment streams and in sites in reference streams in 1992–1999. The y-axis scaling is different among streams.

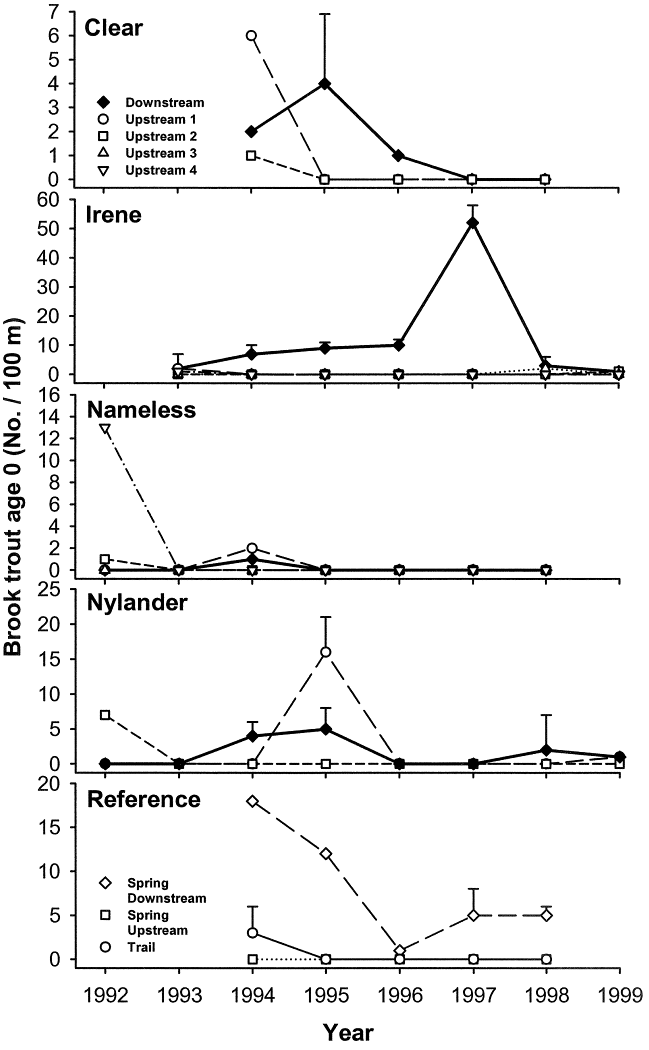


Figure 3. Population estimates (+95% C.I.) for young-of-year brook trout (age 0) in sites upstream and downstream of barriers in treatment streams and in sites in reference streams in 1992 through 1999. The y-axis scaling is different among streams.

bined with isolation upstream of the barriers, did not correspond with enhancement of wild cutthroat trout populations. In Clear and especially Irene and Nylander creeks, the post-removal abundance of cutthroat trout was generally greater downstream, not upstream, of barriers (Fig. 4). However, abundances of cutthroat trout in downstream sites tended to be lower than the abundances of the co-occurring brook trout population (Fig. 2). Other than an initial decline in Trail Creek, we did not observe notable temporal patterns in abundances of cutthroat trout in the reference streams, and the magnitude of population estimates was similar to population estimates in treatment streams (Fig. 4). Longitudinal differences in cutthroat trout abundance (upstream - downstream) did not increase as hoped for under an isolation-management strategy (Fig. 5). We did not detect significant correlations between longitudinal differences in abundance and the number of years after removal of non-native fishes in any of the four treatment or reference streams. Values for Kendall's τ ranged from -0.20 (Clear Creek, $p = 0.62$) to 0.29 (Nameless Creek, $p = 0.36$), confirming the absence of significant enhancement of wild cutthroat trout. The statistical power ($1 - \beta$) of these correlation tests averaged 0.81 (range 0.56 – 0.99). The best response occurred in Nameless Creek, where there was a relative increase in the initial abundance of cutthroat trout upstream of barriers from a low difference of -4.5 to a high of 2.75 (+7.25 fish/100 m 2 years after removal). In years 2 through 6, however, the longitudinal difference remained relatively constant at only 1.6 fish/100 m.

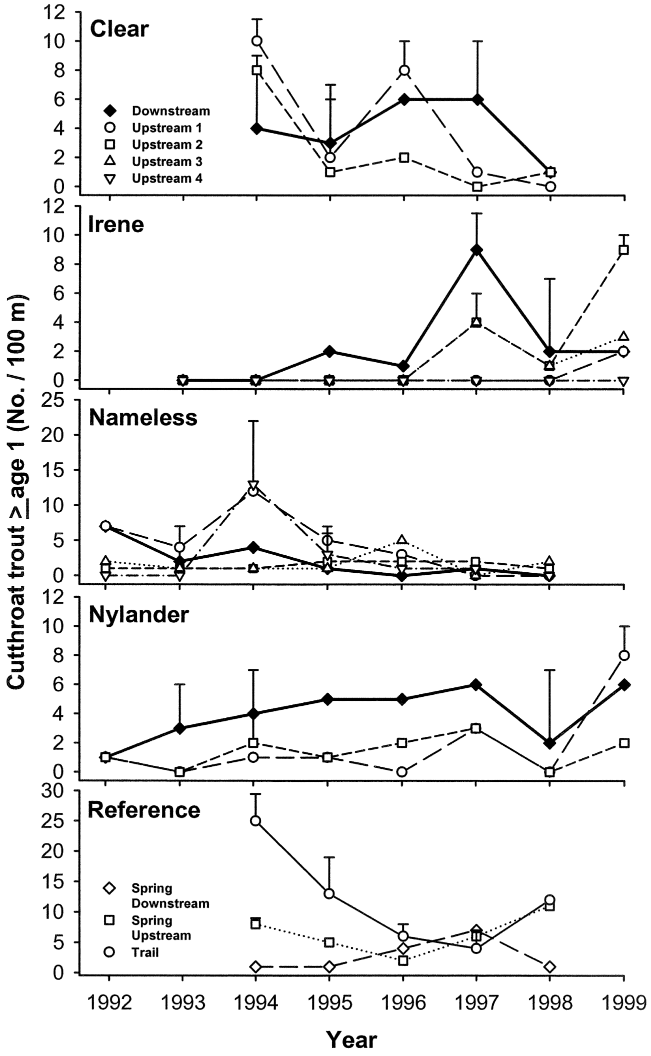


Figure 4. Population estimates (+ 95% C.I.) for wild cutthroat trout ≥ age 1 in sites upstream and downstream of barriers in treatment streams and in sites in reference streams in 1992–1999. The y-axis scaling is different among streams.

We found only limited evidence for increased body condition of cutthroat trout upstream of barriers. We did not detect significant trends in the longitudinal difference in relative weight of cutthroat trout in Nameless or Nylander creeks or in reference streams (τ ranged from -0.20 to 0.67; power ranged from 0.52 to 0.90). We did find a positive correlation between the longitudinal difference and number of years after removal of non-native fishes in Clear Creek ($\tau = 1.0$, $p = 0.04$, $n = 4$). The trend was for a consistent increase in the longitudinal difference from -15.3 in 1994 to 1.3 in 1998, suggesting that by the end of the study cutthroat trout upstream of the barrier increased from a marked deficit in condition to approximately equivalent condition relative to cutthroat trout downstream of the barrier. Sample sizes of cutthroat trout of sufficient size for reliable calculation of relative weight (Kruse & Hubert 1997) were too low for trend analyses in Irene Creek. Across the duration of the study, relative weights of cutthroat trout av-

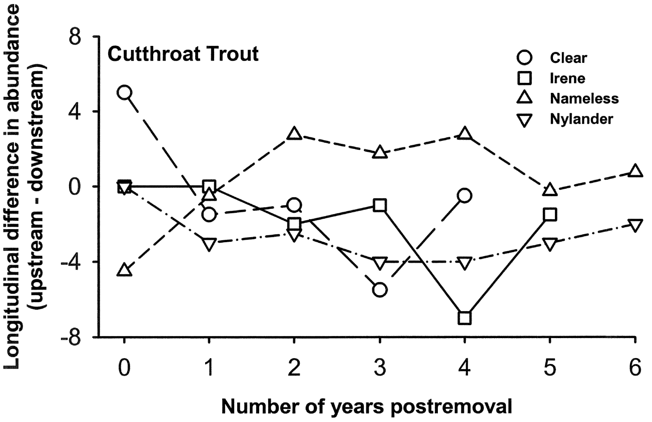


Figure 5. Longitudinal differences in abundance of wild cutthroat trout ≥ age 1 before and after removal of non-native trout, calculated by subtracting the population estimate (trout/100 m) in the downstream site from the mean population estimate of the upstream sites in each stream for each year.

eraged 94.1 (SE = 1.7, n = 66) in sites upstream of barriers, 92.1 (1.7, 47) downstream of barriers, and 95.4 (1.5, 43) in reference streams.

Stocking of hatchery-origin cutthroat trout upstream of barriers failed to enhance populations for more than 1 or 2 years after release (Table 2). Our recaptures of marked hatchery cutthroat trout suggested a rapid loss of stocked fish downstream over the barriers. Three separate stocking events occurred in each of the treatment streams (12 total), with initial stocking densities that ranged from 18 to 138 fish/100 m. Sampling in the year following release indicated that abundances of hatchery cutthroat trout stocked upstream of barriers declined by 87% to 100%, with <1% of the original stocks remaining after 3 years. In 1992 cutthroat trout stocked upstream of the barrier in Nameless Creek declined in abundance from 34 to 7 fish/100 m within 2 months. Stocked fish were, however, found downstream of the barrier at a density of 17 fish/100 m, suggesting significant downstream movement. Cutthroat trout stocked into Nylander Creek (42 fish/100 m in 1991) and Clear Creek (138 fish/100 m in 1995) were never recaptured at sites upstream of barriers in subsequent years. By contrast, stocked cutthroat trout were recaptured in sites downstream of barriers, particularly in Clear Creek. In several years, abundance estimates for stocked cutthroat trout in sites downstream of barriers exceeded abundance estimates for sites upstream of barriers.

Discussion

There was little evidence of enhancement of wild cutthroat trout populations upstream of barriers following isolation and removal of brook trout. In fact, average abundances of cutthroat trout upstream of barriers remained lower than downstream in three of the four treatment streams (negative longitudinal differences in abundance), indicating that fewer cutthroat trout persisted in isolation than coexisted with brook trout.

One explanation for this pattern is that brook trout had only a limited effect on cutthroat trout and that a significant release from competition did not occur. We consider this explanation unlikely for several reasons. Removal of brook trout from the study reaches decreased

Table 2. Decline in hatchery cutthroat trout stocked upstream of migration barriers in four streams in 1990 through 1999.[a]

			Abundance of hatchery cutthroat trout (number/100 m)									
Stream	*Fin clip*	*Number stocked (year)*	*1990*	*1991*	*1992*	*1993*	*1994*	*1995*	*1996*	*1997*	*1998*	*1999*
Clear Creek												
upstream	RP	2006 (1993)				134	8	2	0	0	0	
downstream							14	2	0	0	0	
upstream	LP	2006 (1994)					134	15	1	0	0	
downstream								10	1	0	0	
upstream	AD	2065 (1995)						138	0	0	0	
downstream									0	1	8	
Irene Creek												
upstream	RP	1003 (1990)	28	0	0	0.3	0	0	0	0	0	0
downstream				0	0	0	0	0	0	0	0	0
upstream	AD	2016 (1991)		56	0	0.5	0.3	0	0	0	0	0
downstream					0	0	0	0	0	0	0	0
upstream	LP	1007 (1998)									28	0
downstream												1
Nameless Creek												
upstream	RP	508 (1990)	18	0	0.5	0	0	0	0	0	0	
downstream				0	0	0	0	0	0	0	0	
upstream	AD	1008 (1991)		35	4.5	1.5	0.3	0.3	0	0	0	
downstream					2	0	0	1	0	0	0	
upstream	LP	1000 (1992)			34 (7)[b]	0.5	0.5	0	0	0	0	
downstream					(17)[b]	1	1	1	0	0	0	
Nylander Creek												
upstream	RP	1002 (1990)	84	ns	0	0	0	0	0	0	0	0
downstream				ns	0	0	0	0	0	0	0	0
upstream	AD	504 (1991)		42	0	0	0	0	0	0	0	0
downstream					2	0	0	0	0	0	0	0
upstream	LP	1540 (1998)									128	2
downstream												2

[a] *Stocks were identified by a fin clip (RP, right pelvic; LP, left pelvic; AD, adipose). Shown are the number of cutthroat trout stocked (year stocked) upstream of barriers and their subsequent abundance through time both upstream and downstream of the barriers (ns, not sampled).*

[b] *Abundance of stocked cutthroat trout determined 2 months after stocking.*

total trout numbers by 35% to 83%, a marked reduction in fish biomass in small, high-elevation streams that are generally considered resource-limited for trout (Fausch 1998). The regularity, intensity, and character of mechanisms underlying competition between cutthroat trout and brook trout are not clear. However, competitive interactions between the species have been hypothesized to contribute to the long-term decline of cutthroat trout in other systems and to determine patterns of distribution (Griffith 1972, 1988; Fausch 1989; Young 1995; Dunham et al. 1999; Kruse et al. 2000). Also, the presence of brook trout appears to limit reintroductions of cutthroat trout in mountain streams (Harig et al. 2000).

Another possibility is that there is a considerable time lag before a detectable response to isolation management occurs, given lengthy generation times for cutthroat trout in higher-elevation streams (4 years or longer; Gresswell 1988; Behnke 1992). The duration of our study might have been too short to allow depressed populations opportunity to recover (e.g., Clear Creek was sampled for 4 years following removal of non-native fishes), especially if the resilience of small populations was low in marginal headwater habitats. However, two of the four streams were sampled for 6 years following removal of non-native fishes; it seems unlikely that in this time evidence for numerical enhancement of cutthroat trout populations would remain absent.

Perhaps the most plausible hypothesis for failure of isolation management to enhance cutthroat trout is that isolated segments of headwater mountain streams lacked critical resources. Resources were apparently adequate to sustain populations at relatively low, pre-isolation levels, but the heterogeneity and connectivity of habitat needed to meet the seasonal requirements of cutthroat trout may be limited upstream of barriers, which could have inhibited population growth. Cutthroat trout in some stream systems migrate downstream to reach deep, low-velocity habitats to overwinter, then return to headwaters in search of spawning habitat (Jakober et al. 1998; Brown 1999; Schmetterling 2000). Lack of deep pools has been related to failure of translocations of greenback cutthroat trout (*O. c. stomias*) (Harig & Fausch 2002). The apparent loss of stocked cutthroat trout downstream over barriers in the present study is consistent with downstream migration to reach overwintering habitats. Loss to downstream emigration has similarly hampered establishment of arctic grayling (*Thymallus arcticus*) upstream of barriers in Yellowstone National Park (Kaya 2000).

Some immediate conservation benefits to cutthroat trout were realized as a result of isolation. Installation of the barriers and removal of non-native trout appeared to minimize the risk of hybridization with rainbow trout and generally inhibited reinvasion by brook trout (but regarding the efficacy of barriers, see Thompson & Rahel 1998). Rainbow trout and other non-native cutthroat trout exist in major tributaries of the Green River watershed; hence, continued maintenance of barriers will be necessary to exclude these species. Removal of non-native brook trout also greatly reduced the species' abundance upstream of barriers, although subsequent removals may be required because electrofishing did not eradicate brook trout from complex habitats (Thompson & Rahel 1996).

These successes need to be weighed against the potential for longer-term risks of isolation in apparently incomplete, fragmented habitats. The viability of small, isolated populations is threatened in the long term by stochastic processes and the potential loss of genetic heterogeneity (Wiens 1997). Extreme and fluctuating environmental conditions characterize headwater streams in mountainous regions, and chance phenomena including forest fires, freezing, and dewatering of stream channels could extirpate fish from isolated habitat fragments (Schlosser & Angermeier 1995; Rieman & Clayton 1997). Adequate levels of immigration are necessary to avoid the deleterious effects of inbreeding, including loss of genetic variation that could increase the risk of extinction (Saunders et al. 1991; Propst et al. 1992; Kruse et al. 2001). Actual population sizes of salmonids necessary for longer-term viability may be as high as 2500 individuals (Allendorf et al. 1997), and 8–25 km of stream may be required to encompass sufficient habitat to support a population of that size (Hilderbrand & Kershner 2000). Harig et al. (2000) determined that isolated reaches needed to exceed 5.7 km for successful establishment of greenback cutthroat trout in Rocky Mountain streams. The isolated populations we studied, however, occupied stream reaches ranging from 1.2 to 3.6 km in length, with estimated total population sizes of <200.

Isolation management at larger spatial scales in drainage networks might avoid potentially negative long-term effects by increasing habitat heterogeneity and connectivity and allowing for fluvial life histories (Dunham et al. 1997). But such strategies involve a tremendous effort to remove non-native fishes and to ensure that unwanted species do not recolonize. Habitat alteration such as increasing pool habitats and improving riparian conditions to benefit cutthroat trout in coordination with isolation also might promote enhancement of populations (Binns & Remmick 1994; Harig & Fausch 2002). Management agencies have been involved in reconnecting two isolated populations of Colorado River cutthroat trout in the Little Snake River drainage of Wyoming and Colorado by building a barrier to upstream fish migration downstream of the confluence of the streams and then poisoning non-native trout in the intervening waters (Young et al. 1996; Wyoming Game and Fish Department 1999). A similar project is now underway in the LaBarge Creek drainage of Wyoming, where several isolated populations of cutthroat trout (including those in Nameless and Clear creeks) will be united into a single, large population (Sexauer 2000).

Despite potentially serious drawbacks, isolation management may offer the only immediate solution for protection of native fishes that cannot withstand predation, hybridization, or competition with non-native species (Minckley et al. 1991; Shafer 1995). For example, native galaxiid fishes in New Zealand remain abundant only upstream of barriers that prevent colonization by non-native, piscivorous brown trout (Townsend 1996). Populations of genetically pure Yellowstone cutthroat trout may owe their persistence to irrigation diversion dams that prevent invasion by non-native trout (Kruse et al. 2000). Recovery of threatened greenback cutthroat trout has relied on establishing new populations isolated from non-native trout by natural or artificial barriers (Stuber et al. 1988; Harig et al. 2000).

However, an isolation approach combined with stocking did not achieve numerical enhancement of cutthroat trout populations during our study and may threaten longer-term viability by fragmenting populations of small size in restricted habitats. We urge careful consideration of the risks inherent in an isolation-management approach to the longer-term protection and enhancement of threatened populations prior to commitment of substantial resources to implement and maintain such a program. If isolation management of inland cutthroat trout appears to be the best option for immediate preservation of threatened populations, we suggest that isolated stream reaches be as long as possible and that habitat enhancements be considered to provide the full range of resources needed to sustain all life stages.

Acknowledgments

We thank R. Remmick and H. Sexauer of the Wyoming Game and Fish Department for useful discussion, technical assistance, and comments on the manuscript. P. Thompson kindly provided data and advice. M. McManus of the Missouri Department of Conservation, offered statistical recommendations. J. Anderson, T. Brunger, N. Elliot, J. Hawley, H. Johnstone, P. Mavrakis, A. Novinger, A. Schrank, and Y. Taniguchi were dedicated field assistants. A. Dolloff, G. Hayward, W. Hubert, B. Rieman, M. Wilzbach, and M. Young provided insightful reviews. Funding was provided by the Wyoming Game and Fish Department and the Department of Zoology and Physiology at the University of Wyoming.

Literature Cited

Allendorf, F. W. et al. 1997. Prioritizing Pacific salmon stocks for conservation. Conservation Biology **11:**140–152.

Behnke, R. J. 1992. Native trout of western North America. Monograph 6. American Fisheries Society, Bethesda, Maryland.

Binns, N. A., and R. Remmick. 1994. Response of Bonneville cutthroat trout and their habitat to drainage-wide habitat management at Huff Creek, Wyoming. North American Journal of Fisheries Management **14:**669–680.

Brown, R. S. 1999. Fall and early winter movements of cutthroat trout, *Oncorhynchus clarki*, in relation to water temperature and ice conditions in Dutch Creek, Alberta. Environmental Biology of Fishes **55:**359–368.

De Staso, J., and F. J. Rahel. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. Transactions of the American Fisheries Society **123:**289–297.

Dunham, J. B., G. L. Vinyard, and B. E. Rieman. 1997. Habitat fragmentation and extinction risk of Lahontan cutthroat trout. North American Journal of Fisheries Management **17:**1126–1133.

Dunham, J. B., M. M. Peacock, B. E. Rieman, R. E. Schroeter, and G. L. Vinyard. 1999. Local and geographic variability in the distribution of stream-living Lahontan cutthroat trout. Transactions of the American Fisheries Society **128:**875–889.

Fausch, K. D. 1989. Do gradient and temperature affect distributions of, and interactions between, brook charr (*Salvelinus fontinalis*) and other resident salmonids in streams? Physiological Ecology Japan **1:**303–322.

Fausch, K. D. 1998. Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales. Canadian Journal of Fisheries and Aquatic Sciences **55:**218–231.

Gregory, J. S., and J. S. Griffith. 2000. First-winter survival of caged wild and hatchery cutthroat trout in allopatry and in sympatry with brook trout. Intermountain Journal of Sciences **6:**217–222.

Gresswell, R. E. 1988. Status and management of cutthroat trout. Symposium 4. American Fisheries Society, Bethesda, Maryland.

Griffith, J. S. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. Journal of the Fisheries Research Board of Canada **29:**265–273.

Griffith, J. S. 1988. A review of competition between cutthroat trout and other salmonids. Pages 134–140 in R. E. Gresswell, editor. Status and management of cutthroat trout. Symposium 4. American Fisheries Society, Bethesda, Maryland.

Harig, A. L., and K. D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. Ecological Applications **12:**535–551.

Harig, A. L., K. D. Fausch, and M. K. Young. 2000. Factors influencing success of Greenback cutthroat trout translocations. North American Journal of Fisheries Management **20:**994–1004.

Hilderbrand, R. H., and J. L. Kershner. 2000. Conserving inland cutthroat trout in small streams: how much stream is enough? North American Journal of Fisheries Management **20:**513–520.

Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society **127:**223–235.

Kaya, C. M. 2000. Arctic grayling in Yellowstone: status, management and recent restoration efforts. Yellowstone Science **8:**12–17.

Kruse, C. G., and W. A. Hubert. 1997. Proposed standard weight (W_s) equations for interior cutthroat trout. North American Journal of Fisheries Management **17:**784–790.

Kruse, C. G., W. A. Hubert, and F. J. Rahel. 2001. Consideration of isolation for conserving headwater Yellowstone cutthroat trout populations. Northwest Science **75:**1–11.

Kruse, C. G., W. A. Hubert, and F. J. Rahel. 2000. Status of Yellowstone cutthroat trout in Wyoming waters. North American Journal of Fisheries Management **20:**692–704.

Melvin, S. M., L. H. MacIvor, and C. R. Griffin. 1992. Predator enclosures: a technique to reduce predation at piping plover nests. Wildlife Society Bulletin **20:**143–148.

Minckley, W. L., G. K. Meffe, and D. L. Soltz. 1991. Conservation and management of short-lived fishes: the cyprinodontoids. Pages 247–

282 in W. L. Minckley and J. E. Deacon, editors. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson.

Moyle, P. B., and G. M. Sato. 1991. On the design of preserves to protect native fishes. Pages 155–173 in W. L. Minckley and J. E. Deacon, editors. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson.

Novinger, D. C. 2000. Reversals in competitive ability: do cutthroat trout have a thermal refuge from competition with brook trout? Ph.D. dissertation. University of Wyoming, Laramie.

Propst, D. L., J. A. Stefferud, and P. R. Turner. 1992. Conservation and status of Gila trout, *Oncorhynchus gilae.* Southwestern Naturalist **37:**117–125.

Rieman, B., and J. Clayton. 1997. Wildfire and native fish: issues of forest health and conservation of sensitive species. Fisheries **22:**6–15.

Rinne, J. N., and P. R. Turner. 1991. Reclamation and alteration as management techniques, and a review of methodology in stream renovation. Pages 219–244 in W. L. Minckley and J. E. Deacon, editors. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson.

SAS Institute. 1999. SAS/STAT user's guide. Version 8.0. SAS Institute, Cary, North Carolina.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology **5:**18–29.

Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392–401 in J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. Symposium 17. American Fisheries Society, Bethesda, Maryland.

Schmetterling, D. A. 2000. Seasonal movements of fluvial westslope cutthroat trout in the Blackfoot River drainage, Montana. North American Journal of Fisheries Management **20:**711–719.

Schroeter, R. E. 1998. Segregation of stream-dwelling Lahontan cutthroat trout and brook trout: patterns of occurrence and mechanisms for displacement. M.S. thesis. University of Nevada, Reno.

Sexauer, H. 2000. LaBarge watershed fisheries management plan for Colorado River cutthroat trout. Wyoming Game and Fish Department, Cheyenne.

Shafer, C. J. 1995. Values and shortcomings of small reserves. BioScience **45:**80–88.

Simberloff, D., J. A. Farr, J. Cox, and D. W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? Conservation Biology **6:**59–70.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W.H. Freeman, San Francisco.

Stuber, R. J., B. D. Rosenlund, and J. R. Bennett. 1988. Greenback cutthroat trout recovery program: management overview. Pages 71–74 in R. E. Gresswell, editor. Status and management of cutthroat trout. Symposium 4. American Fisheries Society, Bethesda, Maryland.

Thompson, P. D., and F. J. Rahel. 1996. Evaluation of depletion-removal electrofishing of brook trout in small Rocky Mountain streams. North American Journal of Fisheries Management **16:**332–339.

Thompson, P. D., and F. J. Rahel. 1998. Evaluation of artificial barriers in small Rocky Mountain streams for preventing the upstream movement of brook trout. North American Journal of Fisheries Management **18:**206–210.

Townsend, C. R. 1996. Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. Biological Conservation **78:**13–22.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. LA-8787-NERP. Los Alamos National Laboratory, Los Alamos, New Mexico.

Wiens, J. A. 1997. Metapopulation dynamics and landscape ecology. Pages 43–62 in I. A. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics and evolution. Academic Press, New York.

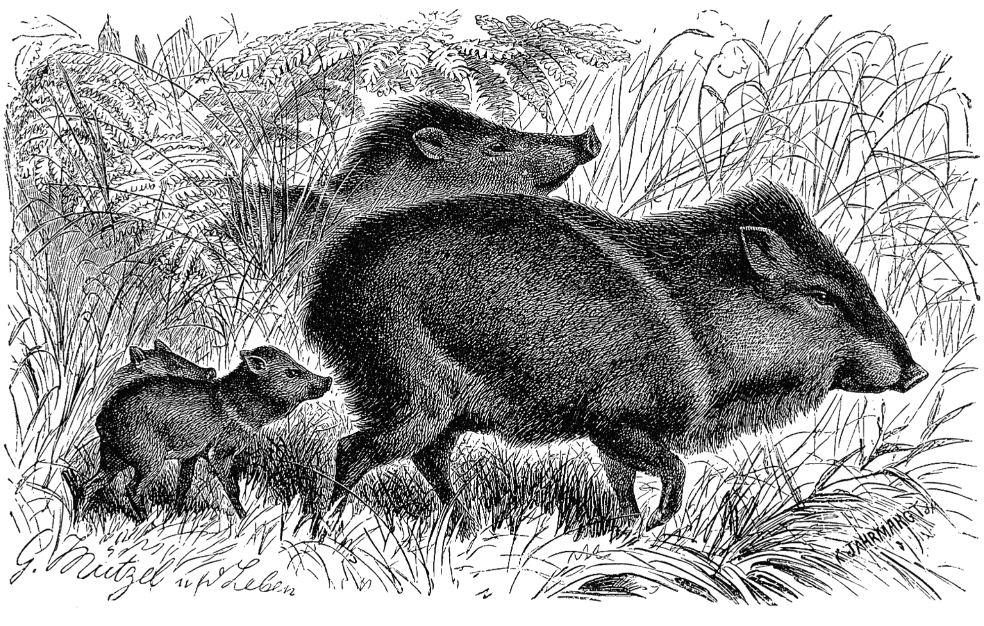
Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. The American Naturalist **125:** 879–887.

Wyoming Game and Fish Department (WGFD). 1987. Comprehensive management plan for Colorado River cutthroat trout in Wyoming. Fish Division, WGFD, Cheyenne.

Wyoming Game and Fish Department (WGFD). 1999. Annual fisheries progress report on the 1998 work schedule. Fish Division, WGFD, Cheyenne.

Young, M. K. 1995. Conservation assessment for inland cutthroat trout. General technical report RM-256. U. S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Young, M. K., R. N. Schmal, T. W. Kohley, and V. G. Leonard. 1996. Conservation status of Colorado River cutthroat trout. General technical report RM-GTR-282. U. S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.



Issues in Species Recovery: An Example Based on the Wyoming Toad

VICTORIA J. DREITZ

*The identification and recovery of endangered species is difficult because of their rarity, the continuing threats to their survival, and inadequate funding for research and conservation. There have been some success stories, but also a number of failures. Have biologists learned from our failures, or are we repeating the same mistakes? While habitat availability and cost are important limitations to species recovery, other, more easily addressed issues also hamper recovery programs. The Wyoming toad (*Bufo baxteri*) is an endangered species whose recovery has been stalled by problems that are common to species recovery efforts, especially for animals without significant "charisma." I summarize the research undertaken on the Wyoming toad since its listing, highlight the difficulties in building a scientifically based recovery program, and identify some of the unmet challenges impeding recovery. Although specific to the Wyoming toad, these recommendations are relevant to recovery programs facing similar issues.*

Keywords: Bufo baxteri*, endangered species, reintroduction, recovery, Wyoming toad*

In a perfect world, recovery programs would have adequate funding, with public and scientific support, and would be built on a foundation of reliable data. In reality, many of these essential ingredients are missing from most recovery programs. For example, the lack of ongoing training to help workers remain abreast of new methods and ideas (Anderson et al. 2003), the appointment of inexperienced personnel to key positions (Reading and Miller 1994), and the lack of coordination among agencies may particularly affect recovery programs. Because recovery programs are often carried out with a thin margin for error, they require strong, qualified leadership with up-to-date knowledge on species and conservation methods.

Suggested modifications to the Endangered Species Act, as well as critiques and assessments of recovery plans, have been published since the early 1990s (Tear et al. 1993, Hoekstra et al. 2002). The recovery program for the Wyoming toad (*Bufo baxteri*) lacks many of the essential ingredients. Because these deficiencies are commonplace, the case of the Wyoming toad provides perspective on other species recovery efforts. I examine the recovery efforts for the Wyoming toad using the framework of critical elements associated with recovery plans for aquatic-breeding amphibians (Semlitsch 2002). I summarize the research undertaken since the toad's listing, highlight the difficulties in building a scientifically based recovery program, and identify unmet challenges in hopes of illuminating some of the problems that arise in species recovery efforts.

Recognizing a species in trouble

The Wyoming toad is endemic to the Laramie Plain and was first described by George Baxter in 1946 (Porter 1968, Baxter and Stone 1985). This toad, a relic from the retreat of Pleistocene glaciation, has been considered a subspecies of the Canadian toad, *Bufo hemiophrys* (Porter 1968, Baxter and Stone 1985). However, Wyoming toads are separated from the range of Canadian toads by at least 750 kilometers (km) and are considered a distinct species by Packard (1971), Smith and colleagues (1998), and Crother and colleagues (2000). From their discovery through the early 1970s, Wyoming toads were considered common and abundant within their restricted range (Baxter and Stone 1985), but rapid declines (Baxter and Meyer 1982, Baxter et al. 1984) presaged their likely extinction by the mid-1980s (Lewis et al. 1985). In 1984, the Wyoming toad was listed as endangered (USFWS 1984).

A single population of Wyoming toads was discovered in 1987 at Mortenson Lake, in Albany County, Wyoming (Odum and Corn 2005). This location was purchased by The Nature Conservancy, and Mortenson Lake National Wildlife Refuge (MLNWR) was established in 1993. The refuge, an im-

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poundment in a complex of lakes and irrigation canals about 6 km north of the Laramie River, was originally a private ranch leased to a fishing club. Reproduction by Wyoming toads was recorded at MLNWR in 1988 (Freda et al. 1988), but the number of egg masses declined until no reproduction was observed after 1991 (Parker 2000, Parker and Anderson 2003, Odum and Corn 2005). By 1993, the few toads that could be found were collected from MLNWR for captive breeding, and the Wyoming toad was considered extinct in the wild (Odum and Corn 2005). Between 1995 and 1999, more than 9500 postmetamorphic toads were reintroduced at MLNWR (Odum and Corn 2005). Egg masses were reported in 1998 and 1999, presumably from toads reintroduced in 1995 or later (Parker 2000). At least one egg mass, which later hatched, was observed at MLNWR in 2002, and at least three, which also hatched, in 2004 (Michelle Geraud, US Fish and Wildlife Service [USFWS], Cheyenne, WY, personal communication, 21 December 2005).

The Wyoming toad is currently found at MLNWR and at one new reintroduction site (2005) between Laramie and Centennial, Wyoming. Genetic diversity is low (Jennings et al. 2001), and chytrid fungus (*Batrachochytrium dendrobatidis*) has been identified as contributing to mortality of individuals (Jennings et al. 2001; Allen P. Pessier, Zoological Society of San Diego, San Diego, CA, personal communication, 29 December 2005). The population at MLNWR is not currently self-sustaining, relying on annual supplementation with captive-reared animals (Odum and Corn 2005).

Although the Wyoming toad was listed in 1984, it was its rediscovery in 1987 that stimulated the formation of an *ad hoc* recovery group by USFWS and the Wyoming Game and Fish Department (WGFD), which also included regular participants from the University of Wyoming, The Nature Conservancy, and various zoos (Ronald E. Beiswenger, University of Wyoming, Laramie, WY, personal communication, 12 February 2006). A recovery plan was adopted in 1991 (USFWS 1991). The plan outlined basic goals but did not include specific objectives or methods to meet those goals. In 1992, the Albany County Wyoming Toad Task Force was convened as requested by the governor of Wyoming, with the support of the Environmental Protection Agency. The objective was to resolve conflicts between the mosquito control program subscribers and protection measures for the Wyoming toad. This group was active only between 1993 and 1995 (Ronald E. Beiswenger, University of Wyoming, Laramie, WY, personal communication, 12 February 2006). Captive breeding was initiated in 1993, and the American Zoo and Aquarium Association (AZA) approved a species survival plan in 1996 (Spencer 1999).

The Wyoming Toad Recovery Team was appointed in 2001, 17 years after the Wyoming toad was listed. That same year, the IUCN (World Conservation Union) Species Survival Commission Conservation Breeding Specialist Group (CBSG) facilitated a workshop including the recovery team, scientists, and interested citizens. The goal of the workshop was to "better understand the factors leading to the precipitous decline of the Wyoming toad, and to develop a set of alternative population management options" (Jennings et al. 2001). The workshop focused on disease, anthropogenic impacts, and population modeling, all within the context of a "shared vision" to "prevent extinction of the species in the wild" (Jennings et al. 2001). The formation of two recovery groups (the *ad hoc* group and the formal recovery team) and the CBSG workshop paralleled recovery actions for the endangered Houston toad (*Bufo houstonensis*) (Brown and Mesrobian 2005).

Monitoring

The success of recovery efforts since 1992 has been measured by monitoring activities that are limited to one or two surveys a year (early summer and fall) conducted by a variable number of untrained observers (P. Stephen Corn, US Geological Survey, Missoula, MT, personal communication, 21 December 2005). The semiannual surveys entail volunteers walking around Mortenson Lake through areas with saturated soils (habitats preferred by toads). If a toad is sighted, it is noted. Toads are not handled. Because observers are continuously moving through the search area, it is assumed that animals were not previously sighted during the survey (Ronald E. Beiswenger, University of Wyoming, Laramie, WY, personal communication, 12 February 2006; Erin Muths, US Geological Survey, Fort Collins, CO, personal communication, 13 December 2005). The results of these surveys are limited to counts of toads observed, categorized by life history stage (juvenile or adult). Although this information provides a minimum bound on the number of toads present, inferences from this type of count-based survey are biased because detection rate (i.e., percentage of animals seen, heard, or trapped) varies among counts (Nichols 1992, Williams et al. 2002). This survey provides quantitative information neither on breeding success nor on the fraction of the population sampled (i.e., there is no estimate of detection probability).

Use of methods lacking scientific rigor can lead to erroneous conclusions (Anderson et al. 2003), with potentially disastrous effects on species persistence (Steidl et al. 2000). For example, overestimating population size can lead to a false sense of security and a subsequent reduction of recovery efforts, and underestimating a population can precipitate hurried or unsuitable actions. Appropriate use of data, and a clear recognition of the inferences drawn from those data, is critical. Available data on the Wyoming toad are limited in scope (see below), and the only available population estimates use closed-population models from a study conducted in the period 1990–1992 (Withers 1992, Odum and Corn 2005).

Research on Wyoming toads

Research undertaken on the Wyoming toad includes field studies, captive breeding efforts, and disease identification. The most positive and numerous research activities have been in the veterinary and zoological communities, where endocrinologists and pathologists have worked successfully to breed Wyoming toads and identify diseases.

Field studies. Field research on Wyoming toads has missed the mark. The few studies conducted to date have been hampered by the scarcity of animals and by flawed methods. Both research and monitoring have been constrained by the reluctance of the *ad hoc* recovery group and regulatory agencies (USFWS, WGFD) to allow methods that involve more than minimal handling of animals (P. Stephen Corn, US Geological Survey, Missoula, MT, personal communication, 21 December 2005).

Two master's theses dominate the field research. Withers (1992) described the general natural history of Wyoming toads, in collaboration with Corn (1993), and compared habitats used by toads with habitats available in the immediate vicinity of Mortenson Lake. These data suggested that Wyoming toads mature earlier (males at two years and females at three years) than other, higher-elevation bufonids in the region (Withers 1992, Corn 1993, Carey et al. 2005, Odum and Corn 2005). Few Wyoming toads were observed to survive more than one to two years after reaching adult size, but this was most likely due to mortality from chytrid fungus (Withers 1992, Odum and Corn 2005). The interpretation of habitat use was hampered by significant differences in habitat measures between the years of the study (1991 and 1992).

Parker (2000) and Parker and Anderson (2003) compared the use of habitat by adult wild Wyoming toads and captive-reared Wyoming toads using radio telemetry in 1998 and 1999. Because there was no reproduction at MLNWR from 1992 to 1998, toads described as "wild" were most likely individuals reintroduced in 1996 or 1997. Thus, a comparison is misleading. The determination of habitat use and preference is fraught with difficulties such as spatial and serial autocorrelation, nonindependence of proportions, and definitions of habitat availability (e.g., Aebischer et al. 1993, Arthur et al. 1996). These concerns call into question many of the conclusions drawn from this study regarding preferred habitat (Parker 2000, Parker and Anderson 2003).

It is inappropriate to base management actions for a critically endangered species on unpublished and non-peer-reviewed reports (Reading and Miller 1994). The collection of accurate demographic data on Wyoming toads has long been recognized as essential to understanding the population dynamics of the species (USFWS 1991, Jennings et al. 2001). An overarching research agenda, including a well-designed monitoring program, is necessary (Boersma et al. 2001, Semlitsch 2002, Dodd 2005). Monitoring can provide reliable information from which important data gaps can be addressed, often in discrete, manageable, and affordable units. While the information mentioned above may be useful within the appropriate context, the rigorous evaluation of reintroduction efforts will go further toward developing a successful recovery program. This is especially important because reintroductions are necessary to sustain the Wyoming toad population in the wild.

Captive breeding. Maintaining animals in an unnatural environment, facilitating breeding, performing genetic screening, and investigating causes of disease in the field and in captivity are both challenging and critical to the success of the recovery program. The captive breeding effort for the Wyoming toad is the most successful aspect of the recovery program. Captive populations are maintained at eight AZA institutions following the AZA species survival plan (Spencer 1999). The development of captive husbandry protocols (Spencer 1999, Jennings et al. 2001) and the recognition of disease (Jennings et al. 2001, Pessier et al. 2002) in the Wyoming toad provide a sound basis for continued research and the provision of animals for reintroduction purposes. However, the captive breeding program should not be viewed as a panacea (Snyder et al. 1996). Simply adding animals to an area is unlikely to result in recovery (Dodd 2005). The captive breeding program for the Wyoming toad still faces unresolved issues. Most captive animals do not live longer than three years, but breeding success is highest in toads that are more than three years old (Jennings et al. 2001). This may indicate a difference between metabolic and chronological age in captive animals, but whether this difference is due to disease, nutrition, or other factors requires further investigation.

Disease identification. The Wyoming toad is afflicted by disease, both in captivity and in the wild. Bacterial infections ("red leg"), fungal infections (chytrid fungus), edema syndrome (Jennings et al. 2001), and short tongue syndrome (Jennings et al. 2001, Pessier et al. 2002) are documented, ongoing problems. Mycotic dermatitis (*Basidiobolus ranarum*) was identified as the cause of mortality in toads (104 of 147, or 71 percent; Taylor et al. 1999), but the pathogen was later determined to be chytrid fungus (Odum and Corn 2005). This disease is implicated in the decline of the boreal toad in the Rocky Mountains (Muths et al. 2003) and has most likely played a prominent role in the decline of Wyoming toads (Corn 2003).

Evaluation of reintroduction

For most amphibians, especially those that are endangered, reintroduction results are bleak (Dodd 2005). The amphibian reintroduction programs that have enjoyed the most success have followed the steps outlined by Dodd and Seigel (1991). These steps include knowing the causes of decline, committing to long-term monitoring, and adhering to the critical elements presented by Semlitsch (2002). Dodd (2005) notes, "Long-term research and monitoring, absolutely essential in any conservation program, are doubly important to ensure the success of HS/RRT [reintroduction] projects" (p. 270).

Efforts to reintroduce Wyoming toads to MLNWR have focused on releasing postmetamorphic toads (Odum and Corn 2005). Although the number of animals reintroduced has been documented, the success of reintroductions has not been evaluated. In response to the continued scarcity of toads in the wild and the proven ability to rear toads in captivity, in 2001 the USFWS requested quantitative information on the potential for reintroduction of captive-reared postmetamorphic toads to MLNWR. A one-year pilot study (Muths and

Dreitz 2003) was financially supported to estimate oversummer survival of reintroduced postmetamorphs and provide guidelines for a long-term monitoring program. The goal was not to provide specific answers, but rather to elucidate an avenue to address questions such as "What is the minimum yearly release number needed to sustain a viable population of Wyoming toads at a reintroduction site?" and "What is the appropriate monitoring protocol to detect trends in a population of Wyoming toads?" The pilot study was designed to follow a sampling approach accounting for imperfect detection based on mark–release–recapture procedures of the robust design (Kendall et al. 1997). Muths and Dreitz (2003) followed standard protocols (Heyer et al. 1994, Williams et al. 2002), including a priori simulations to estimate the number of animals to be released. Although survival was low, postmetamorphs did survive through the summer (Muths and Dreitz 2003). The pilot study field-tested protocols and methods and documented modifications to those protocols necessary to provide data for a long-term monitoring program for the Wyoming toad (Muths and Dreitz 2003).

Considerations for recovery

More than 25 years have passed since the Wyoming toad was recognized as critically imperiled, and 21 years since it was listed as an endangered species. Biological problems, including a precipitous decline in population numbers in the early 1990s and the presence of a lethal fungus (Jennings et al. 2001), have made study difficult and reintroduction an equivocal proposition. Since listing, there have been only four formal studies of the Wyoming toad: two theses (Withers 1992, Parker 2000, Parker and Anderson 2003), a three-year (1990–1992) project by the USFWS (Corn 1993, Odum and Corn 2005), and a pilot study (Muths and Dreitz 2003). Only the study by Muths and Dreitz (2003) provided guidelines for monitoring the reintroduction of captive-reared toads.

Semlitsch (2002) identified critical elements associated with successful recovery programs. He first discussed spatial and temporal scales. Defining the spatial scale for the Wyoming toad recovery effort is straightforward because of the toad's limited historical range. The temporal scale will most likely be dictated by the production of animals from captive husbandry, the development of disease identification tools, and the development of remedial actions in the face of disease. Below we address three additional points identified by Semlitsch (2002) in the context of the Wyoming toad.

Location of translocation sites relative to historical range and quality of habitat. Chytrid fungus (Jennings et al. 2001), pesticides, herbicides, and nonnative predators (e.g., stocked brown trout, *Salmo trutta*) are potential threats to Wyoming toads at MLNWR. Sites other than MLNWR should be identified using a priori criteria such as appropriate habitat characteristics, food availability, and predator and disease factors. Results from the pilot study at MLNWR (Muths and Dreitz 2003) can be used to evaluate candidate reintroduction sites where limitations are likely to be similar, that is, where few, if any, wild individuals are present and where released animals have low genetic diversity. New sites should be surveyed thoroughly for the presence of amphibians and of diseases such as chytrid fungus.

At least two applications for "safe harbor" agreements have been submitted (USFWS 2004), and one reintroduction site has been established on private property (R. Andrew Odum, Toledo Zoological Society, Toledo, OH, personal communication, 21 December 2005). Wyoming toads, including both adults and tadpoles, were released at the reintroduction site in 2005 (Jodi Bush, USFWS, Cheyenne, WY, personal communication, 22 September 2005), although the extent to which these sites were surveyed before the release is unknown. Postrelease surveys, which follow the field protocols of the semiannual sampling at MLNWR (i.e., no handling, toads sighted, no estimate of detection rate), are conducted only semiweekly (summer 2005) because of staffing limitations (Jodi Bush, USFWS, Cheyenne, WY, personal communication, 22 September 2005).

Translocation and reintroduction procedures. Given the assumption that captive rearing and reintroduction are the most practical recovery options for the Wyoming toad, we should examine both the methods and other associated elements carefully. For the Wyoming toad, the questions of where to gather animals to reintroduce into depopulated areas and whether to use captive or wild-caught animals are moot—there are no known extant populations in the wild. The genetic issues inherent in small, captive populations are being addressed by members of the Wyoming Toad Recovery Team (R. Andrew Odum, Toledo Zoological Society, Toledo, OH, personal communication, 21 December 2005).

Eggs collected in the wild are the first choice for translocation (Semlitsch 2002). Griffith and colleagues (1989) showed that wild-collected stock survived at twice the rate of captive-reared animals. Successful toad introductions involve translocations of eggs or juveniles at several sites, with releases in multiple years boosting the chances of success (Denton et al. 1997). Although documentation is limited, unsuccessful translocations of other bufonids have used postmetamorphic animals (Dodd and Seigel 1991, Muths et al. 2001).

Important population parameters (survival and reproduction) can be estimated and a monitoring program can be implemented that accounts for detection rate. Without such a monitoring scheme, an assessment of life history parameters is limited to imprecise and most likely unreliable estimates. Reintroducing egg masses provides an estimate of recovery effort needed to produce breeding animals, but cannot provide estimates for specific population parameters, such as survival. For example, if 1000 egg masses are reintroduced and 50 adult toads return to breed, we know the magnitude of effort necessary to produce 50 breeding adults. Accounting for detection rate using individually identifiable animals will yield useful data sooner than releasing eggs and waiting until toads mature and return to breed. Moreover, it provides an opportunity to quantify the success of the efforts in biologically meaningful terms. A two-pronged approach, using both eggs and individually identifiable juveniles, may be the most effective. This approach puts toads on the ground through the release of egg masses, and it reliably estimates population parameters that are necessary to build, maintain, and eventually complete such a reintroduction program.

Although reintroduction appears to be the tool of choice for recovery of the Wyoming toad, I highlight the recommendations of Dodd and Seigel (1991) and Dodd (2005). The motivation to employ reintroduction should be examined carefully. For example, is the reintroduction program attractive because it provides good publicity? If breeding in the wild occurs soon after the reintroduction, will success be declared, regardless of the long-term outlook? Sometimes reintroduction is chosen without adequately addressing the factors that put the species at risk in the first place. Often these factors, such as disease, are not obvious and require significant investment to elucidate properly (Dodd 2005).

Measuring success and long-term management. According to Boersma and colleagues (2001), "One cannot possibly know whether management is working and whether it needs to be adaptively altered unless its effects are monitored" (p. 648). It follows that it is impossible to declare a reintroduction successful without long-term monitoring to determine the ability of the population to sustain itself through time (Semlitsch 2002). It is impossible, using current data, to infer the status of the population, project the population's long-term viability, or evaluate the Wyoming toad recovery effort. Although new releases occurred in 2005, follow-up observations of the reintroduction effort rely on field surveys that cannot adequately evaluate the success of the reintroduction.

Communication. Measuring success and accomplishing short- and long-term management goals depends on clear articulation of the goals. It is likely that logistical stumbling blocks and miscommunication are not unusual and are, in fact, symptomatic of collaborative recovery efforts (Reading and Miller 1994). Miscommunication can undermine the success of a conservation program (e.g., Saterson et al. 2004). The case of the Wyoming toad is instructive. A critical misunderstanding occurred because of lack of dialogue regarding the goals of the Wyoming toad pilot project (Muths and Dreitz 2003). Specifically, there was a disparity between the questions addressed in the pilot project (Muths and Dreitz 2003), as requested by the USFWS, and the questions to which the recovery team expected answers. Agreement among management agencies on priorities is of paramount importance for acquiring adequate support and targeting success (Reading and Miller 1994). In addition, miscommunication regarding the number of animals available for release probably jeopardized the results of the pilot study (Muths and Dreitz 2003).

The assignment of inexperienced personnel to key positions has been noted as a substantive problem in endangered species recovery (Reading and Miller 1994) and may be particularly applicable to the recovery of the Wyoming toad, the most endangered amphibian in the United States. The problem of inadequate experience or expertise is not unique to endangered species recovery, but is symptomatic in the wildlife profession. Anderson and colleagues (2003) noted, "Perhaps our greatest failure as a profession has been the near total lack of meaningful science education.... [P]rofessionals must be given the opportunity to keep abreast of a large array of general technical advances" (p. 302). The Wyoming Toad Recovery Team also suffers from gaps in leadership: The coordinator resigned in 2004, and as of December 2005, no new coordinator had been designated. Strong leadership is essential for project direction and communication (Reading and Miller 1994).

The original recovery plan was completed in 1991. Although a revision is currently under way, there have been no revisions in 15 years, in spite of considerable advances in statistical modeling of population parameters (Williams et al. 2002) and molecular techniques (Wayne and Morin 2004). Available drafts of the revised recovery plan for the Wyoming toad (the last available draft was dated 2001) list several goals under "Part II Recovery," including "identify scientific criteria needed for population estimates" and "collect accurate demographic and ecological data." However, recently proposed and field-tested methods accounting for detection rate have been questioned in terms of their statistical efficacy and their field techniques for handling animals (Erin Muths, US Geological Survey, Fort Collins, CO, personal communication, 13 December 2005). Recovery plans need to be dynamic and responsive to advances in all relevant fields. Boersma and colleagues (2001), however, suggest that revised recovery plans may be no more effective than those without revision.

A second aspect of communication concerns informing the public. Miscommunication in the form of overly optimistic progress reports can mislead the recovery team or the public. Examples of this can be found in recovery efforts for other species, such as the black-footed ferret (*Mustela nigripes*) (Reading and Miller 1994) and the Houston toad (Yaffee 1982). Recent press releases about the recovery program for Wyoming toads focus on captive husbandry and the release of postmetamorphs, but no mention is made of the lack of data on the survival of released animals or the difficulty of obtaining such estimates.

Conclusions

Reintroducing a species is a separate exercise from monitoring its status. However, reintroduction without monitoring contributes little to the long-term success of recovery efforts and the persistence of the species (Dodd and Seigel 1991, Dodd 2005). An effective reintroduction and monitoring program for Wyoming toads is likely to be accomplished by a two-pronged approach focusing on the reintroduction of eggs and of individually identified postmetamorphic toads. According to Semlitsch (2002), "Monitoring procedures that do not distinguish between translocated [reintroduced] and wild-produced animals or between generations *through some mark-release-recapture procedures* will not be good measures of success" (p. 626; italics added). A program that releases eggs and individually identifiable juvenile toads can address immediate concerns over the use of captive-bred progeny and can address longer-term goals of providing information on life history parameters for management needs and program assessment.

A successful amphibian recovery program must attend to critical elements (*sensu* Semlitsch 2002), including the collection and use of defensible data. The most positive actions for Wyoming toads have been in the fields of veterinary science and husbandry. Endocrinologists and pathologists have worked successfully to identify the physiological processes that govern breeding in Wyoming toads and to investigate disease, nutritional problems, and other challenges involved in captive husbandry. While this aspect of toad recovery work has excelled, however, field research has faltered. Two pertinent issues are a general lack of funding for "noncharismatic" microfauna and an excessive concern over the fate of individual animals (e.g., as a result of handling), as opposed to the species as a whole, both of which have interfered with the development and implementation of necessary research. Unfortunately, many research opportunities are no longer available because of the decline in Wyoming toad numbers between 1993 and 2003.

The Wyoming toad has faced political and resource problems less severe than those that have hampered conservation of the Houston toad (Brown and Mesrobian 2005), but it still provides a good example of the fine-scale difficulties that can plague a recovery program. The example of the Wyoming toad demonstrates that listing a species is no guarantee that sufficient recovery efforts will be implemented or that communication among cooperating entities will occur. Seventeen years is too long a gap between the identification of an endangered species and the organization of a recovery team. Nearly 15 years have elapsed since revisions were made to the recovery plan for the Wyoming toad (more revisions are currently in preparation; Ronald E. Beiswenger, University of Wyoming, Laramie, WY, personal communication, 12 February 2006). In recovery planning, more attention should be focused on communication and on the timely production of adequate and achievable recovery goals and criteria, including the use of research to determine the direction and success of recovery plans. The Wyoming toad provides one more case that emphasizes the dire need to improve recovery efforts of endangered species.

Acknowledgments

I am indebted to Erin Muths of the US Geological Survey–Fort Collins Science Center, who participated in the development of this manuscript and in the monitoring pilot study conducted on Wyoming toads. She provided expertise on amphibians, particularly on historical and current perspectives of Wyoming toad ecology and conservation efforts, and many hours of discussion on recovery efforts of threatened and endangered amphibians. I thank Ronald E. Beiswenger, P. Stephen Corn, Michelle Geraud VanAcker, Andy Kouba, R. Andrew Odum, Allen P. Pessier, G. Brint Spencer, and Bill Turner for sharing unpublished information about the Wyoming toad recovery program. Erin Muths, Paul M. Lukacs, P. Stephen Corn, Paul F. Doherty Jr., B. Lee Lamb, Barry Noon, Kenneth Wilson, and three anonymous reviewers provided helpful comments on earlier drafts of the manuscript.

References cited

Aebischer NJ, Robertson A, Kenward RE. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74: 1313–1325.

Anderson DR, Cooch EG, Gutierrez RJ, Krebs CJ, Lindberg MS, Pollock KH, Ribic CA, Shenk TM. 2003. Rigorous science: Suggestions on how to raise the bar. Wildlife Society Bulletin 31: 296–305.

Arthur SM, Manly BFJ, McDonald LL, Garner GW. 1996. Assessing habitat selection when availability changes. Ecology 77: 215–227.

Baxter GT, Meyer JS. 1982. Progress Report: An Investigation of the Status of the Wyoming Toad in Albany County, Wyoming, and Possible Causes of the Decline in Numbers of Wyoming Populations of Anuran Amphibians. Laramie (WY): Department of Zoology, University of Wyoming.

Baxter GT, Stone MD. 1985. Amphibians and Reptiles of Wyoming. 2nd ed. Cheyenne (WY): Wyoming Game and Fish Department.

Baxter GT, Stromberg MR, Dodd CK Jr. 1984. The status of the Wyoming toad (*Bufo hemiophrys baxteri*). Environmental Conservation 9: 338, 348.

Boersma PD, Kareiva P, Fagan WF, Clark JA, Hoekstra JM. 2001. How good are endangered species recovery plans? BioScience 51: 643–649.

Brown LE, Mesrobian A. 2005. Houston toads and Texas politics. Pages 150–167 in Lannoo MJ, ed. Amphibian Declines: The Conservation Status of United States Species. Berkeley: University of California Press.

Carey C, Corn PS, Jones MS, Livo LJ, Muths E, Loeffler CW. 2005. Environmental and life history factors that limit recovery in southern Rocky Mountain populations of boreal toads (*Bufo boreas*). Pages 222–236 in Lannoo MJ, ed. Amphibian Declines: The Conservation Status of United States Species. Berkeley: University of California Press.

Corn PS. 1993. Population Ecology of the Endangered Wyoming Toad (*Bufo hemiophyrs baxteri*): 1992 Results. Fort Collins (CO): US Fish and Wildlife Service.

———. 2003. Deteriorating status of western amphibians: Can we generalize about causes? Pages 249–255 in Linder G, Krest SK, Sparling DW, eds. Amphibian Decline: An Integrated Analysis of Multiple Stressor Effects. Pensacola (FL): Society of Environmental Toxicology and Chemistry.

Crother BI, et al. 2000. Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico, with Comments Regarding Confidence in Our Understanding. St. Louis (MO): Society for the Study of Amphibians and Reptiles. Herpetological Circular no. 29.

Denton JS, Hitchings SP, Beebee TJC, Gent A. 1997. A recovery program for the natterjack toad (*Bufo calamita*) in Britain. Conservation Biology 11: 1329–1338.

Dodd CK Jr. 2005. Population manipulation. Pages 265–270 in Lannoo MJ, ed. Amphibian Declines: The Conservation Status of United States Species. Berkeley: University of California Press.

Dodd CK Jr, Seigel RA. 1991. Relocations, repatriations, and translocations of amphibians and reptiles: Are they conservation strategies that work? Herpetologica 47: 336–350.

Freda J, Gern B, McLeary D, Baxter G. 1988. 1988 Recovery Efforts for the Endangered Wyoming Toad, *Bufo hemiophrys* baxteri. Laramie (WY): Department of Zoology, University of Wyoming.

Griffith B, Scott JM, Carpenter JW, Reed C. 1989. Translocation as a species conservation tool: Status and strategy. Science 245: 477–480.

Heyer WR, Donnelly MA, McDiarmid RW, Hayek LC, Foster MS. 1994. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Washington (DC): Smithsonian Institution Press.

Hoekstra JM, Clark JA, Fagan WF, Boersma PD. 2002. A comprehensive review of endangered species act recovery plans. Ecological Applications 12: 630–640.

Jennings M, Beiswenger R, Corn PS, Parker M, Pessier A, Spencer B, Miller P, eds. 2001. Population and Habitat Viability Assessment for the Wyoming Toad (*Bufo baxteri*). Final Workshop Report. Apple Valley (MN): IUCN/SSC Conservation Breeding Specialist Group.

Kendall WL, Nichols JD, Hines JE. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology 78: 563–578.

Lewis DL, Baxter GT, Johnson KM, Stone MD. 1985. Possible extinction of the Wyoming toad, *Bufo hemiophrys baxteri*. Journal of Herpetology 19: 166–168.

Muths E, Dreitz VJ. 2003. Preliminary Development of a Monitoring Program for Wyoming Toad Populations. Fort Collins (CO): US Geological Survey–Fort Collins Science Center.

Muths E, Johnson TL, Corn PS. 2001. Experimental repatriation of boreal toad (*Bufo boreas*) eggs, metamorphs, and adults in Rocky Mountain National Park. Southwestern Naturalist 46: 106–113.

Muths E, Corn PS, Pessier AP, Green DE. 2003. Evidence for disease-related amphibian decline in Colorado. Biological Conservation 110: 357–365.

Nichols JD. 1992. Capture–recapture models. BioScience 42: 94–102.

Odum RA, Corn PS. 2005. *Bufo baxteri* Porter, 1968, Wyoming toad. Pages 390–392 in Lannoo MJ, ed. Amphibian Declines: The Conservation Status of United States Species. Berkeley: University of California Press.

Packard GC. 1971. Inconsistency in application of the biological species concept to disjunct populations of anurans in southeastern Wyoming and north-central Colorado. Journal of Herpetology 5: 191–193.

Parker J. 2000. Habitat use and movements of the Wyoming toad, *Bufo baxteri:* A study of wild juvenile, adult, and released captive-raised toads. Master's thesis. University of Wyoming, Laramie, WY.

Parker JM, Anderson SH. 2003. Habitat use and movements of repatriated Wyoming toads. Journal of Wildlife Management 67: 439–446.

Pessier AP, Roberts DR, Linn M. 2002. Short tongue syndrome, lingual squamous metaplasia and suspected hypovitaminosis A in captive Wyoming toads, *Bufo baxteri*. Pages 151–153 in Bradley T, ed. Proceedings, Association of Reptilian and Amphibian Veterinarians: Ninth Annual Conference, October 9–12, 2002, Reno, Nevada. N.p.: The Associations.

Porter KR. 1968. Evolutionary status of a relict population of *Bufo hemiophrys* Cope. Evolution 22: 583–594.

Reading RP, Miller BJ. 1994. The black-footed ferret recovery program: Unmasking professional and organizational weaknesses. Pages 73–100 in Clark TW, Reading RP, Clarke AL, eds. Endangered Species Recovery: Finding the Lessons, Improving the Process. Washington (DC): Island Press.

Saterson KA, Christensen NL, Jackson RB, Kramer RA, Pimm SL, Smith MD, Wiener JB. 2004. Disconnects in evaluating the relative effectiveness of conservation strategies. Conservation Biology 18: 597–599.

Semlitsch RD. 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. Conservation Biology 16: 619–629.

Smith HM, Chiszar D, Collins JT, van Breukelen F. 1998. The taxonomic status of the Wyoming toad, *Bufo baxteri* Porter. Contemporary Herpetology 1998 (1). (22 June 2006; *www.cnah.org/ch/ch/1998/1/index.htm*)

Snyder NFR, Derrickson SR, Beissinger SR, Wiley JW, Smith TB, Toone WD, Miller B. 1996. Limitations of captive breeding in endangered species recovery. Conservation Biology 10: 338–348.

Spencer GB. 1999. The Wyoming toad SSP. Endangered Species Bulletin 24: 18–19.

Steidl RJ, DeStefano S, Matter WJ. 2000. On increasing the quality, reliability and rigor of wildlife science. Wildlife Society Bulletin 28: 518–521.

Taylor SK, Williams ES, Thorne ET, Mills KW, Withers DI, Pier AC. 1999. Causes of mortality of the Wyoming toad. Journal of Wildlife Disease 35: 49–57.

Tear TH, Scott JM, Hayward PH, Griffith B. 1993. Status and prospects for success of the Endangered Species Act—a look at recovery plans. Science 262: 976–977.

[USFWS] US Fish and Wildlife Service. 1984. Endangered and threatened wildlife and plants; determination that *Bufo hemiophrys baxteri* (Wyoming toad) is an endangered species. Federal Register 49 (11): 1992–1994.

———. 1991. Wyoming Toad Recovery Plan. Denver (CO): US Fish and Wildlife Service, Region 6.

———. 2004. Programmatic Safe Harbor Agreement and receipt of an application for an enhancement of survival permit associated with proposed restoration and reintroduction activities for Wyoming toads within suitable wetland habitat of Albany County, WY. Federal Register 69 (94): 26878–26879.

Wayne RK, Morin PA. 2004. Conservation genetics in a new molecular age. Frontiers in Ecology and the Environment 2: 89–97.

Williams BK, Nichols JD, Conroy MJ. 2002. Analysis and management of animal populations. San Diego (CA): Academic Press.

Withers DI. 1992. The Wyoming toad (*Bufo hemiophrys baxteri*): An analysis of habitat use and life history. Master's thesis. University of Wyoming, Laramie.

Yaffee SL. 1982. Prohibitive Policy: Implementing the Federal Endangered Species Act. Cambridge (MA): MIT Press.

Communications

Ecological Applications, 28(2), 2018, pp. 275–283

Demographic drivers of a refugee species: large-scale experiments guide strategies for reintroductions of hirola

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Abstract. Effective reintroduction strategies require accurate estimates of vital rates and the factors that influence them. The hirola (*Beatragus hunteri*) is the rarest antelope on Earth, with a global population size of <500 individuals restricted to the Kenya–Somali border. We estimated vital rates of hirola populations exposed to varying levels of predation and rangeland quality from 2012 to 2015, and then built population matrices to estimate the finite rate of population change (λ) and demographic sensitivities. Mean survival for all age classes and population growth was highest in the low-predation–high-rangeland-quality setting ($\lambda = 1.08 \pm 0.03$ [mean ± SE]), and lowest in the high-predation–low-rangeland-quality setting ($\lambda = 0.70 \pm 0.22$). Retrospective demographic analyses revealed that increased fecundity (the number of female calves born to adult females annually) and female calf survival were responsible for higher population growth where large carnivores were absent. In contrast, variation in adult female survival was the primary contributor to differences in population growth attributable to rangeland quality. Our analyses suggest that hirola demography is driven by a combination of top-down (predation) and bottom-up (rangeland quality) forces, with populations in the contemporary geographic range impacted both by declining rangeland quality and predation. To enhance the chances of successful reintroductions, conservationists can consider rangeland restoration to boost both the survival and fecundity of adult females within the hirola's historical range.

Key words: *endangered species; habitat quality; life table response experiment; predation; rangeland; recruitment; survival; ungulate; vital rate.*

INTRODUCTION

A species' geographic range can be viewed as a proxy of its realized niche, in which a combination of factors (e.g., resource availability, predation, interspecific competition) combine to influence vital rates and subsequent population growth. Species exhibiting rapid range collapse may be confined to habitats in which low rates of survival, recruitment, or both prevent positive population growth (Pulliam and Danielson 1991, Caughley 1994). For such "refugee species" (sensu Kerley et al. 2012), there is strong risk of conflating persistence within a habitat to suitability of that habitat, thereby obfuscating the efforts most likely to lead to recovery (Van Horne 1983, Lea et al. 2016).

The forces that affect wildlife populations, and thus extirpation and eventual extinction, encompass bottom-up and top-down processes that are dynamic in space and through time. Understanding ecological processes can be used to identify refugee species, thereby steering conservation efforts (Sinclair and Krebs 2002, Wallach et al. 2015). Nevertheless, recovery efforts often are conducted without an a priori understanding of the relative roles of these ecological processes, glossing over the possibility that species may currently exist as refugees and leading to ineffective reintroductions in suboptimal habitats (Balmford and Cowling 2006, Tanentzap et al. 2012, Morrison 2013). While the escalation of extinction

Manuscript received 22 May 2017; revised 28 September 2017; accepted 2 October 2017. Corresponding Editor: Jonathan N. Pauli.

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risk has led to heightened urgency to identify effective conservation strategies, many efforts still fail to incorporate evidence-based practices that could increase their impact (Sutherland et al. 2004). Experimental approaches can inform the degree to which populations are limited top-down, bottom-up, or both; for example, Armstrong and Perrott (2000) and Armstrong et al. (2002) combined food supplementation with stochastic simulation models to demonstrate that Stitchbird (*Notiomystis cincta*) reintroductions were limited by food on predator-free islands. In light of the widening gap between conservation efforts and continued declines in populations, the scientific community increasingly is emphasizing the importance of evidence, experimental or otherwise, to ground management interventions for species of conservation concern in the most rigorous science possible (Beale et al. 2013, Tulloch et al. 2015).

The hirola antelope (*Beatragus hunteri*) is a critically endangered species from a once-widespread lineage. Hirola declined from over 15,000 individuals in the 1960s to <500 individuals today (IUCN 2008), most precipitously in the 1980s following a rinderpest outbreak, such that their geographic range has contracted to a narrow swath of rangeland between the Tana River and the Boni Forest. However, following eradication of rinderpest by 2001 (Mariner et al. 2012), hirola populations did not recover to pre-outbreak levels (Ali et al. 2017, Fig. 1). Our recent work has demonstrated that range degradation, through tree encroachment, may underlie continued suppression of hirola populations (Ali et al. 2017). Additionally, some have speculated that a combination of heightened predation and reduced rangeland quality are responsible for its current status as the world's most endangered antelope (Probert et al. 2015). Such uncertainty characterizes the plight of many species of conservation concern, and can translate to variable outcomes in reintroduction efforts (Sarrazin and Barbault 1996, Sutherland et al. 2004, Armstrong and Seddon 2008). Recovery efforts for hirola have occurred mostly through community-based conservancies and sanctuaries (e.g., the Ishaqbini Community Conservancy in eastern Kenya; Measham and Lumbasi 2013), because the vast majority (>90%) of hirola occur outside formally protected areas alongside pastoralists and their livestock.

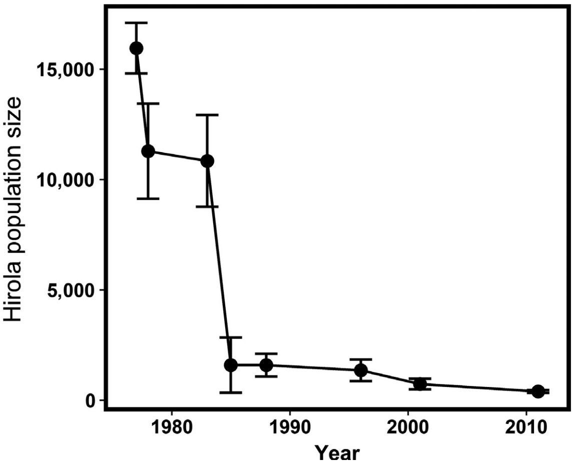

FIG. 1. Estimated hirola population trends from 1977–2011 (mean ± SE). The population crash in the mid-1980s is the result of a rinderpest outbreak in the Horn of Africa. Data courtesy of the Kenya Department of Resource Surveys and Remote Sensing. See Appendix S1 for methods for aerial surveys.

Vital rates entail the survival, growth, and reproduction of individuals, and responses of these vital rates to environmental conditions therefore determine population dynamics. We sought to quantify the relative importance of age-specific survival and fecundity to population growth of hirola, with the intent of centering recovery plans on the processes most likely to reverse population declines (Johnson et al. 2010). Between 2012 and 2015, we quantified vital rates under three ecological conditions: (1) a predator-proof sanctuary with relatively high rangeland quality because of minimal livestock grazing (hereafter "sanctuary"), nested within the broader Ishaqbini Community Conservancy; (2) the Ishaqbini Community Conservancy (hereafter "conservancy") with similarly high rangeland quality but in which large carnivores occurred; and (3) an area outside the conservancy (hereafter "rangelands") with similar numbers of large carnivores to the conservancy (Appendix S1: Table S1), but with lower rangeland quality (due to high levels of livestock grazing that reduced forage availability). Our study provides a rare example of how large-scale experiments can be used to understand species declines and guide reintroduction efforts for a critically endangered species (see also Saltz and Rubenstein 1995, Sarrazin and Legendre 2000, and Steury and Murray 2004). This is especially important considering that hirola are restricted to the Kenya–Somalia border, a remote and volatile area where wildlife populations are difficult to monitor.

MATERIALS AND METHODS

Study area

We conducted this work in Ijara (latitude 1°36′33.95″ S, longitude 40°32′35.43″ E) and Fafi (latitude 0°25′23.26″ S, longitude 40°13′46.42″ E) sub-counties of Garissa County in eastern Kenya (Appendix S1: Fig. S1). Ijara is one of the driest regions in Kenya with an average annual rainfall ranging from 350–550 mm. Xeric conditions are ideal for hirola, which thrive in open, semiarid grasslands (Kingdon 1982). Livestock production is the most common land use in the region and includes production of domestic goat (*Capra hircus*), sheep (*Ovis aries*), cattle (*Bos indicus*), camel (*Camelus dromedarius*), and donkey (*Equus asinus*). Native species of large carnivores include lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), spotted hyenas (*Crocuta crocuta*), and African wild dogs (*Lycaon pictus*), which are common both in the conservancy and in the rangelands (Appendix S1: Table S1).

Demographic study design

Environmental setting 1: sanctuary.—In August 2012, a 25-km^2 predator-proof sanctuary (latitude 1°52′24.94″ S, longitude 40°11′13.55″ E) was established within Ishaqbini Community Conservancy through a partnership between local communities, the Kenya Wildlife Service, and the Northern Rangelands Trust in an effort to curtail ongoing hirola declines (Appendix S1: Fig. S1). The sanctuary fence is 2.5 m tall with electrified (6,000–7,000 V) strands of wires spaced at 30 cm with wire mesh along the lower 1.5-m section. Dedicated personnel maintain the fence and patrol the sanctuary on a daily basis. Prior to translocating hirola into the sanctuary, we removed livestock and large carnivores (six spotted hyenas and six cheetahs), and established three permanent rain-catchment troughs. We then translocated hirola from the outskirts of Ishaqbini Community Conservancy into the sanctuary. We used a combination of helicopter drives and net capture; additionally, 12 individuals were enclosed within the sanctuary at the time of construction for a total of 48 individuals (i.e., ~10% of the global population; 5 males, 39 females, and 4 calves; King et al. 2011). We immobilized net captured individuals with a combination of 3 mg Etorphine hydrochloride (M99; a narcotic) and 30 mg Azaperone (Stresnil; a tranquilizer) with 6 mg Diprenorphine hydrochloride as a reversal. Prior to release, we fixed uniquely numbered ear tags on each individual to aid in subsequent identification and monitoring. Individuals settled into six distinct groups after the first six months and maintained this social structure throughout the study period (2012–2015). The sex and age composition of the enclosed herd approximated the social structure and densities reported for hirola throughout their geographic ranges (Andanje 2002).

Environmental setting 2: conservancy.—Located on the eastern bank of the Tana River in Kenya and with an area of 240 km^2, the Ishaqbini Community Conservancy (1°54′19.56″ S, 40°12′49.89″ E; Appendix S1: Fig. S1) was established in 2005 by Terra Nuova (an Italian non-government organization for conservation and rural development; Njoroge et al. 2015). In an attempt to improve rangeland quality for hirola and other wildlife, livestock grazing has been minimized since 2008, thereby providing more grass biomass relative to rangelands (Appendix S1: Fig. S2). About six hirola groups use the conservancy at varying times of the year. We restricted our analyses to 38 individuals (slightly lower than the ~10% of the global population; King et al. 2011) in three resident groups that occupied the conservancy for the duration of our study. Hirola have stable groups and are faithful to particular areas, so we were able to identify 38 unique individuals throughout the year using natural marks including ear nicks, horn size and shape, scars, and coloration (see also Bro-Jørgensen and Durant 2003).

Environmental setting 3: rangelands.—From August 2012 to December 2012, we deployed GPS PLUS collars (Vectronic Aerospace, Berlin, Germany) on nine adult females from seven different groups (group size = 7.0 ± 2.0 [mean ± SE], range = 5–11; ~15% of the global population) spread in a 1,000 km^2 area outside the conservancy and the sanctuary (Appendix S1: Fig. S1). GPS collars allowed us to relocate the seven groups weekly to estimate vital rates through resighting (Cormack 1964, Johnson et al. 2010). In collaring individuals, we followed the same capture procedures as the translocation effort (see *Environmental setting 1: sanctuary*). The rangelands were characterized by lower grass biomass due to intensive livestock grazing (Appendix S1: Fig. S2) and comparable abundances of large carnivores to conservancy lands (Appendix S1: Table S1). This third environmental setting is representative of the hirola's current range. All procedures were conducted with a veterinary team under the authority of the Kenya Wildlife Service (KWS) and under permit number KWS/CRA/5001.

Demographic data collection and analysis

We used weekly resightings of groups from all three settings to estimate age-specific survival rates of calves, female sub-adults, and adults, and fecundity of adult females (see below; Andanje 2002, Johnson et al. 2010). We summarized the weekly totals from re-sighting to generate an average monthly count of females per setting, which we used to develop Kaplan-Meier (KM) models and generate survival rates for every year for the entire experimental period (3 yr). During each survey, we identified all observed individuals and searched for any missing individuals that were counted in the previous survey(s) for a period of up to two weeks. Searching for missing individuals entailed intensive bouts of searching, during which we covered a 7–12 km radius in concentric circles from the centroid at which we detected the rest of the group. Following these counts, and in light of the high fidelity and cohesion of individuals within groups (Andanje 2002), we interpreted any missing individuals as evidence of mortality. Subsequently, and toward the last week of every month, we conducted a verification survey to validate our observed counts. Verifications involved a combination of Pearson correlations (Lawrence and Lin 1989), Brier scores (Brier 1950), and Cohen's weighted kappa methods (Cohen 1968) to quantify agreement between resighting by multiple observers (Appendix S1: Table S2).

Similar to other alcelaphine antelopes, the majority of adult females (>50%) exhibit a birth pulse at the beginning of the short rains in October–November, although breeding can occur throughout the year (Rutberg 1987, Andanje 2002). Hirola have 7–8 month gestation periods (Kingdon 1982), and we began noticing gravid females ~2–3 months before parturition. Therefore, we used a post-birth census to estimate adult fecundity, measured as the average proportion of adult females that gave birth to calves over each 12-month period. This proportion integrates three rates, none of which we measured directly (the probability of pregnancy, the probability of birth given pregnancy, and calf sex ratio), with a fourth rate, the litter size of hirola, which did not vary. Females give birth to a single calf at approximately 3 yr old and live up to 10 yr (Andanje 2002). We assumed a 50:50 sex ratio for all calves (we could not distinguish sexes of calves) in estimating female fecundities; this is typical for ungulates when sample sizes are large or when multi-year data is used (Raithel et al. 2007). Post-breeding censuses are used commonly for field studies that have logistical and other challenges (Cooch et al. 2003); this approach allowed us to count and employ sight–resight methods on adult females with calves, since calves often have reduced mobility and adult-female–calf pairs may temporarily disassociate from groups.

We used the survival package in R version 3.2 (R Core Team 2013, Therneau 2013) to generate mean cumulative survival rates for each age class per year (Kaplan and Meier 1958, White and Garrott 1990), and the popbio package (Stubben and Milligan 2007) to develop an age-structured matrix for each setting in each transition year (for a total of nine matrices). To implement matrix models, we followed Andanje (2002) in modeling hirola demography with three age classes (calves [i.e., individuals born within the monitoring year], female sub-adults between 1 and 2 yr old, and female adults >2 yr) to account for differences in survival and fecundity. Following Caswell (2001), we constructed a female-based post-birth model with a 1-yr projection interval using a 3 × 3 matrix

$$A = \begin{pmatrix} 0 & 0 & S_{\mathrm{ad}} & F_{\mathrm{ad}} \\ S_{\mathrm{c}} & 0 & 0 & \\ 0 & S_{\mathrm{sa}} & S_{\mathrm{ad}} & \end{pmatrix} \begin{pmatrix} \text{Calves} \\ \text{Subadults} \\ \text{Adults} \end{pmatrix}$$

where each matrix element represents a vital rate for each of the classes (calves, sub-adults, and adults; Morris and Doak 2002) defined as S_{c}, survival of calves; S_{sa}, survival of sub-adults; S_{ad}, survival of adults; and F_{ad}, fecundity rate of adult females. At the beginning of each survey, we identified the proportion of individuals in each age class, and matched these with corresponding survival and fecundity rates.

With a post-breeding census approach, non-zero matrix elements in the top row of the matrix represent the product of adult fecundity and survival. From matrices, we estimated the finite rate of population change (λ) as the dominant eigenvalue (Caswell 2001) and calculated the geometric means for each setting across all the three transition years (2012–2013, 2013–2014, 2014–2015). We plotted the KM estimates of annual survival and the cumulative hazard curves for all the age classes in the three settings (Appendix S1: Fig. S3). To account for uncertainty in model selection, we estimated the standard errors of estimates of population parameters by full-model averaging (Johnson and Omland 2004, Symonds and Moussalli 2011). From the model output, we extracted the coefficients, standard errors and associated degrees of freedom. We conducted a series of Z tests in R to evaluate differences in λ between pairs of environmental settings, and we calculated both analytical sensitivity and elasticity estimates for lower level vital rates across each environmental setting in the popbio package (Stubben and Milligan 2007).

We conducted a life table response experiment (LTRE) to decompose effects of environmental settings on λ into contributions from setting-specific vital rates (Bruna and Oli 2005, Barclay et al. 2011). LTRE analysis quantifies the real contributions of variation in vital rates to differences in λ between two or more populations (Horvitz et al. 1997). We calculated contributions from demographic matrices for the 2012–2015 period using averaged vital rates estimated from each population to facilitate pairwise (settings) comparisons (sanctuary vs. conservancy, sanctuary vs. rangelands, conservancy vs. rangelands). We calculated the change in λ between each paired *setting* as $\Delta\lambda = \lambda_i - \lambda_j$, which can also be estimated using

$$\sum_{m} (x_{m_i} - x_{m_j}) * s_{ij}$$

where $(x_{m_i} - x_{m_j})$ is the difference in vital rate m for a pair of settings, and s_{ij} is the mean sensitivity of λ to changes in vital rate m evaluated for a "mean" matrix (i.e., midway between the two matrices being compared) between the pair of settings being compared (Bruna and Oli 2005). Thus, each term in the summation represents the contribution of vital rate m to the $\Delta\lambda$ arising between a pair of settings.

RESULTS

We tracked telemetered hirola from the time they were fitted with GPS collars (between August and December 2012) through December 2015. Adult survival was generally higher than sub-adult and calf survival across all three settings and years, with survival rates highest in the sanctuary for all three age classes (Fig. 2). Of particular note were (1) increases in adult survival due to heightened rangeland quality (S_{ad} sanctuary $\approx$ S_{ad} conservancy > S_{ad} rangelands; Fig. 2A); (2) increases in sub-adult survival due to large carnivore exclusion (S_{sa} sanctuary > S_{sa} conservancy $\approx$ S_{sa} rangelands; Fig. 2B); (3) increases in calf survival due to large carnivore exclusion (S_{c} sanctuary > S_{c} conservancy $\approx$ S_{c} rangelands; Fig. 2C); and (4) increases in fecundity due to large carnivore exclusion (F_{ad} sanctuary > F_{ad} conservancy $\approx$ F_{ad} rangelands; Fig. 2D). Elasticity of adult survival was higher in the conservancy and rangelands

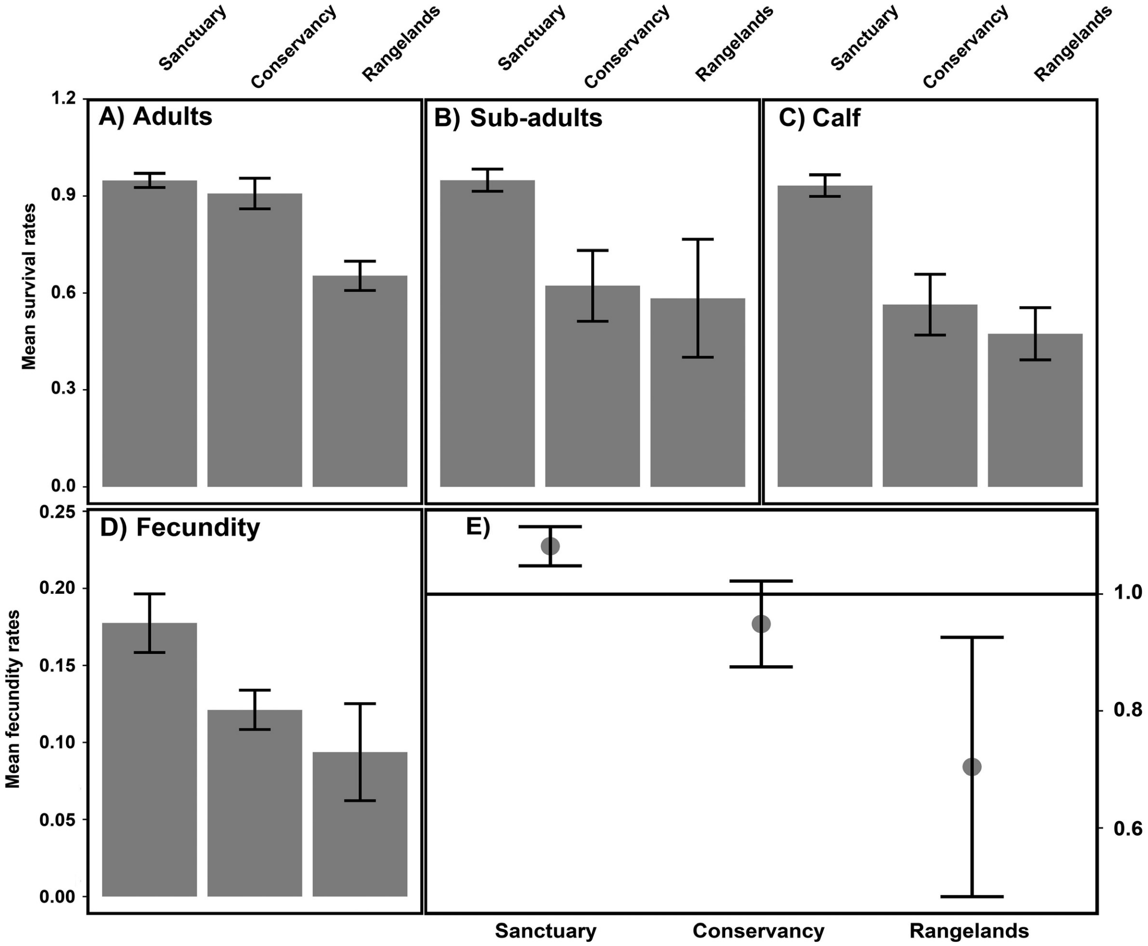

FIG. 2. Survival rates (mean ± SE) for hirola in the sanctuary, conservancy, and rangelands for (A) adult, (B) sub-adult, and (C) calf age classes from 2012–2015; (D) estimated adult fecundity rates (mean ± SE) of hirola in the sanctuary, conservancy, and rangelands from 2012–2015; and (E) estimated population growth rates (mean λ ± SE) of hirola in the sanctuary, conservancy, and rangelands.

TABLE 1. Differences in survival rates, adult fecundity, and sensitivities for age classes between pairs of settings from 2012–2015 study periods.

	Differences and range in vital rate			Sensitivity and range		
Age class	Sanctuary vs. Conservancy	Sanctuary vs. Rangelands	Conservancy vs. Rangelands	Sanctuary vs. Conservancy	Sanctuary vs. Rangelands	Conservancy vs. Rangelands
Survival						
Calf	**0.37 (0.20–0.60)**	**0.46 (0.19–0.80)**	0.09 (0.02–0.16)	0.09 (0.08–0.10)	0.09 (0.07–0.11)	0.07 (0.03–0.09)
Sub-adult	**0.33 (0.03–0.70)**	**0.37 (0.20–0.60)**	0.04 (−0.10–0.17)	0.09 (0.07–0.10)	0.09 (0.06–0.10)	0.06 (0.02–0.09)
Adult	0.04 (0.01–0.10)	**0.30 (0.10–0.63)**	**0.25 (0.11–0.53)**	0.86 (0.84–0.89)	0.86 (0.83–0.90)	0.91 (0.86–0.98)
Fecundity	**0.06 (0.05–0.10)**	**0.08 (0.02–0.12)**	0.03 (−0.03–0.06)	0.47 (0.38–0.58)	0.47 (0.36–0.57)	0.34 (0.08–0.54)

Notes: Values are means. Statistically significant differences ($P < 0.05$) between settings are shown in boldface type. The first environmental setting is the reference for the difference between pairs of environmental settings.

compared to the sanctuary (Appendix S1: Table S3). However, the mean sensitivities for sub-adult and calf survival in all three paired settings were statistically indistinguishable (Table 1).

The finite rate of population change (λ) of hirola was highest in the sanctuary (1.08 ± 0.03 [mean ± SE]), followed by the conservancy (0.95 ± 0.07) and the rangelands (0.70 ± 0.22; Fig. 2E). The finite rate of population change was higher in the sanctuary compared to the conservancy ($Z = 1.65$, $P < 0.05$; Fig. 2E), higher in the conservancy compared to the rangelands ($Z = 1.07$, $P = 0.05$; Fig. 2E), and higher

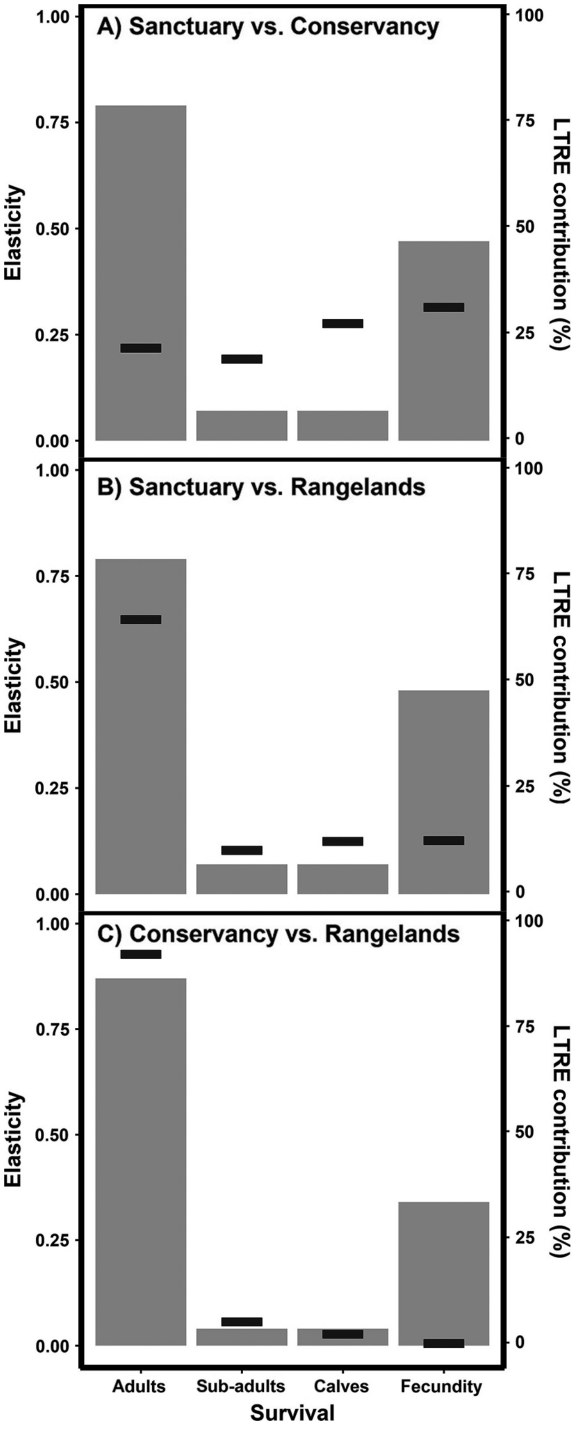

FIG. 3. Results from a life table response experiment (LTRE) indicating the elasticity (bars) and percent contributions (heavy lines) of vital rates for 2012–2015 to changes in λ for hirola for paired settings: (A) sanctuary vs. conservancy, (B) sanctuary vs. rangelands, and (C) conservancy vs. rangelands.

in the sanctuary compared to the rangelands ($Z = 1.71$, $P < 0.01$; Fig. 2E). Fecundity and calf survival were the most important contributors to λ following large carnivore exclusion (Fig. 3A), whereas adult survival was the primary contributor to increased λ stemming from differences in rangeland quality (Fig. 3B, C).

Overall, adult survival contributed most to differences in λ between the conservancy and the rangelands, explaining 90% of the overall change in λ between the two settings (Fig. 3C). Similarly, change in adult survival between the sanctuary and rangelands explained 64% of the overall change in λ between the two settings (Fig. 3B). However, between the sanctuary and conservancy settings, fecundity explained much of the overall change in λ between the two settings (Fig. 3A). For calves, most mortality occurred within the first six months of life, particularly in the conservancy and in the rangelands (Appendix S1: Fig S3).

DISCUSSION

By utilizing a large-scale, large carnivore exclosure and capitalizing on natural variation in rangeland quality, we quantified demographic drivers of the critically endangered hirola antelope in eastern Kenya. Following a rinderpest (*Morbillivirus*) outbreak in 1985 (Andanje 2002), hirola numbers have been suppressed for nearly 30 years (Fig. 1). Although rinderpest was eradicated from Kenya by 2001 (Mariner et al. 2012), hirola populations have never recovered to pre-crash levels, an observation that was the primary motivation for this study. Vital rates for hirola across environmental settings and age classes were suppressed to varying degrees by a combination of predation and rangeland quality, with a decreasing trend in population growth from the sanctuary ($\lambda > 1$) to the conservancy ($\lambda \approx 1$) to the rangelands ($\lambda < 1$). We interpret differences in population growth between the sanctuary and conservancy to reflect the effect of predation by large carnivores, which reduces fecundity and calf survival (Fig. 2A). Population growth between the conservancy and rangelands appears to have shifted from approximately stable to negative, which we attribute to higher rangeland quality in the conservancy.

Some combination of predation and poor range quality was responsible for suppressed population growth of hirola. Population crashes triggered by rinderpest in the mid-1980s have reduced hirola to precariously low numbers, such that their ability to rebound after rinderpest eradication seems compromised by poor habitat quality due to tree encroachment over the past 30 years (Ali et al. 2017). Additionally, and while hirola and large carnivores have coexisted for thousands of years in eastern Kenya, density-dependent predation may prevent positive population growth, confining hirola to a predator pit (Walters et al. 1975, Ballard et al. 2001). In conjunction with efforts to restore grassland habitats, the persistence of hirola likely will also require in situ predator-proof sanctuaries to provide a source for future reintroductions.

Our work strongly suggests that hirola are a refugee species, in which survival and fecundity are not sufficiently high to sustain populations in the remaining habitat (which itself is a fraction of their historical geographic range [Ali et al. 2017]). Overall, the combined effect of increased rangeland quality (stemming from low numbers of livestock) and exclusion of large carnivores resulted in positive population growth of hirola. The reduction in population growth via reduced rangeland quality is consistent with other studies that point to the importance of variation in adult survival in driving population dynamics of tropical ungulates (Owen-Smith and Mason 2005). In contrast, bolstered population growth following predator exclusion fits the life-history paradigm developed in temperate regions, in which calf survival and adult fecundity regulate population dynamics (Gaillard et al. 1998, Raithel et al. 2007). In sum, hirola require some combination of high-quality rangeland and reduced rates of predation, relative to current levels, for populations to persist.

As our study is on a large, critically endangered mammal, our inferences are limited by small sample sizes and at least three potential shortcomings. First, we conducted our work over a relatively short period of time (3 yr) relative to the lifespan of hirola, during which environmental stochasticity (droughts, floods) was minimal and therefore did not feature in our demographic matrices. Second, each environmental setting in our study was represented by a single replicate, in which predator exclusion and livestock production altered the abundance of large carnivores and rangeland quality. Because each setting was not replicated, there is some potential for unmeasured, cryptic effects to influence our results. Finally, some of the demographic pathways by which large carnivores reduced population growth are not known. Although the reduction in adult survival and calf survival show a clear signature of direct killing by predators, it is conceivable that reductions in pregnancy and parturition could have arisen from carnivore-induced stress (e.g., Creel et al. 2009, Sheriff et al. 2015) or behavioral shifts to lower-quality habitats (e.g., Ford et al. 2014, Ford and Goheen 2015, Ng'weno et al. 2017), although the existence and strength of such effects are idiosyncratic and system specific (Kauffman et al. 2010, Middleton et al. 2013).

In African savannas, ungulates exhibit pronounced variation in their abundance through time (Sinclair 1983, Owen-Smith and Mason 2005), and such temporal variation is typically associated with some combination of heterogeneity in rangeland quality and predation (Mduma et al. 1999, Sinclair et al. 2003, Owen-Smith and Mason 2005, Grange et al. 2015). Additionally, our findings are congruent with those indicating that tree encroachment (resulting from elephant extirpation and overgrazing) triggered rangeland degradation and loss of habitat for hirola; tree encroachment was not associated with increased rates of predation (Ali et al. 2017). Since the mid-1980s, hirola have remained at low population densities throughout their geographic range, during which time large-carnivore abundance has remained relatively constant in these areas (Ali et al. 2017). In light of this, and while predation by large carnivores certainly suppresses population growth, we believe rangeland degradation is a major, largely unappreciated threat underlying chronic low numbers of hirola.

The finite rate of population change of hirola was driven by fecundity and calf survival following large carnivore exclusion, whereas adult survival was the primary contributor to increased population growth that stemmed from enhanced rangeland quality. Therefore, and to the extent that large-carnivore control is both unethical and infeasible, the persistence of hirola may depend on the reversion of tree encroached areas to grasslands in eastern Kenya. Our work provides evidence that can be used to integrate hirola conservation and future reintroduction efforts with rangeland restoration. Restoration efforts will require strong local support, and conservation agencies may consider implementing restoration practices that are compatible with local livelihoods. From a parallel study, we found that locals were strongly supportive of manual tree removal, grass seeding, elephant conservation, and resting range from livestock as restoration solutions to promote grass growth and potential recovery of hirola (A. Ali, et al. *unpublished manuscript*). Such efforts hold promise in bolstering hirola populations in landscapes occupied by large carnivores, humans, and their livestock.

ACKNOWLEDGMENTS

Our work was made possible by the support of the Kenya Wildlife Service, communities in Ijara and Fafi sub-counties of Garissa County, Garissa County officials, Ishaqbini Community Conservancy, Northern Rangelands Trust, Association of Zoos and Aquariums, British Ecological Society, Chicago Zoological Society, Denver Zoo, Disney Worldwide Conservation Fund, Houston Zoo, Idea Wild, International Foundation for Science, IUCN/SSC Antelope Specialist Group, Mohamed Bin Zayed Species Conservation Fund, National Museums of Kenya, People's Trust for Endangered Species, Rufford Foundation, St. Louis Zoo's Center for Conservation in the Horn of Africa, University of Wyoming's Berry Biodiversity Conservation Center, University of Wyoming's Haub School, and the Zoological Society of London. We thank individuals from all of these organizations for their foresight and generosity. We thank Jeff Beck, Anna Chalfoun, and David McDonald for comments on a previous draft. Last, a special thanks to Martha Fischer for her continued enthusiasm and encouragement with this research. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

Ali, A. H., A. T. Ford, J. S. Evans, M. M. Hayes, A. M. Kibara, J. King, D. Evans, and J. R. Goheen. 2017. Resource selection and landscape change reveal mechanisms suppressing population recovery for the world's most endangered antelope. Journal of Applied Ecology. https://doi.org/10.1111/1365-2664.12856.

Andanje, S. A. 2002. Factors limiting the abundance and distribution of hirola (*Beatragus hunteri*) in Kenya. Dissertation. Newcastle University, UK.

Armstrong, D. P., and J. K. Perrott. 2000. An experiment testing whether condition and survival are limited by food supply in a reintroduced Hihi population. Conservation Biology 14:1171–1181.

Armstrong, D. P., and P. J. Seddon. 2008. Directions in reintroduction biology. Trends in Ecology and Evolution 23:20–25.

Armstrong, D. P., R. S. Davidson, W. J. Dimon, J. K. Perrott, I. Castro, J. G. Ewen, R. Griffiths, and J. Taylor. 2002. Population dynamics of reintroduced forest birds on New Zealand islands. Journal of Biogeography 29:609–621.

Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter, and J. C. deVos Jr. 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. Wildlife Society Bulletin 29:99–115.

Balmford, A., and R. M. Cowling. 2006. Fusion or failure? The future of conservation biology. Conservation Biology 20:692–695.

Barclay, J. H., N. M. Korfanta, and M. J. Kauffman. 2011. Long-term population dynamics of a managed burrowing owl colony. Journal of Wildlife Management 75:1295–1306.

Beale, C. M., S. van Rensberg, W. J. Bond, M. Coughenour, R. Fynn, A. Gaylard, R. Grant, B. Harris, T. Jones, and S. Mduma. 2013. Ten lessons for the conservation of African savannah ecosystems. Biological Conservation 167:224–232.

Bjørkvoll, E., A. M. Lee, V. Grøtan, B. E. Sæther, A. Stien, S. Engen, S. Albon, L. E. Loe, and B. B. Hansen. 2015. Demographic buffering of life histories? Implications of the choice of measurement scale. Ecology 97:40–47.

Brier, G. W. 1950. Verification of forecasts expressed in terms of probability. Monthly Weather Review 78:1–3.

Bro-Jørgensen, J., and S. M. Durant. 2003. Mating strategies of topi bulls: getting in the centre of attention. Animal Behaviour 65:585–594.

Bruna, E. M., and M. K. Oli. 2005. Demographic effects of habitat fragmentation on a tropical herb: life-table response experiments. Ecology 86:1816–1824.

Caswell, H. 2001. Matrix population models. John Wiley & Sons, New York, NY.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Cohen, J. 1968. Weighted kappa: Nominal scale agreement provision for scaled disagreement or partial credit. Psychological Bulletin 70:213–220.

Cooch, E. G., G. Gauthier, and R. F. Rockwell. 2003. Apparent differences in stochastic growth rates based on timing of census: a cautionary note. Ecological Modelling 159:133–143.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429–438.

Creel, S., J. A. Winnie, and D. Christianson. 2009. Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. Proceedings of the National Academy of Sciences USA 106:12388–12393.

Ford, A. T., and J. R. Goheen. 2015. An experimental study on risk effects in a dwarf antelope, *Madoqua guentheri*. Journal of Mammalogy 96:918–926.

Ford, A. T., J. R. Goheen, T. O. Otieno, L. Bidner, L. A. Isbell, T. M. Palmer, D. Ward, R. Woodroffe, and R. M. Pringle. 2014. Large carnivores make savanna tree communities less thorny. Science 346:346–349.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: constant adult survival and variable recruitment. Trends in Ecology and Evolution 13:58–63.

Grange, S., F. Barnier, P. Duncan, J. M. Gaillard, M. Valeix, H. Ncube, S. Périquet, and H. Fritz. 2015. Demography of plains zebras (*Equus quagga*) under heavy predation. Population Ecology 57:201–214.

Horvitz, C., D. W. Schemske, and H. Caswell. 1997. The relative "importance" of life-history stages to population growth: prospective and retrospective analyses. Pages 247–271. Springer US, Boston, MA.

IUCN SSC Antelope Specialist Group. 2008. *Beatragus hunteri*. The IUCN red list of threatened species. Version 2014.2. www.iucnredlist.org

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19:101–108.

Johnson, H. E., L. S. Mills, T. R. Stephenson, and J. D. Wehausen. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecological Applications 20:1753–1765.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. Ecology 91:2742–2755.

Kerley, G. I. H., R. Kowalczyk, and J. P. G. M. Cormsigt. 2012. Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a marginal habitat? Ecography 35:519–529.

King, J., S. Andanje, C. Musyoki, R. Amin, J. Goheen, D. Lesimirdana, and A. H. Ali. 2011. Aerial survey of hirola (*Beatragus hunteri)* and other large mammals in southeast Kenya. Unpublished report to the Kenya Wildlife Service. Kenya Wildlife Service, Kenya.

Kingdon, J. 1982. East African mammals. Volume III C. Academic Press, London, UK.

Lawrence, I., and K. Lin. 1989. A concordance correlation coefficient to evaluate reproducibility. Biometrics 45:255–268.

Lea, J. M., G. I. Kerley, G. H. Hrabar, T. J. Barry, and S. Shultz. 2016. Recognition and management of ecological refugees: A case study of the Cape mountain zebra. Biological Conservation 203:207–215.

Mariner, J. C., J. A. House, C. A. Mebus, A. E. Sollod, D. Chibeu, B. A. Jones, P. L. Roeder, B. Admassu, and G. G. van't Klooster. 2012. Rinderpest eradication: appropriate technology and social innovations. Science 337:1309–1312.

Mduma, S. A., A. Sinclair, and R. Hilborn. 1999. Food regulates the Serengeti wildebeest: A 40-year record. Journal of Animal Ecology 68:1101–1122.

Measham, T. G., and J. A. Lumbasi. 2013. Success factors for community-based natural resource management: Lessons from Kenya and Australia. Environmental Management 52:649–659.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, R. C. Cook, J. G. Cook, S. E. Albeke, H. Sawyer, and P. J. White. 2013. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. Ecology Letters 16:1023–1030.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Sinauer, Sunderland, Massachusetts, USA.

Morrison, M. L. 2013. Wildlife restoration: techniques for habitat analysis and animal monitoring. Island Press, Washington, D.C., USA.

Ng'weno, C. C., N. J. Maiyo, A. H. Ali, A. K. Kibungei, and J. R. Goheen. 2017. Lions influence the decline and habitat shift of hartebeest in a semiarid savanna. Journal of Mammalogy 98:1078–1087.

Njoroge, P., M. Muchane, W. Wamiti, D. K. Kamau, and M. Githiru. 2015. Avifauna of Ishaqbini community conservancy in Ijara District, NE Kenya. Scopus 28:15–24.

Owen-Smith, N., and D. R. Mason. 2005. Comparative changes in adult vs. juvenile survival affecting population trends of African ungulates. Journal of Animal Ecology 74:762–773.

Probert, J., B. Evans, S. Andanje, R. Kock, and R. Amin. 2015. Population and habitat assessment of the critically endangered hirola (*Beatragus hunteri)* in Tsavo East National Park, Kenya. Oryx 49:514–520.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist 137:50–66.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795–803.

Rutberg, Allen. T. 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. American Naturalist 130:692–710.

Saltz, D., and D. I. Rubenstein. 1995. Population dynamics of a reintroduced Asiatic wild ass (*Equus hemionus*) herd. Ecological Applications 5:327–335.

Sarrazin, F., and R. Barbault. 1996. Reintroduction: challenges and lessons for basic ecology. Trends in Ecology and Evolution 11:474–478.

Sarrazin, F., and S. Legendre. 2000. Demographic approach to releasing adults versus young in reintroductions. Conservation Biology 14:488–500.

Sheriff, M. J., E. K. McMahon, C. J. Krebs, and R. Boonstra. 2015. Predator-induced maternal stress and population demography in snowshoe hares: the more severe the risk, the longer the generational effect. Journal of Zoology 296:305–310.

Sinclair, A. R. E. 1983. Adaptations of African ungulates and their effects on community function. Ecosystems of the world. Pages 401–426 *in* Tropical savannas. Bourliere, editor. Elsevier, Amsterdam, The Netherlands.

Sinclair, A., and C. J. Krebs. 2002. Complex numerical responses to top–down and bottom–up processes in vertebrate populations. Philosophical Transactions of the Royal Society B 357:1221–1231.

Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator–prey system. Nature 425:288–290.

Steury, T. D., and D. L. Murray. 2004. Modeling the reintroduction of lynx to the southern portion of its range. Biological Conservation 117:127–141.

Stubben, C., and B. G. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22:1–23.

Sutherland, W. J., A. S. Pullin, P. M. Dolman, and T. M. Knight. 2004. The need for evidence-based conservation. Trends in Ecology and Evolution 19:305–308.

Symonds, M. R., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13–21.

Tanentzap, A. J., K. J. Kirby, and E. Goldberg. 2012. Slow responses of ecosystems to reductions in deer (Cervidae) populations and strategies for achieving recovery. Forest Ecology and Management 264:159–166.

Therneau, T. 2013. A package for survival analysis in S. R package version 2.37-2. http://CRAN.R-project.org/package=survival

Tulloch, A. I. T., R. F. Maloney, L. N. Joseph, J. R. Bennett, M. M. I. Di Fonzo, W. J. M. Probert, S. M. O'Connor, J. P. Densem, and H. P. Possingham. 2015. Effect of risk aversion on prioritizing conservation projects. Conservation Biology 29:513–524.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Wallach, A. D., W. J. Ripple, and S. P. Carroll. 2015. Novel trophic cascades: apex predators enable coexistence. Trends in Ecology and Evolution 30:146–153.

Walters, C. J., R. Hilborn, and R. Peterman. 1975. Computer simulation of barren-ground caribou dynamics. Ecological Modelling 1:303–315.

White, G. C., and R. A. Garrott. 1990. Analysis of radio-tracking data. Academic, San Diego, California, USA.

SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1664/full

DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.480tf.

Legend of the wolf

Predators are supposed to exert strong control over ecosystems, but nature doesn't always play by the rules.

BY EMMA MARRIS

The return of grey wolves to the western United States has sparked debate over their role in structuring ecosystems.

In the summer of 2008, Kristin Marshall was driving through Yellowstone National Park in Wyoming. Marshall, a graduate student at the time, had come to the park to study willow shrubs — specifically, how much they were being eaten by elk.

She pulled to the side of the road and was preparing to hike to one of her study plots when she ran into two sisters from the Midwest, who were touring the park. The women asked what Marshall was doing and she said, "I am a researcher. I am working in that willow patch down there."

The tourists gushed: "We watched all about the willows on this nature documentary. We hear that all the willows are doing so much better now because the wolves are back in the ecosystem." That stopped Marshall

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short. "I didn't want to say, 'No, you are wrong, they aren't actually doing that well.'"

Instead, she said: "The story is a probably a little more complicated than what you saw on the nature documentary." That was the end of the conversation; the tourists seemed uninterested in the more-complicated story of how beavers and changes in hydrology might be more important than wolves for willow recovery. "I can't say I blame them," says Marshall, now an ecologist with the US National Oceanic and Atmospheric Administration in Seattle, Washington. "What you see on TV is captivating."

On television and in scientific journals, the story of how carnivores influence ecosystems has seized imaginations. From wolves in North America to lions in Africa and dingoes in Australia, top predators are thought to exert tight control over the populations and behaviours of other animals, shaping the entire food web down to the vegetation through a 'trophic cascade'. This story is popular in part because it supports calls to conserve large carnivores as 'keystone species' for whole ecosystems. It also offers the promise of a robust rule within ecology, a field in which researchers have yearned for more predictive power.

> *"Predators can be important, but they aren't a panacea."*

But several studies in recent years have raised questions about the top-predator rule in the high-profile cases of the wolf and the dingo. That has led some scientists to suggest that the field's fascination with top predators stems not from their relative importance, but rather from society's interest in the big, the dangerous and the vulnerable. "Predators can be important," says Oswald Schmitz, an ecologist at Yale University in New Haven, Connecticut, "but they aren't a panacea."

PREDATORS ON TOP

In the early years of ecology, predators did not get so much respect. Instead, researchers thought that plants were the dominant forces in ecosystems. The theory was that photosynthesis from these primary producers determined how much energy was available in an area, and what could live there. Bottom-up control was all the rage.

Interest in top-down trophic cascades emerged in 1963, when ecologist Robert Paine of the University of Washington in Seattle started to exclude predators from study plots at his coastal research site. He pried predatory starfish off intertidal rocks and hurled them into deeper waters. Without the starfish to control their numbers, mussels eventually carpeted the plots and kept limpets and algae from taking hold in the region. A new ecosystem emerged (see *Nature* **493,** 286–289; 2013).

After this and other aquatic studies, the conventional wisdom in the field was that top-down trophic cascades happened only in rivers, lakes and the sea. An influential 1992 paper[1] by Donald Strong at the University of California, Davis, asked: "Are trophic cascades all wet?" As if in answer, ecologists began looking for similar carnivore stories on land.

They soon found them. In 2000, a review[2] tallied 41 terrestrial studies on trophic cascades, most of which showed that predation had significant effects on the number of herbivores in an area, or on plant damage, biomass or reproductive output. These studies were all on small plots involving small predators: birds, lizards, spiders and lots of ants.

Research on terrestrial trophic cascades moved to much larger scales with the work of John Terborgh and William Ripple. In 2001, Terborgh, an ecologist at Duke University in Durham, North Carolina, reported[3] on dramatic ecosystem changes that came after a dam was built in Venezuela. Flooding from the dam created islands that were too small to support big predators such as jaguars and harpy eagles. The population densities of their prey — rodents, howler monkeys, iguanas and leaf-cutter ants — boomed to 10–100 times those on the mainland. Seedlings and saplings were devastated.

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In the same year, Ripple, an ecologist at Oregon State University in Corvallis, published a key paper[4] on the most famous, and probably the best-studied, example of a terrestrial carnivore structuring an ecosystem: Yellowstone's wolves. The ecosystem offered a natural experiment because the US National Park Service had the park's exterminated wolves (*Canis lupus*) by 1926 and then reinstated them in the 1990s, after public sentiment and ecological theory had shifted. In 1995, 14 wolves from Alberta, Canada, were introduced into the park. Seventeen from British Columbia followed in 1996. By 2009, there were almost 100 wolves in 14 packs in the Yellowstone area. (That number is now down to 83 in 10 packs.)

During the years when there were no wolves, ecologists grew increasingly worried about the aspen trees (*Populus tremuloides*) in the park. It seemed that intensive browsing by Rocky Mountain elk (*Cervus elaphus*) was preventing trees from reaching adult height, or 'recruiting'. In the early twentieth century, aspen covered between 4% and 6% of the winter range of the northern Yellowstone herd of elk; by the end of the century, they accounted for only 1% (ref. 4).

When Ripple and his co-authors checked aspen growth against the roaming behaviour of wolves in three packs, they found that aspen grew tallest in streamside spots that saw high wolf traffic. That pattern hinted at an indirect behavioural cascade: rather than limiting browsing by reducing elk populations throughout the park, wolves apparently made elk more skittish and less likely to browse in the tightly confined stream valleys, where prey have limited escape routes (see 'The tangled web'). A 2007 study[5] by Ripple and Robert Beschta, also of Oregon State, seemed to strengthen the behavioural-cascade hypothesis. It found that the five tallest young aspen in stream-side stands where there were downed logs — a potential trip hazard for elk — were taller than the five tallest young aspen in stands away from streams or without downed logs.

Similar evidence of indirect wolf effects emerged from a study of willows. In 2004, Ripple and Beschta found[6] that the shrubs were returning in narrow river valleys, where the researchers thought that the chances of wolves attacking elk were greatest.

More recently, Ripple has been documenting the regrowth of cottonwood trees. "When we look around western North America, we see a big decrease in tree recruitment after wolves were removed. And when wolves returned to Yellowstone, the trees started growing again. It is just wonderful to walk through that new cottonwood forest."

TALES FROM TREES

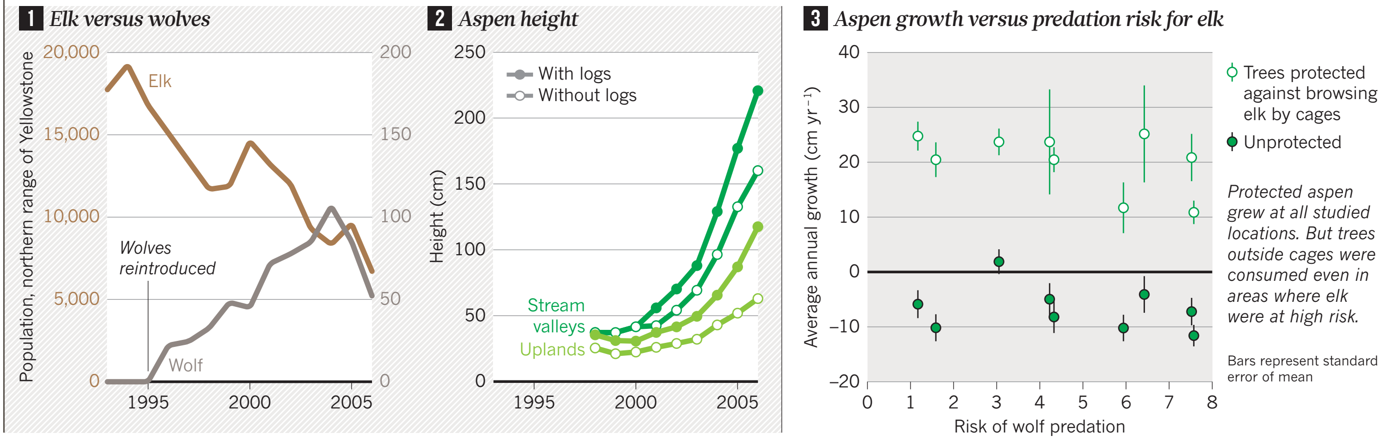
But some ecologists had their doubts. The first major study[7] critical of the wolf effect appeared in 2010, led by Matthew Kauffman of the Wyoming Cooperative Fish and Wildlife Research Unit in Laramie. When researchers drilled boreholes into more than 200 trees in Yellowstone and analysed growth patterns, they found that the recruitment of aspen had not ended all at once. Some trees had reached adult size as late as 1960, long after the wolves had gone. And some stands had stopped growing new adults as early as 1892, well before the wolves left. The aspen petered out over decades, as elk populations slowly grew, suggesting that the major influence on the trees is the size of the elk population, rather than elk behaviour in response to wolves. And although wolves influence elk numbers, many other factors play a part, says Kauffman: grizzly bears are increasingly killing elk; droughts deplete elk populations; and humans hunt elk that migrate out of the park in winter.

When Kauffman and his colleagues studied[7] aspen in areas where risk of attack by wolves was high or low, they obtained results different from Ripple's. Rather than look at the five tallest aspen in each stand, as Ripple had done, they tallied the average tree height and used locations of elk kills to map the risk of wolf attacks. By these measures, they found no differences between trees in high- and low-risk areas.

Questions have also emerged about the well-publicized relationship between wolves and willows. Marshall and two colleagues investigated the controls on willow shrubs by examining ten years' worth of data

The tangled web

Researchers disagree on whether the return of wolves to Yellowstone National Park (**1**) sparked a resurgence of aspen trees by limiting browsing by elk. One study found that aspen grow better in stream areas with fallen trees (**2**), where elk may feel most vulnerable to wolves. But another study found that aspen fare poorly even in areas where elk are most at risk from wolves (**3**).



1 *Elk versus wolves* **2** *Aspen height* **3** *Aspen growth versus predation risk for elk*

Protected aspen grew at all studied locations. But trees outside cages were consumed even in areas where elk were at high risk.

Bars represent standard error of mean

SOURCE: 1 & 2: REF. 5; 3: REF. 7

from open plots and plots surrounded by cages to keep the elk out. Her team found[8] that the willows were not thriving in all the protected sites. The only plants that grew above 2 metres — beyond the reach of browsing elk — were those in areas where simulated beaver dams had raised the water table.

If beavers have a key role in helping willows to thrive, as Marshall's study suggests, the shrubs face a tough future because the park's beaver populations have dropped. Researchers speculate that the removal of wolves in the 1920s allowed elk to eat so much willow that there was none left for the beavers, causing an irreversible decline.

"The predator was gone for at least 70 years," says Marshall. "Removing it has changed the ecosystem in fundamental ways." This work suggests that wolves did meaningfully structure the Yellowstone ecosystem a century ago, but that reintroducing them cannot restore the old arrangement.

Arthur Middleton, a Yale ecologist who works on Yellowstone elk, says that such studies have disproved the simple version of the trophic cascade story. The wolves, elk and vegetation exist in an ecosystem with hundreds of other factors, many of which seem to be important, he says.

DINGO DEBATE

Another classic example of a trophic cascade has come under attack in Australia. The standard story there is that the top predator, the dingo (*Canis lupus dingo*), controls smaller introduced predators such as cats and foxes, allowing native marsupials to thrive. But Ben Allen, an ecologist at the Department of Agriculture, Fisheries and Forestry in Toowoomba, has compared[9] areas where dingoes are poisoned with areas where they are left alone, and found no difference in marsupial abundance. He is quite cynical, he says, about "this idea that top predators are wonderful for the environment and will put everything back to the Garden of Eden".

Allen's opponents counter that he has failed to show that the poisoning regimens actually reduce dingo population densities. Chris Johnson, an ecologist the University of Tasmania in Hobart, says he is "very critical" of Allen's experimental design and methods. The dingo effect is real, says Johnson.

Ripple is not worried about these debates, which he views as quibbling over details that do not undermine the overall strength of the tropic-cascade hypothesis. In fact, when he published a major review[10] this year of the effects that predators exert over ecosystems, he left out studies critical of the wolf and dingo trophic-cascade theories; he says that there was no room for them in the space he had to work with. Ripple is particularly concerned with documenting the impacts of Earth's top carnivores because so many are endangered. "We are losing these carnivores at the same time that we are learning about their ecological effects," he says. "It is alarming, and this information needs to be brought forth."

The debate has been harsh at times, but in quieter moments the different factions all tend to talk in similar terms about the great complexity of ecosystems and the likelihood that the truth lies somewhere in the middle. James Estes, an ecologist at the University of California, Santa Cruz, and one of the fathers of the trophic-cascade idea, says that the evidence for cascades mediated by changes in animal behaviour rather than by changes in animal number is "thin", at the moment — and that many of the effects that have been documented are spotty and badly need to be rigorously mapped out. Still, he adds, "When all is said and done, and everyone is dead 100 years from now, Bill [Ripple] will be closer to right".

Although Ripple stresses the role of the top carnivores, he agrees they are not the end of the story. "I believe in the combination of top-down and bottom-up, working in unison," he says. "They are both playing out on any given piece of ground and the challenge will be to discover what determines their interactions and relative effects."

Schmitz has some thoughts on how to do that. His own smaller-scale work on invertebrates has convinced him that neither bottom-up nor top-down theories adequately capture the story of ecosystems. He is starting to look at the middle players, such as elk, beavers and grass-eating grasshoppers. These herbivores, he says, integrate influences from both the top (such as predation pressure) and the bottom (such as the nutritional quality of plants). "It is not really bottom-up or top-down but trophic cascades from the middle out," he says. "That is where we will evolve. It is knowing what the middle guy is going to do that gives you the predictive ability."

It remains to be seen whether theories such as this middle-out idea will grip researchers and the public as much as the theory of top-down cascades. Many researchers have doubts. They worry that tales of predators shaping their ecosystems are so attractive that they have unrivalled control over discourse. "Everyone likes to think of the big wolf or the big bear looking after the environment," says Allen. "We do love a good story." ■ SEE EDITORIAL P.139

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1. Strong, D. R. *Ecology* **73,** 747–754 (1992).
2. Schmitz, O. J., Hambäck, P. A. & Beckerman, A. P. *Am. Nat.* **155,** 141–153 (2000).
3. Terborgh, J. *et al. Science* **294,** 1923–1926 (2001).
4. Ripple, W. J., Larsen, E. J., Renkin, R. A. & Smith, D. W. *Biol. Conserv.* **102,** 227–234 (2001).
5. Ripple, W. J. & Beschta, R. L. *Biol. Conserv.* **138,** 514–529 (2007).
6. Ripple, W. J. & Beschta, R. L. *Forest Ecol. Management* **200,** 161–181 (2004).
7. Kauffman, M. J., Brodie, J. F. & Jules, E. S. *Ecology* **91,** 2742–2755 (2010).
8. Marshall, K. N., Hobbs, N. T. & Cooper, D. J. *Proc. R. Soc. B* **280,** 20122977 (2013).
9. Allen, B. L. in *Wolves: Biology, Behavior and Conservation* (eds Maia, A. P. & Crussi, H. F.) Ch. 3 (Nova, 2012).
10. Ripple, W. J. *et al. Science* **343,** 1241484 (2014).

The Journal of Wildlife Management 79(3):513–517; 2015; DOI: 10.1002/jwmg.852

Note

Insufficient Sampling to Identify Species Affected by Turbine Collisions

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ABSTRACT We compared the number of avian species detected and the sampling effort during fatality monitoring at 50 North American wind facilities. Facilities with short intervals between sampling events and high effort detected more species, but many facilities appeared undersampled. Species accumulation curves for 2 wind facilities studied for more than 1 year had yet to reach an asymptote. The monitoring effort that is typically invested is likely inadequate to identify all of the species killed by wind turbines. This may understate impacts for rare species of conservation concern that collide infrequently with turbines but suffer disproportionate consequences from those fatalities. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS avian, fatality, monitoring, North America, turbine collisions, wind energy.

Wind power is rapidly expanding in the United States, with more electric generating capacity added than any other source in 2012 (Wiser and Bolinger 2013). Some stakeholders have raised concerns about fatalities caused when birds collide with wind turbines, and 1–2 years of post-construction monitoring are undertaken at many wind facilities to collect information on fatalities caused by turbine collisions. Over 220 species of birds have been collectively documented in fatality monitoring at wind facilities in North America (Loss et al. 2013). Most of these species fall under some level of protection from treaties and laws, such as the Convention for the Protection of Migratory Birds between the United States and Great Britain (acting on behalf of Canada), the United States Endangered Species Act, the Canadian Species at Risk Act, and the United States Bald and Golden Eagle Protection Act.

Ultimately, understanding the impacts of wildlife collisions with wind turbines requires knowledge of what species are killed by turbines, how many individuals are killed per year, and the consequences of those fatalities to the populations of species killed. Guidelines from the United States Fish and Wildlife Service (USFWS) state specifically that post-construction monitoring should "estimate the number and species composition of fatalities" (USFWS 2012:34). The majority of studies, development of statistical estimators, and reviews of wind–wildlife interactions have focused on the estimation of the number of fatalities. However, most studies of fatalities caused by wind turbines ultimately group data across species to estimate overall mortality rates by taxonomic groups (Johnson et al. 2002, Arnett et al. 2008, Loss et al. 2013). These studies may be useful in comparing relative fatality levels at different sites or across different causes of mortality (e.g., fossil fuel vs. wind energy generation; Government Accountability Office 2006, Sovacool 2009), but their utility is limited by the lack of species-specific information.

Several nonexclusive reasons may explain why species are not found or are found infrequently during fatality monitoring. Some species may effectively avoid turbines, and these species are unlikely to experience population-level effects of turbine fatalities. Other species may be infrequent in fatality monitoring because they are rare. Rarity is a problem for many species of conservation concern. Because they are rare, fatalities are infrequent, and therefore, difficult to detect, but those deaths may have disproportionately large impacts on populations. For example, the cerulean warbler (*Setophaga cerulean*) experienced severe declines during the 20th century and is considered vulnerable by the International Union for Conservation of Nature (Buehler et al. 2013). Although only 2 cerulean warbler fatalities were documented in publicly available monitoring data (Loss et al. 2013), those observations may represent a nontrivial stressor on populations of this struggling species. Finally, species may be undersampled.

We examined the relationship between sampling effort and the number of species observed dead at wind facilities in North America to assess the ability of fatality monitoring studies to accurately describe the community of avian species affected. Many approaches exist to estimate species richness from observation data (e.g., Gotelli and Colwell 2001, Dorazio et al. 2006), and many are applicable to fatality monitoring. Although these approaches can indicate how many species were likely missed, there is no way to determine which particular species

Received: 4 August 2014; Accepted: 17 January 2015
Published: 5 March 2015

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were missed without further sampling. Hull et al. (2013) found the species accumulation curve for birds killed by collisions at 2 wind facilities in Tasmania began to asymptote after approximately 7 years of monitoring. Most studies in North America are of a shorter duration, suggesting these studies may not be capable of detecting the full range of species actually killed. Nevertheless, a wide body of literature on species accumulation curves and sampling effort suggests longer studies of a large number of turbines with short sampling intervals will detect more species than small, short studies with longer sampling intervals (Gotelli and Colwell 2001), and further analysis of how fatality studies accumulate species is warranted.

METHODS

We used data from 1995 to 2011 that were aggregated for a study of North American turbine fatalities (Loss et al. 2013) to assess the effect of effort on the number of species detected in wind turbine fatality monitoring. Our unit of interest was the wind facility, and we aggregated data from multiple studies at the same wind facility, including studies that sampled only 1 section or phase of the wind facility. For each facility, we calculated the total number of turbine-months of sampling effort, which was defined as the sum of the number of searched turbines multiplied by the study duration in months. We then modeled the total number of unique species documented at that wind facility across all studies and years as a logarithmic function of sampling effort. To correct for species richness, we repeated this using the percentage of species known to occur in or migrate through the state that were observed during fatality monitoring as the independent variable because site-specific estimates of richness were not feasible. We used state lists because they appeared to be the most inclusive community-level data available. For example, Breeding Bird Survey data poorly samples nocturnal species and arctic breeders. We ignored fatalities that could not be identified to species. Because turbine-months fail to incorporate differences in search intervals, we categorized each wind facility as having a short search interval (1–7 days) or a long search interval (>7 days) and compared species accumulation between these interval lengths. We selected the search intervals because surveys typically occurred either weekly or monthly for most facilities.

We also created species accumulation curves at 2 wind facilities to better characterize the patterns of accumulation at single wind facilities. Both Shiloh I Wind Power Project in Solano County, California (Kerlinger et al. 2007) and Wolfe Island Wind Plant in Frontenac Islands, Ontario (Stantec 2010, 2011*a*–*c*, 2012) had short sampling intervals (3–7 days), were monitored for at least 1 year, and reported the dates and species of avian fatality observations. This data structure allowed us to aggregate fatalities into weekly samples and produce species accumulation and sample-based rarefaction curves for each wind facility. We also used the Chao 1 method to calculate the expected number of species for each wind facility (Gotelli and Colwell 2011).

RESULTS

We calculated total turbine-months and number of species observed for 50 North American wind facilities (Fig. 1). Sampling effort explained 46 and 63% of the variation in the number of species and 33 and 56% of the variation in the percent of species

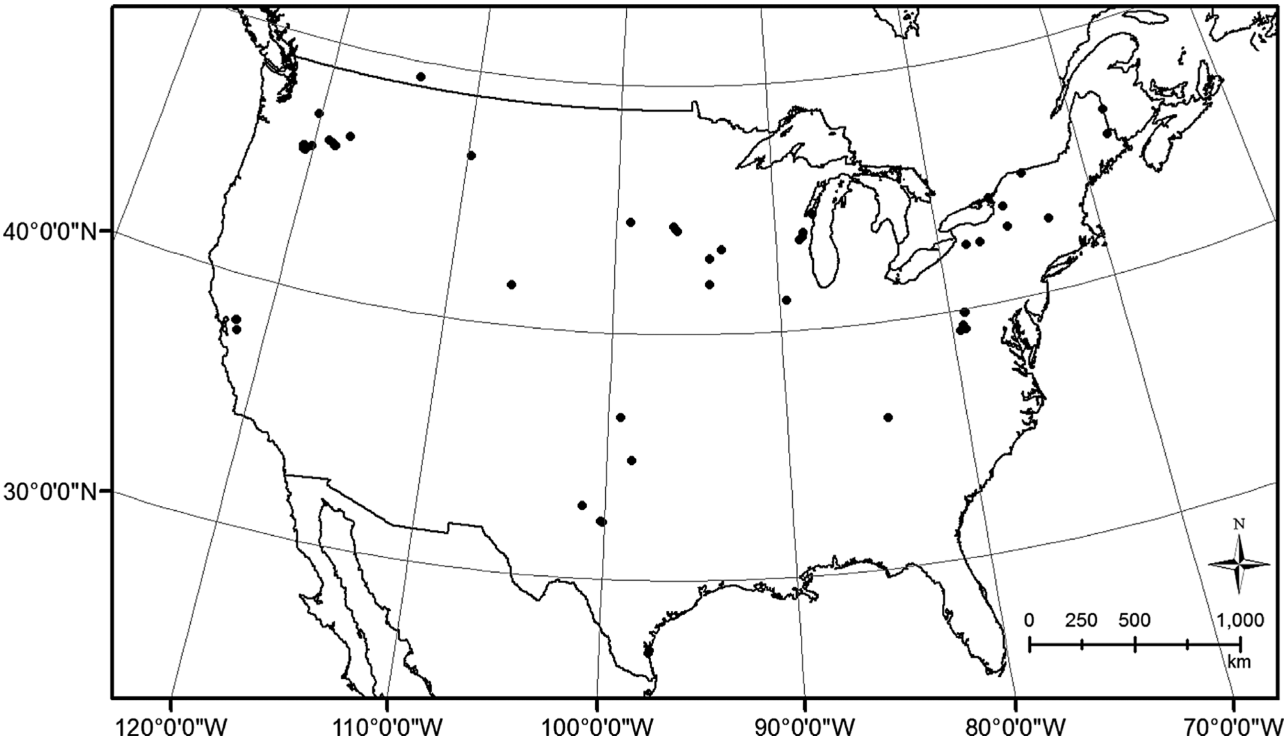

Figure 1. Locations of wind energy facilities used to estimate the relationship between mortality monitoring effort and the number of bird species observed.

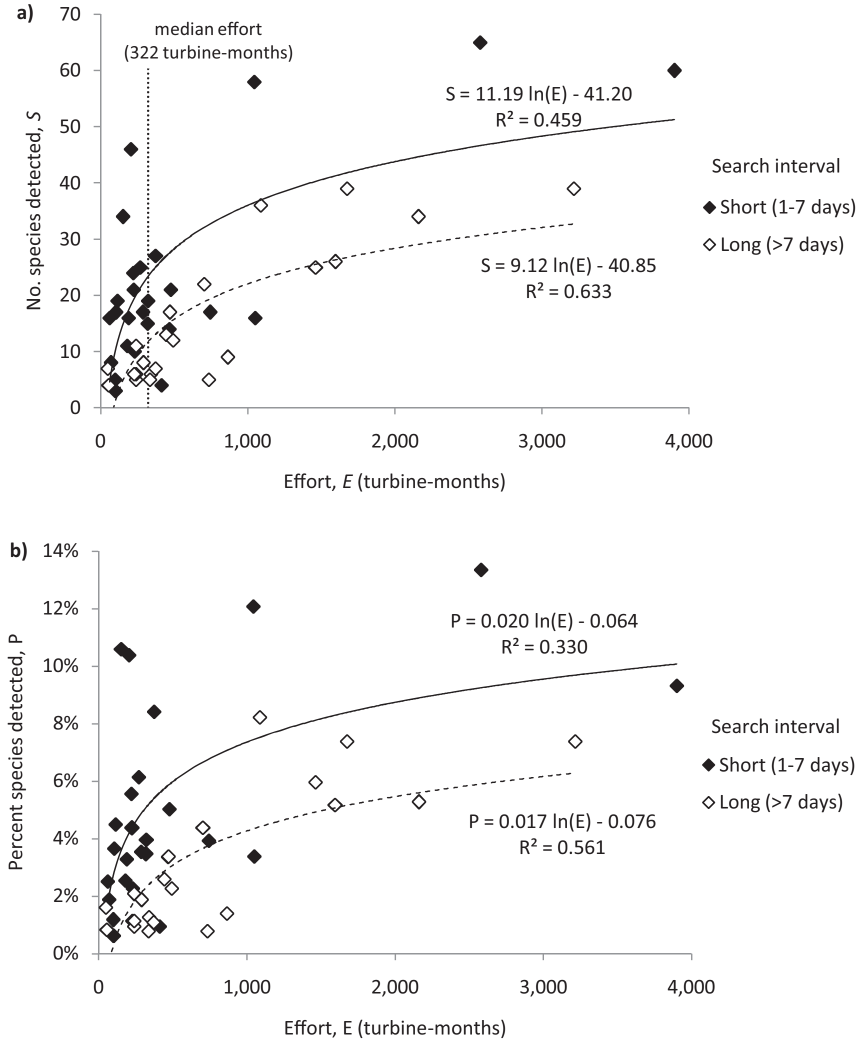

Figure 2. Number of species (a) and (b) percent of birds occurring in the state detected during fatality monitoring at 50 North American wind facilities sampled between 1995 and 2011 based on sampling interval and the sampling effort (number of turbines multiplied by the duration of study in months). The lines describe the relationships between species and effort for studies with short sampling intervals (solid) and long sampling intervals (dashed).

detected at wind facilities studied with short and long sampling intervals, respectively (Fig. 2). Facilities that had greater effort or short sampling intervals detected more species than wind facilities with low effort or long sampling intervals (Fig. 2).

Weekly surveys of 50 turbines at Shiloh I Wind Power Project accumulated species at a relatively constant rate through 52 weeks of monitoring (Fig. 3a). In contrast, weekly surveys at 86 turbines at Wolfe Island Wind Plant accumulated species quickly at the initiation of monitoring and in early spring each year (Fig. 3b). We estimated 66 (SD = 14) species were killed by Shiloh I turbines, with 35 observed, and 131 (14) species were killed by Wolfe Island turbines, with 65 observed. Furthermore, neither Shiloh I nor Wolfe Island appeared to have reached an asymptote after 1 and 2.5 years of study, respectively.

DISCUSSION

The wind facilities we included varied in species richness, abundance of species, number of turbines, proportion of turbines sampled, area, habitat types, sampling methodology, time of year studied, and other factors. Despite this latent variation in the data, there was still a clear relationship between effort and the number of species detected. This relationship remained when we attempted to correct for species richness using state and province species lists. Most of the wind facilities appeared to be undersampled with respect to species detection, with relatively low sampling effort and few species detected (Fig. 2). We note that the data we used came from publicly available studies and may not reflect the levels of sampling effort that exist in privately collected fatality studies. The patterns of accumulation at Shiloh I Wind Power Project and Wolfe Island Wind Plant suggest that sampling >2 years may be warranted to detect all affected species. Moreover, the faster rates of species accumulation during early spring at Wolfe Island highlight the importance of covering migratory periods during fatality studies.

Generally, studies with weekly (or more frequent) sampling detected more species than studies with longer sampling intervals. Long periods between sampling make it more likely

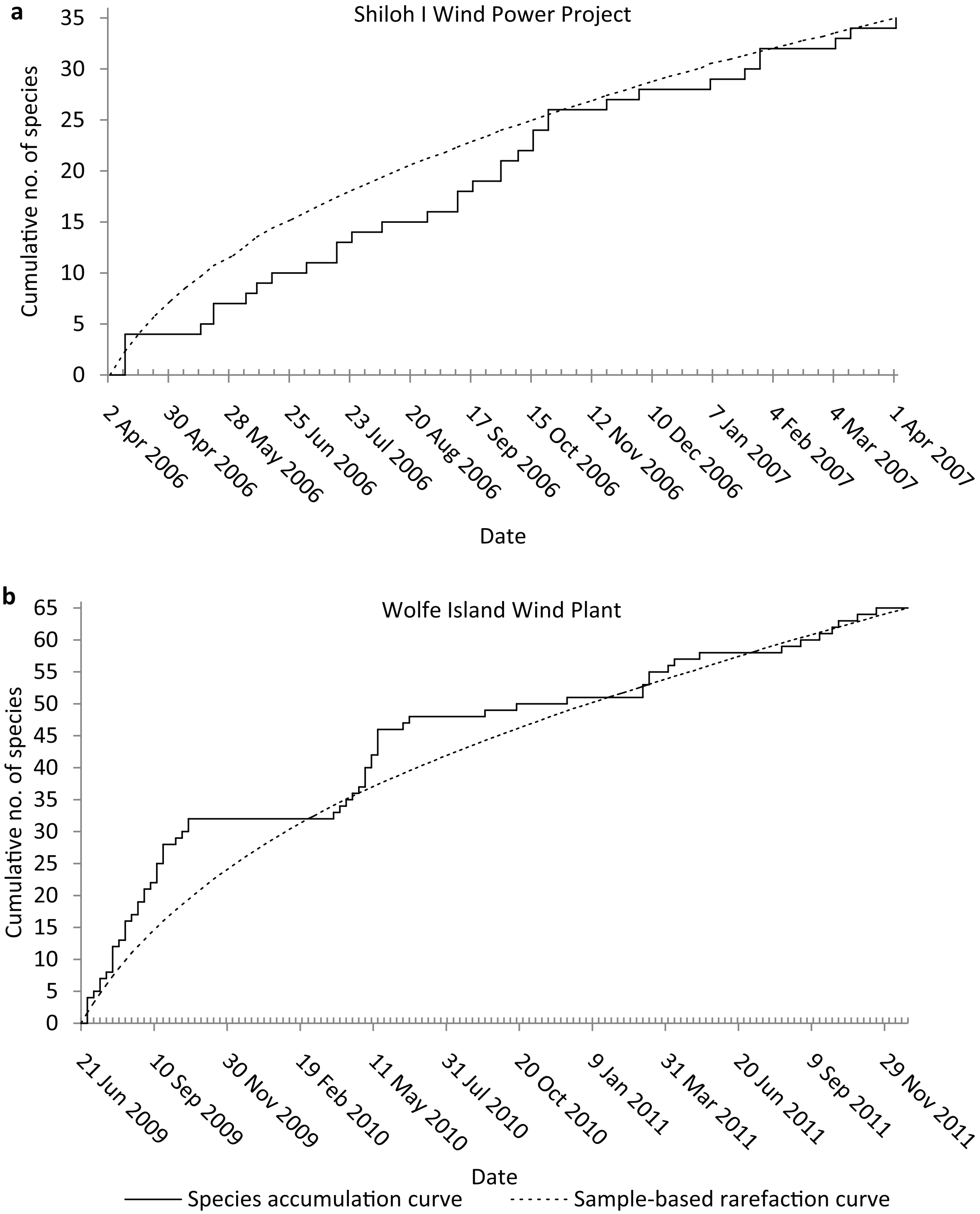

Figure 3. Species accumulation (solid) and sample-based rarefaction (dashed) curves for (a) a 52-week study at 50 turbines at Shiloh I Wind Power Project in Rio Vista, California, and (b) a 131-week study at 86 turbines at Wolfe Island Wind Plant in Frontenac Islands, Ontario.

that any new species that is killed will be removed by scavengers or otherwise degrade to anonymity before it can be observed. Although applying a correction factor for scavenger removal can reduce the resulting bias in estimates of fatalities across taxonomic groups (Smallwood 2013), it cannot indicate the identities of those individuals that went undetected. Thus, a study that is sufficient to estimate the number of fatalities caused by turbines could still be insufficient to determine which species are affected. The proportions of each species in fatality data multiplied by the total fatalities were used to calculate species-specific fatality levels for birds colliding with communication towers (Longcore et al. 2013) and wind turbines (Zimmerling et al. 2013), but this approach is likely to produce inaccurate estimates for wind fatality data where the species composition of fatalities is not fully described.

MANAGEMENT IMPLICATIONS

Though fatality estimates provide useful information about wildlife impacts of wind energy production, managers cannot assess risks to populations or species without characterization of the identities of the animals that are killed. Available fatality data were insufficient to conclude that species not observed were not in fact affected by turbine fatality. Even the studies with short sampling intervals and long study duration at Shiloh and Wolfe Island were unable to determine with confidence that all affected species of conservation concern were identified. In light of these limitations, managers may need to seek alternate methods or additional data when addressing rare species of conservation concern at wind facilities. For example, it may be possible to estimate the pool of species at risk, or rare species, that will likely occur around a facility (and thus may be killed but rarely found) using state lists, or combinations of data from monitoring programs.

ACKNOWLEDGMENTS

This work was completed as part of the U.S. Geological Survey Wind Energy Impact Assessment Methodology project. We thank L. New, S. Smallwood, M. Morrison, and an anonymous reviewer for helpful comments on earlier drafts of this manuscript.

LITERATURE CITED

Arnett, E. B., W. K. Brown, W. P. Erickson, J. K. Fiedler, B. L. Hamilton, T. H. Henry, A. Jain, G. D. Johnson, J. Kerns, R. R. Koford, C. P. Nicholson, T. J. O'Connell, M. D. Piorkowski, and R. D. Tankersley, Jr.. 2008. Patterns of bat fatalities at wind energy facilities in North America. Journal of Wildlife Management 72:61–78.

Buehler, D. A., P. B. Hamel, and T. Boves. 2013. Cerulean warbler (*Dendroica cerulea*). Account 511 *in* A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell. edu/bna/species/511/articles/introduction. Accessed 14 Nov 2014.

Dorazio, R. M., J. A. Royle, B. Söderström, and A. Glimskär. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology 87:842–854.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Gotelli, N. J., and R. K. Colwell. 2011. Estimating species richness. Pages 39–54 *in* A. E. Magurran, and B. J. Gill, editors. Biological diversity: frontiers in measurement and assessment. Oxford University Press, Oxford, United Kingdom.

Hull, C. L., E. M. Stark, S. Peruzzo, and C. C. Sims. 2013. Avian collisions at two wind farms in Tasmania, Australia: taxonomic and ecological characteristics of colliders versus non-colliders. New Zealand Journal of Zoology 41:47–62.

Johnson, G. D., W. P. Erickson, M. D. Strickland, M. F. Shepherd, D. A. Shepherd, and S. A. Sarappo. 2002. Collision mortality of local and migrant birds at a large-scale wind-power development on Buffalo Ridge, Minnesota. Wildlife Society Bulletin 30:879–887.

Kerlinger, P., R. Curry, L. Culp, B. Fischer, A. Hasch, and C. Wilkerson. 2007. Post-construction avian monitoring study for the Shiloh I Wind Power Project Solano County, California. Curry and Kerlinger, L.L.C., McLean, Virginia, USA.

Longcore, T., C. Rich, P. Mineau, B. MacDonald, D. G. Bert, L. M. Sullivan, E. Mutrie, S. A. Gauthreaux, Jr., M. L. Avery, R. L. Crawford, A. M. Manville, E. R. Travis, and D. Drake. 2013. Avian mortality at communication towers in the United States and Canada: which species, how many, and where. Biological Conservation 158:410–419.

Loss, S. R., T. Will, and P. P. Marra. 2013. Estimates of bird collision mortality at wind facilities in the contiguous United States. Biological Conservation 168:201–209.

Smallwood, K. S. 2013. Comparing bird and bat fatality-rate estimates among North American wind-energy projects. Wildlife Society Bulletin 37:19–33.

Sovacool, B. K. 2009. Contextualizing avian mortality: a preliminary appraisal of bird and bat fatalities from wind, fossil-fuel, and nuclear electricity. Energy Policy 37:2241–2248.

Stantec. 2010. Wolfe Island Ecopower Centre post-construction follow-up plan, bird and bat resources, monitoring report No. 2, 2009. Stantec Consulting Ltd, Edmonton, Alberta, Canada.

Stantec. 2011*a*. Wolfe Island Wind Plant post-construction follow-up plan, bird and bat resources, monitoring report No. 3, 2010. Stantec Consulting Ltd, Edmonton, Alberta, Canada.

Stantec. 2011*b*. Wolfe Island Wind Plant post-construction follow-up plan, bird and bat resources, monitoring report No. 4, 2010. Stantec Consulting Ltd, Edmonton, Alberta, Canada.

Stantec. 2011*c*. Wolfe Island Wind Plant post-construction follow-up plan, bird and bat resources, monitoring report No. 5, 2011. Stantec Consulting Ltd, Edmonton, Alberta, Canada.

Stantec. 2012. Wolfe Island Wind Plant post-construction follow-up plan, bird and bat resources, monitoring report No. 6, 2011. Stantec Consulting Ltd, Edmonton, Alberta, Canada.

U.S. Fish and Wildlife Service [USFWS]. 2012. Land-based wind energy guidelines. <http://www.fws.gov/windenergy/docs/weg_final.pdf>. Accessed 24 Jul 2014.

Wiser, R., and M. Bolinger. 2013. 2012 Wind technologies market report. U.S. Department of Energy. <www1.eere.energy.gov/wind/pefs/2012_wind_technologies_market_report.pdf>. Accessed 16 Dec 2013.

Zimmerling, J. R., A. C. Pomeroy, M. V. d'Entremont, and C. M. Francis. 2013. Canadian estimate of bird mortality due to collisions and direct habitat loss associated with wind turbine developments. Avian Conservation and Ecology:8. <http://www.ace-eco.org/vol8/iss2/art10/>. Accessed 4 Feb 2014.

Associate Editor: Michael Morrison.

Research Article

Cougar Exploitation Levels in Utah: Implications for Demographic Structure, Population Recovery, and Metapopulation Dynamics

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Abstract

*Currently, 11 western states and 2 Canadian provinces use sport hunting as the primary mechanism for managing cougar (*Puma concolor*) populations. Yet the impacts of sustained harvest on cougar population dynamics and demographic structure are not well understood. We evaluated the effects of hunting on cougar populations by comparing the dynamics and demographic composition of 2 populations exposed to different levels of harvest. We monitored the cougar populations on Monroe Mountain in south-central Utah, USA, and in the Oquirrh Mountains of north-central Utah from 1996 to 2004. Over this interval the Monroe population was subjected to annual removals ranging from 17.6–51.5% (mean ± SE = 35.4 ± 4.3%) of the population, resulting in a >60% decline in cougar population density. Concurrently, the Oquirrh study area was closed to hunting and the population remained stationary. Mean age in the hunted population was lower than in the protected population ($F = 9.0$; $df = 1, 60.3$; $P = 0.004$), and in a pooled sample of all study animals, females were older than males ($F = 13.8$; $df = 1, 60.3$; $P < 0.001$). Females from the hunted population were significantly younger than those from the protected population (3.7 vs. 5.9 yr), whereas male ages did not differ between sites (3.1 vs. 3.4 yr), suggesting that male spatial requirements may put a lower limit on the area necessary to protect a subpopulation. Survival tracked trends in density on both sites. Levels of human-caused mortality were significantly different between sites ($\chi^2 = 7.5$; $P = 0.006$). Fecundity rates were highly variable in the protected population but appeared to track density trends with a 1-year lag on the hunted site. Results indicate that harvest exceeding 40% of the population, sustained for ≥4 years, can have significant impacts on cougar population dynamics and demographic composition. Patterns of recruitment resembled a source–sink population structure due in part to spatially variable management strategies. Based on these observations, the temporal scale of population recovery will most likely be a function of local harvest levels, the productivity of potential source populations, and the degree of landscape connectivity among demes. Under these conditions the metapopulation perspective holds promise for broad-scale management of this species.* (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1588–1600; 2006)

Key words

connectivity, cougar, demographics, hunting, metapopulation, population dynamics, Puma concolor*, radiotelemetry, refuge, source–sink dynamics, Utah.*

Across western North America sport harvest is the primary mechanism for the population-scale management of *Puma concolor* (Pierce and Bleich 2003). Management regimes vary from public safety and depredation control only in California, to a year-round open season in Texas (Nowell and Jackson 1996). In order to balance hunting opportunities with protection of big game and livestock, most states manage cougar populations at some intermediate level. However, cougars are secretive, long-lived, and utilize large home ranges, making them difficult to manage with precision (Ross et al. 1996). At present, there are no widely accepted methods for the enumeration of cougars across diverse habitat types and climatic regimes (Anderson et al. 1992, Ross et al. 1996). Most techniques (e.g., track counts, scent stations, probability sampling) have limitations that render them marginally useful (Choate et al. 2006) or capable of detecting only large and rapid changes in population size (Van Sickle and Lindzey 1992, Beier and Cunningham 1996). Additionally, cougars occur at low population densities relative to their primary prey, making them sensitive both to bottom-up (e.g., prey declines; Logan and Sweanor 2001, Bowyer et al. 2005) and top-down (e.g., overexploitation; Murphy 1998) perturbations. Assessing cougar population trends is complicated by annual removals of varying intensity. Changes in population size and composition are generally indexed through harvest data and are therefore confounded by nonrandom sampling biases, further hindering reliable trend estimation (Wolfe et al. 2004).

Cougar management in Utah is spatially organized, with 4 broad ecoregions subdivided into 30 different hunting units. Each unit is managed independently in order to apply harvest pressure according to local priorities, which can include density reductions aimed at increasing survival in mule deer (*Odocoileus hemionus*) or bighorn sheep (*Ovis canadensis*) populations. Cougars are therefore managed at 2 different spatial scales. Locally, they are either managed conservatively as a trophy species or liberally as a limiting factor in the population dynamics of native ungulates. The statewide population, however, is managed for sustainable

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hunting opportunities and persistence across its currently occupied range (Mason et al. 1999).

Cougar hunting in Utah is conducted by means of pursuit with trained hounds. The hunting season extends from mid-December to early June, but approximately 75% of the kill occurs during December to March, when snow cover facilitates tracking and pursuit (Mason et al. 1999). Prior to 1998 the sport harvest of cougars occurred under a Limited Entry (i.e., lottery) system in which the number of permits for individual units is restricted. The long-term mean hunter success for this system is 64%. Beginning with the 1997–1998 season the Harvest Objective (i.e., quota) system was introduced for some units. This system employs an unlimited availability of permits to achieve a prescribed level of kill. Hunters are required to report their kill within 48 hours and the unit is closed once the quota is reached. Typically 74% of the quota is achieved, but instances of overharvest do occur. Between 1995 and 2003 legal harvest accounted for 90.0% of the total statewide cougar kill (Hill and Bunnell 2005). The remaining known mortality was distributed among animals killed in response to livestock depredation (6.2%) and other human-caused mortality, including roadkill and accidental trappings (3.8%). Additional unreported mortality such as incidental take during big game hunting seasons and illegal snaring occurs, but the magnitude of this impact is probably small relative to legal harvest. Individual cougars involved in livestock depredation are managed by the Wildlife Services Division of the United States Department of Agriculture, who may employ foot-hold snares as well as hounds to remove offending individuals. Nuisance cougars are defined as animals in urban settings that constitute a potential threat to human safety. These animals are generally controlled by Utah Division of Wildlife Resources (UDWR) personnel using lethal or nonlethal means, as circumstances warrant.

Little is known about both the immediate and long-term effects of sustained harvest on cougar populations (Anderson 1983, Ross et al. 1996). Numerous studies have been conducted on exploited populations (Murphy 1983, Barnhurst 1986, Logan et al. 1986, Ross and Jalkotzy 1992, Cunningham et al. 2000), including 2 removal experiments (Lindzey et al. 1992, Logan and Sweanor 2001), but few of these studies directly addressed the questions of: 1) how harvest affects the demographic structure of a population, and 2) what the long-term implications are for persistence and recovery of exploited populations within a metapopulation context. Moreover, habitat configuration and connectivity are important factors influencing cougar recruitment patterns, but with few exceptions (Beier 1993, 1995, Maehr et al. 2002) this relationship has been largely overlooked.

Recent years have seen the emergence of the idea of managing cougars as a metapopulation based on the effects of natural habitat patchiness (Sweanor et al. 2000, Laundré and Clark 2003) or anthropogenic fragmentation (Beier 1996, Ernest et al. 2003). Because metapopulations transcend administrative boundaries, understanding population response to sustained harvest is vital in order to manage for persistence across landscapes exhibiting varying degrees of natural and human-caused fragmentation.

We assessed the impacts of exploitation on cougar population dynamics by comparing demographic characteristics between an exploited and a semiprotected population. Specific objectives of this study were: 1) determine how harvest levels might influence the dynamics and demographic structure of individual populations, 2) identify the factors that may influence the rate of population recovery, and 3) assess how the distribution of harvest impacts might affect recruitment within a metapopulation context.

Study Area

Cougar habitat in Utah is geographically fragmented, being broadly associated with mesic regions between 1500 m and 3000 m. The Wasatch Mountains and associated high plateaus form the core habitat, longitudinally bisecting the state, whereas the Colorado Plateau and Great Basin ecoregions consist primarily of desert ecosystems, with suitable habitat sparsely distributed among insular mountain ranges (Fig. 1). We selected Monroe Mountain and the Oquirrh Mountains as study areas for this research (Fig. 1). Although differences existed between these sites in terms of size and plant community composition, they were located within 190 km of each other, making them climatically and ecologically similar in a broad sense, but far enough apart to be treated demographically as independent populations. The most pronounced difference between these populations was the level of exploitation to which each was subjected.

Exploited Area

Monroe Mountain comprises part of the Sevier Plateau in the Southern Mountains ecoregion of south-central Utah (38.5°N, 112°W). The site is a high volcanic plateau extending 75 km in a north–south orientation and lies within a west–east geologic transition from basin and range topography to the Colorado Plateau. Hydrologically, Monroe is part of the Great Basin, but climatically and biologically it is more closely associated with other high-elevation regions of the Colorado Plateau and southern Rocky Mountains. The study site covered approximately 1,300 km^2 and encompassed the central unit of the Fishlake National Forest, southeast of Richfield. Other landholders included the Bureau of Land Management (BLM), State of Utah, and various private interests.

The terrain is mountainous with elevations ranging from 1,600–3,400 m. Annual precipitation ranged from 15–20 cm at lower elevations to 60–120 cm on the plateaus above 2,700 m. Approximately 60% of the annual precipitation occurred as snow in January and February, with most of the remainder derived from summer thunderstorms (Ashcroft et al. 1992). Snowpack typically persisted until mid-June at elevations $>$3,000 m. Mean monthly temperatures ranged from $-4.6°$ C in January to 18.7° C in July (Ashcroft et al. 1992).

Plant communities were diverse and varied with elevation and aspect (Edwards et al. 1995). Piñon-juniper woodlands

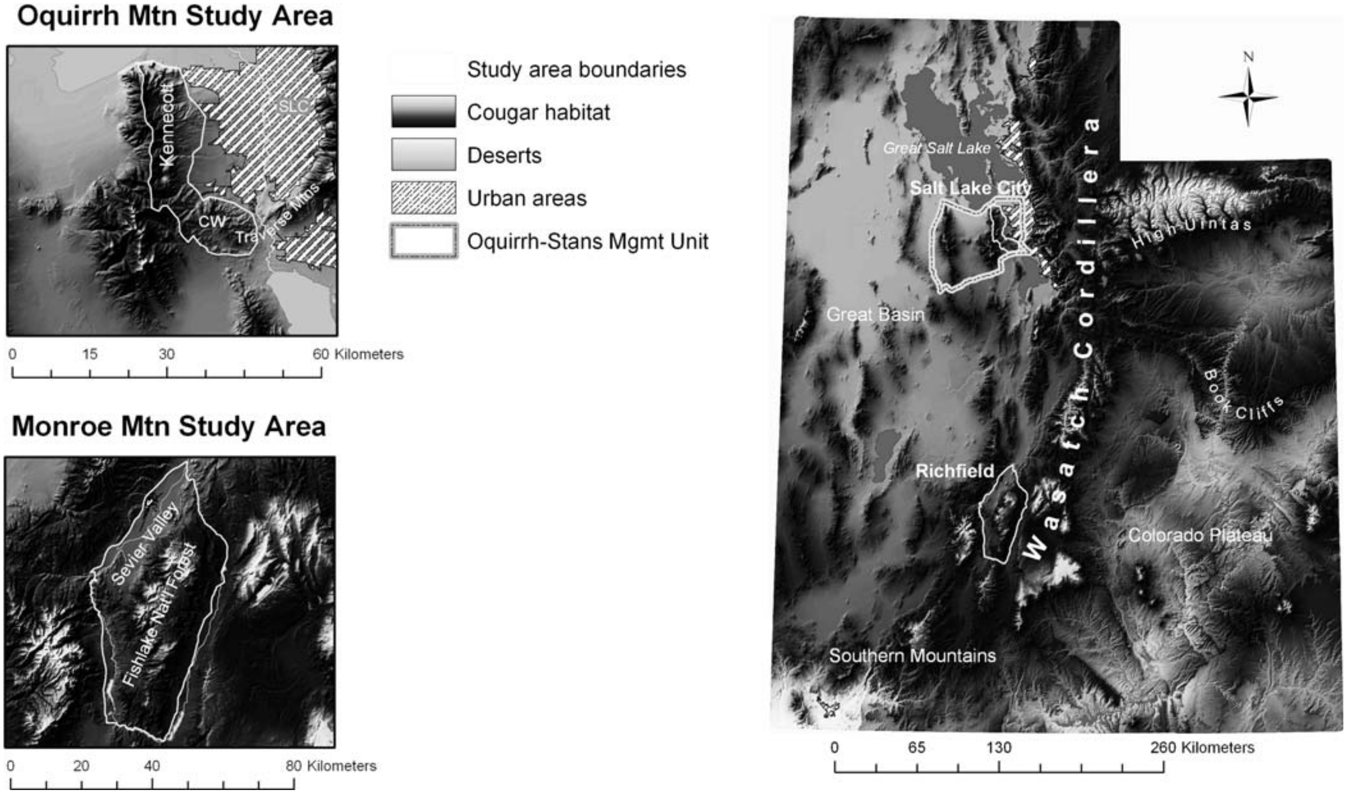

Figure 1. Study-area locations and cougar habitat across Utah, USA, 1996–2004.

(*Pinus edulis, Juniperus scopulorum, Juniperus osteosperma*) comprised the single largest vegetation type covering approximately 44% of the area. Mixed conifer and aspen (*Populus tremuloides*) stands occurred at higher elevations, with gambel oak (*Quercus gambelii*), mountain shrub (e.g., *Cercocarpus ledifolius, Rosa woodsii, Purshia tridentata*), and mixed sagebrush (*Artemisia tridentata*) –grassland meadows interspersed throughout.

Resource exploitation included livestock grazing, logging, and recreation. The UDWR classified Monroe Mountain as Cougar Management Unit 23. Mule deer and elk (*Cervus elaphus*), the primary cougar prey species on this site, were also managed for annual harvests. Human densities around the site varied from 73/100 km^2 to 382/100 km^2 (U.S. Census Bureau), with most of the population scattered among small agricultural communities in the Sevier Valley on the northwestern boundary of the study site.

Protected Area

The Oquirrh-Traverse Mountains complex (hereafter the Oquirrhs) extends 55 km in a north–south orientation on the eastern edge of the Great Basin ecoregion in north-central Utah (40.5°N, 112.2°W). The Oquirrhs are typical of other mountain ranges within this ecoregion in that they form islands of high productivity relative to the surrounding desert basins (Brown 1971) and thus represented the majority of cougar habitat in this area.

The total area of the Oquirrhs measures approximately 950 km^2, but we conducted fieldwork primarily on the northeastern slope of the range on properties owned and managed by the Utah Army National Guard (Camp Williams, Traverse Mountains, 100 km^2) and the Kennecott Utah Copper Corporation (Oquirrh Mountains, 380 km^2). The site was situated at the southern end of the Great Salt Lake, abutting the southwestern side of the greater Salt Lake metro area. Ownership on the southern and western portions of the Oquirrhs was a conglomeration of BLM, grazing associations, and small mining interests, with approximately 45% of the range residing in private ownership.

Elevations on the site vary from lake level at 1,280 m up to 3,200 m. The Traverse Mountains run perpendicular to the Oquirrhs, and range in elevation from 1,650 m to 2,100 m. Annual precipitation ranged from 30–40 cm in the Salt Lake and Tooele valleys to 100–130 cm on the highest ridges and peaks. Most precipitation fell as snow between December and April, with approximately 25% occurring in the form of summer thunderstorms. Mean monthly temperatures ranged from –2.4° C in January to 22.2° C in July (Ashcroft et al. 1992).

Gambel oak and sagebrush were the predominant vegetation on the site. Also prevalent were Utah juniper in the foothills, and canyon maple (*Acer grandidentatum*) in the drainages at low elevations, and across broader areas above 1,800 m. Mountain mahogany (*Cercocarpus spp.*) was present, but relegated to well-drained soils along ridges. North-facing slopes above 2,200 m supported localized montane communities of aspen and Douglas fir (Edwards et al. 1995).

Mining activities have dominated the Kennecott property for >100 years (Roylance 1982), and the site included 2 large open pit mines and attendant infrastructure. Camp Williams was used for military training activities, and consequently exhibited brief fire return intervals. All prominent peaks on the study site supported commercial radio and television transmitters with associated access roads. A limited amount of livestock grazing occurred seasonally. Mule deer and elk were present on this study area as well; however deer were not hunted, whereas elk were subject to intensive management through annual harvests and active translocation projects. The study site was part of the Oquirrh-Stansbury Cougar Management Unit 18, but both of these properties were closed to the public and cougar hunting was prohibited. Human density adjoining the study area varied from 232/100 km^2 in rural Tooele County to 47,259/100 km^2 in urban Salt Lake County (United States Census Bureau).

Methods

We monitored cougar populations within the 2 study areas simultaneously from early 1997 to December 2004. We estimated demographic parameters for each population based on radiotelemetry data collected between 1996 and 2004 on Monroe and from 1997 and 2004 on the Oquirrhs. We calculated estimates of life-history parameters for cougars on the Oquirrh site during 1997 and 1998 from raw data presented in Leidolf and Wolfe (Utah State University, unpublished data). We performed statistical comparisons with the use of SAS (V.8) software. We report all descriptive statistics as mean ± SE unless otherwise noted.

Radiotelemetry and Harvest

We conducted intensive capture efforts during winter (Nov–Apr) each year of the study. We captured cougars by pursuing them into trees, culverts, cliffs, or mine shafts with trained hounds (Hemker et al. 1984). We immobilized each animal with a 5:1 combination of ketamine HCl and xylazine HCl (Kreeger 1996) at a dose of 10 mg ketamine plus 2 mg xylazine/kg of body weight. We administered immobilizing drugs with a Palmer CO_2 pistol (Powder Springs, Georgia), jab stick, or hand-held syringe. We collected tooth (vestigial premolar, P2) samples for age determination by counts of cementum annulations. We sexed, aged, weighed, measured, tattooed with a unique identifier, and equipped with a radiocollar (Advanced Telemetry Solutions, Isanti, Minnesota) and a microchip (AVID Co., Norco, California) every adult animal captured. We checked adult females for evidence of lactation during handling. We tattooed, microchipped, and released all kittens too small to wear a radiocollar. We conducted all procedures in accordance with Utah State University Institutional Animal Care and Use Committee standards (Approval No. 937-R).

We relocated all radio-collared cougars with the use of aerial and ground-based telemetry techniques (Mech 1983). We conducted telemetry flights bimonthly on both sites as weather conditions permitted. We also relocated cougars opportunistically with ground-based telemetry by plotting radiotriangulated locations on United States Geological Survey 7.5′ topographic quads with the use of Universal Transverse Mercator coordinates (zone 12, North American Datum 1927). We stored all locations in a Geographic Information Systems (GIS) database (ArcView, ESRI Products, Redlands, California).

Over the course of the study, radiocollared cougars on Monroe Mountain were not protected from harvest beyond normal legal stipulations outlined in the UDWR hunting proclamations. Annual hunter-kill was regulated by apportionment of a limited number of hunter permits, issued by the UDWR on the decision of the State Wildlife Board. The Camp Williams and Kennecott properties were closed to hunting throughout the study; however, radiocollared cougars leaving those properties were considered legal take on adjacent private and public lands within Unit 18 during the 1997–2001 hunting seasons. Radiocollared cougars on that unit were protected after 2002.

Demographic Parameters

Density.—We measured cougar density as the total number of adult and subadult cougars/100 km^2 present during winter. Our a priori goal was to capture and collar as many individuals as possible. In this sense, we attempted to conduct a census of the population during winter, but during no year were we able to capture all independent cougars. To derive a conservative estimate of the number of unmarked animals on the site, we used 2 methods. First, because males and females can generally be differentiated by track size (Fjelline and Mansfield 1989), we considered multiple track sets of same-sexed animals encountered in the same watershed one individual. Given the large ranges of cougars, we felt that the primary watersheds on the site ($n = 4$; mean ± SD = 361 ± 95 km^2, range = 237–462 km^2) provided a practical threshold for differentiating individuals, as these basins approximated the size of a male home range. This does not negate the possibility that some individuals were double-counted; however, the effect of this error on the population estimate was small due to the number of animals that fell into this category annually. Second, we backcalculated birthdates of radiocollared cougars from age estimations based on tooth wear and counts of cementum annulations and used this information to assess our estimates of uncollared individuals from track evidence and hunter harvest. We excluded males backdated in this manner from the population estimate when they were <3 years old because of the likelihood that they were recent immigrants. Because females tend to be philopatric (Sweanor et al. 2000), we included them in the population estimate as resident subadults at the backcalculated age of 1–2 years. Although there are exceptions to these arbitrary dispersal rules, they provide a reasonable cutoff point for population estimates based on known cougar behavior (Beier 1995, Sweanor et al. 2000). We summed the total number of animals detected (from all means: capture, deaths, tracks) in June at the end of the capture and hunting seasons. This number most accurately represented the population during the period June to December of the preceding year (Choate et al. 2006).

Road densities were high across both study areas. In addition to using 4-wheel-drive vehicles, we conducted winter tracking efforts on horseback and snowmachine in order to reduce bias associated with different levels of access. Using multiple methods also helped to reduce bias in terms of the social classes most vulnerable to detection due to frequent road crossings or small home ranges (Barnhurst 1986). Snow conditions influenced our ability to detect tracks, and therefore dry winters may have some bias associated with population counts; however, this bias was likely consistent between sites, as both study areas are subject to similar weather patterns.

We based study-area boundaries on major roads surrounding the site; therefore we used ecologically relevant vegetative and topographic features to delineate and quantify habitat within the study-site perimeter. We used the criteria of Laing and Lindzey (1991), which excluded valley bottoms and landcover types dominated by urban and agricultural uses. Maps represent geographical area on the planar surface and do not account for slope differences in mountainous terrain where actual surface area is greater. This discrepancy in area calculation leads to an increasing overestimation of population density as the ruggedness of the terrain increases. In order to increase the accuracy of the density estimates we used GIS software (ArcView surface to area ratio extension, Jenness Enterprises, Flagstaff, Arizona) to calculate the surface areas of habitat within study-site perimeters.

Age structure.—We determined age at the time of capture by visual inspection of tooth wear and gumline recession (Ashman et al. 1983, Laundré et al. 2000). In a few cases we used counts of cementum annulations (Matson's Lab, Milltown, Montana). To test for age differences among treatment groups (site and sex combinations), we used a 2-way factorial analysis of variance in a completely randomized design with unequal variances. We adjusted significance levels for pairwise mean comparisons to control experimentwise Type I error with the Tukey-Kramer method.

Cause-specific mortality.—We determined causes of mortality through visual inspection and necropsy of carcasses. When we could not determine cause of death in the field, we submitted the carcass to the Utah State University Veterinary Diagnostics Lab for detailed analysis. We calculated mortality by tallying cause of death among radiocollared animals and unmarked animals found opportunistically during tracking sequences. We pooled all human-related causes by site and tested for proportional differences with the use of chi-square (χ^2) tests.

Survival.—We calculated survival annually for all radiocollared adult and subadult animals from each population. To account for staggered entry and censoring due to the additions and losses of radiocollared animals to the sample, we used a Kaplan-Meier product limit estimator (Kaplan and Meier 1958). We estimated annual survival by defining the start of sample intervals as 1 December of each year. By beginning the sampling interval prior to the beginning of the hunting season (15 Dec), we ensured that human-related mortality is accounted for only once during a single nonoverlapping period in each year. We calculated measures of precision for the computed survival rates from procedures described by Cox and Oakes (1984; cited in Pollock et al. 1989). We compared survival curves between sites with the use of the log-rank test (Pollock et al. 1989).

Fecundity.—We measured fecundity as the proportion of sexually mature females detected with litters-of-the-year (kittens <1 yr) on site during winter. We counted litters during snow tracking and capture efforts. We checked all females taken in the hunt for signs of lactation, which helped account for otherwise undocumented reproduction. Kittens >3 months old are only found with their mothers 20–43% of the time (Barnhurst 1986), but we tracked many female cougars on multiple occasions, thereby increasing the probability of detecting kittens, if present. We did not attempt any analyses on the actual number of kittens born per litter, because of the difficulty in determining the actual number of kittens when ≥ 2 track sets were found. There are 2 potential sources of error in this estimate. First, it is possible that some maternal females experienced whole-litter loss prior to the winter tracking season, and therefore a proportion of nonlactating females or those without kittens may actually have been reproductively active that season. Second, kittens <2 months old are not mobile, and so this cohort would also have been missed through track-based counts. Consequently, both the number of kittens per litter and the proportion of reproductively active females are biased low. The minimum percentage of females caring for young provided an annual estimate of productivity for each population (Barnhurst 1986). We used paired t-tests to detect differences in mean fecundity rates pooled over the entire study interval.

Dispersal.—We tattooed the ears of all kittens handled on the Oquirrh mountain site in the event that they were recaptured as adults. For the Oquirrh Mountain animals, we were able to calculate several crude estimates of dispersal distance and direction opportunistically based on harvest returns of animals marked as kittens. In addition, we monitored subadults captured as transients on Monroe via radiotelemetry for extrasite movements, thus providing some information on coarse-scale movement patterns. We calculated distances as a straight line between capture site and death site or the center of the home range.

Landscape Configuration

We used measures of landscape configuration to assess the overall degree of connectivity of the study sites to surrounding habitats within their respective ecoregions. Connectivity is defined here as "the degree to which the landscape facilitates or impedes [animal] movement among resource patches" (Taylor et al. 1993). We used descriptions provided by Laing and Lindzey (1991) to delineate potential connective habitats between the study areas and neighboring patches. In assessing connectivity for cougars we used only easily quantifiable landscape variables and did not consider potential psychological barriers, although there is some evidence that outdoor lighting may function as such (Beier 1995). We derived the following metrics: size (km^2), shape (perimeter–area ratios), greatest interpatch distance, percent of perimeter connected to neighboring habitat patches, width of connective habitat, and percent of perimeter impermeable to cougar movement. Impermeability refers to landscape features that prohibited, filtered, or redirected animal movement (Ernest et al. 2003, Forman et al. 2003), such as the Great Salt Lake, interstate highways, and urban areas. Some of these features may not form absolute barriers, but they can act as an impediment to animal movement. Perimeter-area ratios are a unitless metric that provided a relative measure of how circular (or how much edge) one study area had relative to the other. We derived these measures in ArcView using the spatial analyst extension and a 30-m digital elevation model of the state of Utah.

Results

Radiotelemetry and Harvest

Capture.—We captured and marked 110 individual cougars on the 2 study sites, representing 145 capture events (Table 1). In addition, we found one dead cougar opportunistically during tracking on the Oquirrh site. We conducted captures on Monroe Mountain from January 1996 to March 2004 and on the Oquirrh site from February 1997 to March 2004. Rugged terrain and frequent animal use of culverts, mine shafts, and lava tubes hindered the collection of ground-based telemetry observations. Consequently most telemetry data were derived from aerial surveys. Monitoring times for Monroe cougars averaged 758 days (range = 2–3140 days) for females, and 194 days (range = 3–662 days) for males. On the Oquirrh site we monitored females for a mean of 810 days (range = 14–2674 days) and males for 399 days (range = 76–1173 days). Differences between sexes reflected the smaller sample of males, their greater tendency to emigrate, and shorter residence times.

Monroe Mountain cougar harvest.—For the period 1990–1995, prior to initiation of this study, a mean of 15.6 (range = 14–19) hunting permits were issued annually, corresponding to a mean kill of 8.7 cougars per year (range = 6–12), and a mean hunter success of 54.0% (range = 40.7–64.9%). In 1996, the number of permits issued increased 33.7% over the 1990–1995 mean. In 1997, the number of permits increased 40% over 1996 levels and 151% over the 1990–1995 mean. Between 1999 and 2000, the number of permits issued decreased to 1990–1995 mean levels and was again decreased for the 2001 season. During the years of heavy harvest (1996–2001), mean per-capita hunting pressure (i.e., the proportion of the population that was legally harvestable) was 87% (range = 68.5–100%). During the years of reduced harvest (2002–2004) mean per-capita hunting pressure was 25.7% (range = 22.7–29.4%; Table 2). During the study 164 permits were issued, 79 cougars were killed (51 M, 28 F), and total hunter success was 48.1%, whereas mean annual hunter success was 46.5% (1996–2001) and 73.3% (2002–2004; Hill and Bunnell 2005). The general decline in the number of hunting tags issued over time was partially in response to preliminary study results.

Table 1. Number of cougars captured according to age and sex classes, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

Age and sex	Monroe	Oquirrhs
Adults		
F	16	20
M	12	7
Subadults		
F	14	2
M	15	3
Kittens		
F	2	9
M	1	9
Totals	60	50

Oquirrh Mountain cougar harvest.—From 1996 to 2001 radiocollared animals on Unit 18 were considered legally harvestable. Cougars on the Camp Williams and Kennecott properties were protected, but these areas were surrounded by private and public lands open to hunting, making any study animal found offsite legal quarry. Beginning in 2002, all radiocollared animals on the unit were protected by law regardless of property ownership to facilitate a concurrent study. During our study 5 radiocollared cougars were killed just outside the study site boundaries (4 M, 1 F). Of these, the 4 males were legally harvested, whereas the female was taken after the 2002 moratorium on radiocollared study animals.

Demographic Parameters

Density.—Estimated high densities (cougars/100 km^2) were similar between sites (Oquirrhs, 2.9; Monroe, 3.2); however, trends in this parameter differed markedly (Fig. 2). Density on Monroe showed a consistent decline during the years of heavy harvest (1997–2001), which leveled off when permits were reduced by 80%, averaging 2.0 ± 0.3 (2002–2004). Oquirrh density showed minimal variation over the study interval averaging 2.8 ± 0.1 (Fig. 2).

Age structure.—Age estimates determined upon initial capture were pooled by sex and site for the entire study period (Table 1). Sexually mature cougars from the Monroe population ($n = 57$) averaged 3.4 ± 0.2 years (F = 3.7 ± 0.4; M = 3.1 ± 0.3). Adult cougars from the Oquirrh population ($n = 33$) averaged 4.6 ± 0.3 years (F = 5.9 ± 0.5; M = 3.4 ± 0.4; Fig. 3). Mean cougar ages differed both by study site (Monroe cougars < Oquirrh cougars; $F = 9.0$, df = 1,60.3, $P = 0.004$) and by sex (F > M; $F = 13.8$; df = 1, 60.3; $P < 0.001$). Further, we found evidence of an interaction between sex and site ($F = 5.31$; df = 1, 60.3; $P = 0.025$). Within the Monroe population male and female mean ages did not differ ($t = 1.21$; df = 54.6; $P = 0.625$), whereas Oquirrh females were significantly older than their male counterparts ($t = 3.70$; df = 30.2; $P = 0.003$). Between sites, Oquirrh females were older than Monroe females ($t =$

Table 2. Cougar harvest characteristics from Monroe Mountain (Unit 23), Utah, USA, 1996–2004.

Hunting season	Estimated population[a]	Permits issued	Cougars killed[b]	% hunter success	% F	% population Hunted[c]	% population Killed
1995–96	35	24	14	58.3	42.9	68.5	40.0
1996–97	42	40	17	42.5	47.1	95.2	40.5
1997–98	33	30	15	50.0	26.7	90.9	45.5
1998–99	26	25	7	28.0	28.6	96.1	26.9
1999–00	21	15	9	60.0	44.4	71.4	42.9
2000–01	15	15	6	40.0	33.3	100.0	40.0
2001–02	17	5	3	60.0	33.3	29.4	17.6
2002–03	20	5	4	80.0	00.0	25.0	20.0
2003–04	22	5	4	80.0	25.0	22.7	18.2
Mean	25.6	18.2	8.8	55.4	31.2	66.6	32.4
SE	3.0	4.1	1.8	17.5	5.0	10.8	3.8

[a] Estimated number of adults and independent subadults from winter capture and tracking efforts.

[b] Legal sport harvest only (Hill and Bunnell 2005).

[c] Per capita hunting pressure, i.e., the ratio of the number of permits issued to the estimated population size (column 3/column 2).

–3.53; df = 38.8; $P = 0.004$), but male ages did not differ between sites ($t = –0.54$; df = 22.5; $P = 0.949$).

Cause-specific mortality.—Mortality on the Monroe site was predominantly human caused (74%), with legal harvest accounting for 81% of human-caused ($n = 26$) and 60% of total mortality ($n = 35$) (Fig. 4). Causes of mortality on the Oquirrh site varied (Fig. 4). All human causes (including roadkill) comprised 53% of the total mortality ($n = 17$) and of this, legal harvest accounted for 44% of all human-caused mortality ($n = 9$) but only 24% of the total. Levels of human-caused mortality differed between sites ($\chi^2 = 7.5$; $P = 0.006$). Various forms of poaching (neck snares, illegal hunter-kill) occurred sporadically on both sites (Monroe, $n = 2$; Oquirrhs, $n = 1$), though alone, this did not represent a significant source of mortality for radio-collared animals.

The second leading cause of death on both sites was intraspecific predation, comprising 17% ($n = 6$) and 18% ($n = 3$) of total mortality on the Monroe and Oquirrh sites, respectively. During the years of high per-capita harvest pressure on Monroe, all victims of intraspecific aggression were resident adult females ($n = 4$), whereas during the period of light harvest all victims were subadult males ($n = 2$). On the Oquirrhs, 1 victim was a predispersal subadult male and 2 were adult females. Notably, one of these instances was an adult female cannibalizing another female with dependent young. Two years later, the survivor in this encounter was killed by an unidentified cougar. Cause of death could not be determined in three cases (2 F, 1 M), but did not appear to be human-related.

In addition to direct mortality, ≥11 kittens from 5 different litters on Monroe were orphaned when their mothers were killed during the winter hunt ($n = 10$) or during summer depredation control actions ($n = 1$). We confirmed the death of one orphaned litter (2 kittens, approx. 6 months old) due to dehydration and malnutrition. On the Oquirrhs, one male kitten was orphaned at the estimated age of 9 months when its mother was killed by an automobile. This animal survived 6 weeks before being taken in a depredation control action on a small ranch just outside of Salt Lake City. A litter of 3 4-month-old kittens died following the disease-related death of their mother. One other male kitten was marked at the age of 7 months following the poaching-related death of its mother in January 2002. It survived at least 2 months before radio contact was lost. Aside from this individual, no other orphans were detected following the deaths of their mothers or as adults on either study area in subsequent years.

Survival.—Adult survival varied between sites and among years (Fig. 5). On Monroe, survival tracked harvest

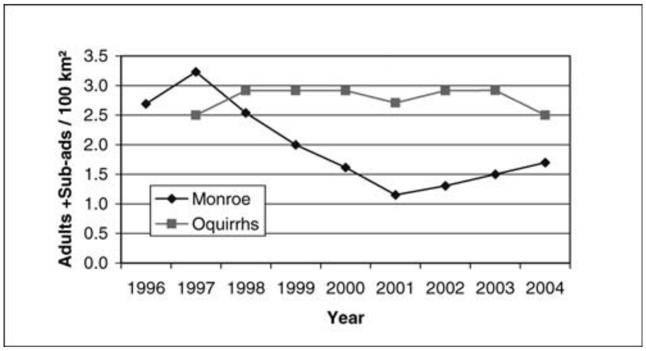

Figure 2. Annual nonjuvenile cougar density as determined from capture, tracking, and harvest, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

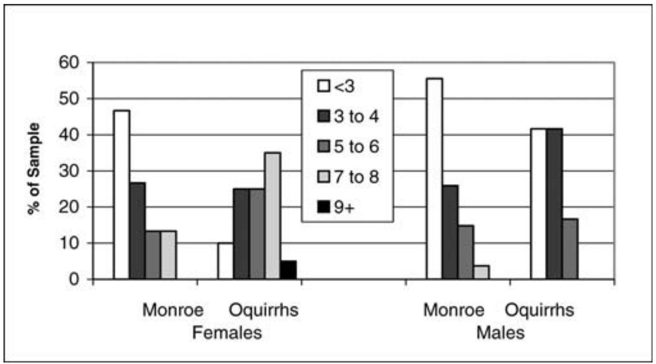

Figure 3. Age distribution of radiocollared cougars by sex, Monroe ($n = 57$) and Oquirrh ($n = 30$) Mountain study sites, Utah, USA, 1996–2004.

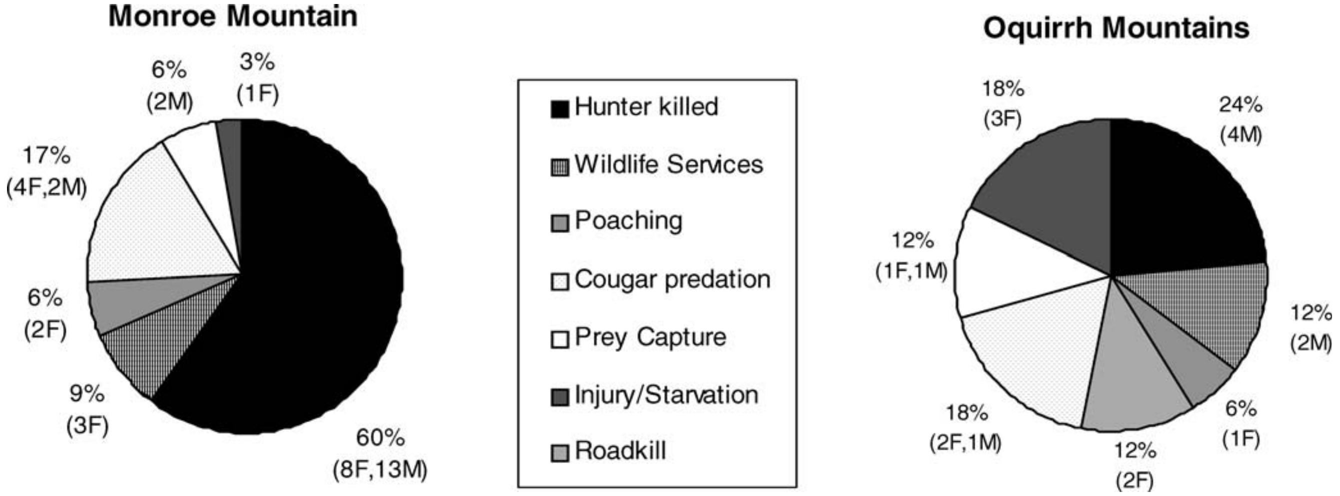

Figure 4. Cause-specific mortality among radiocollared cougars from the Monroe ($n = 35$) and Oquirrh Mountain ($n = 17$), study sites, Utah, USA, 1996–2004.

intensity, ranging from a high of 1.0 in 1996, just prior to the initiation of the treatment period, and declining to a low of 0.36 ± 0.33 (95% CI) in 2001, the end of high per-capita hunting pressure. Survival on the Oquirrhs showed moderate variation, ranging from 0.63 ± 0.28 to 0.91 ± 0.17. Trends in survival mirrored those of density on both sites, averaging 0.64 ± 0.07 (± SE) on Monroe and 0.76 ± 0.04 on the Oquirrhs. Analysis of trends over the entire interval suggested a difference in survival between sites ($\chi^2 = 3.41$; df $= 1$, $P = 0.068$).

Fecundity.—Reproduction varied between sites and years (Fig. 6). The number of litters detected annually ranged from 0–9 on Monroe and from 1–5 on the Oquirrhs, averaging 0.24 ± 0.04 (Monroe) and 0.34 ± 0.05 (Oquirrhs) litters per sexually mature female. Although rates did not differ statistically between sites ($t = -1.23$; df $= 7$; $P = 0.258$), fecundity on Monroe tracked the population decline and included a zero detection rate in 2002, the year following the lowest population estimate. At that time there were ≥ 5 sexually mature females present. The lowest fecundity estimate for the Oquirrh population was recorded the year after a 50% reduction in elk numbers. These animals were removed for reintroductions in other states. The removal was conducted over 2 years and was comprised primarily of cows and calves, the sex and age classes most vulnerable to cougar predation (Murphy 1998). The number of resident females on the Oquirrh site was smaller ($\bar{x} = 9.6$/yr) than on Monroe ($\bar{x} = 15.7$/yr), which may have influenced the variability in fecundity. Litter sizes averaged 1.7 and 1.9 kittens per litter on Monroe and the Oquirrhs, respectively. Based exclusively on the Oquirrh site using only kittens handled and marked (4–10 months post partum), the sex ratio was even (9 F, 9 M).

Dispersal.—Several animals were captured and marked either just prior to, or during dispersal. Four cougars (1 F, 3 M) moved from Monroe to neighboring mountain ranges 19–55 km distant. Two of these (1 F, 1 M) established residency in habitat adjacent to the study area; one was recaptured and his collar removed (fate unknown); and one was harvested 42 km northeast on the Fishlake Plateau (Fig. 7).

Seven dispersals were documented on the Oquirrh site (2 F, 5 M), ranging in distance from 13 to 85 km (Fig. 7). Of these, 3 (1 F, 2 M) settled elsewhere in the Oquirrh Mountains; 1 female moved to the Simpson-Sheeprock Mountains; 2 males moved to the Stansbury Mountains where they were hunter-killed as transients; and 1 male dispersed to the Mt. Timpanogos region of the southern

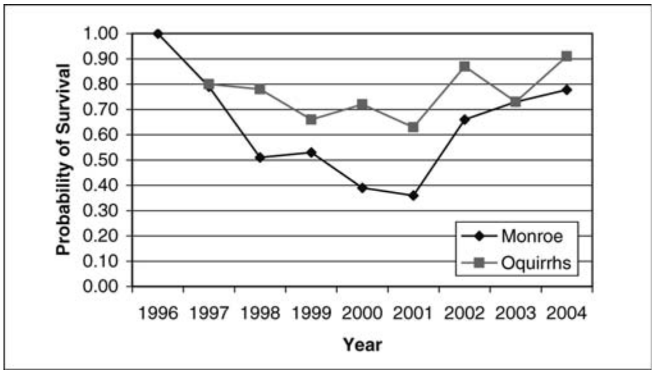

Figure 5. Estimated annual survival rates for radiocollared cougars, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

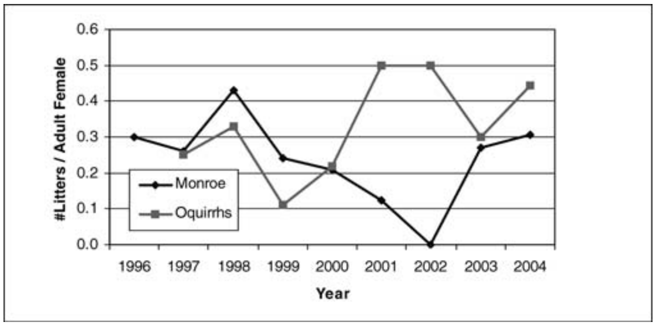

Figure 6. Annual fecundity rates for adult cougars on the Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

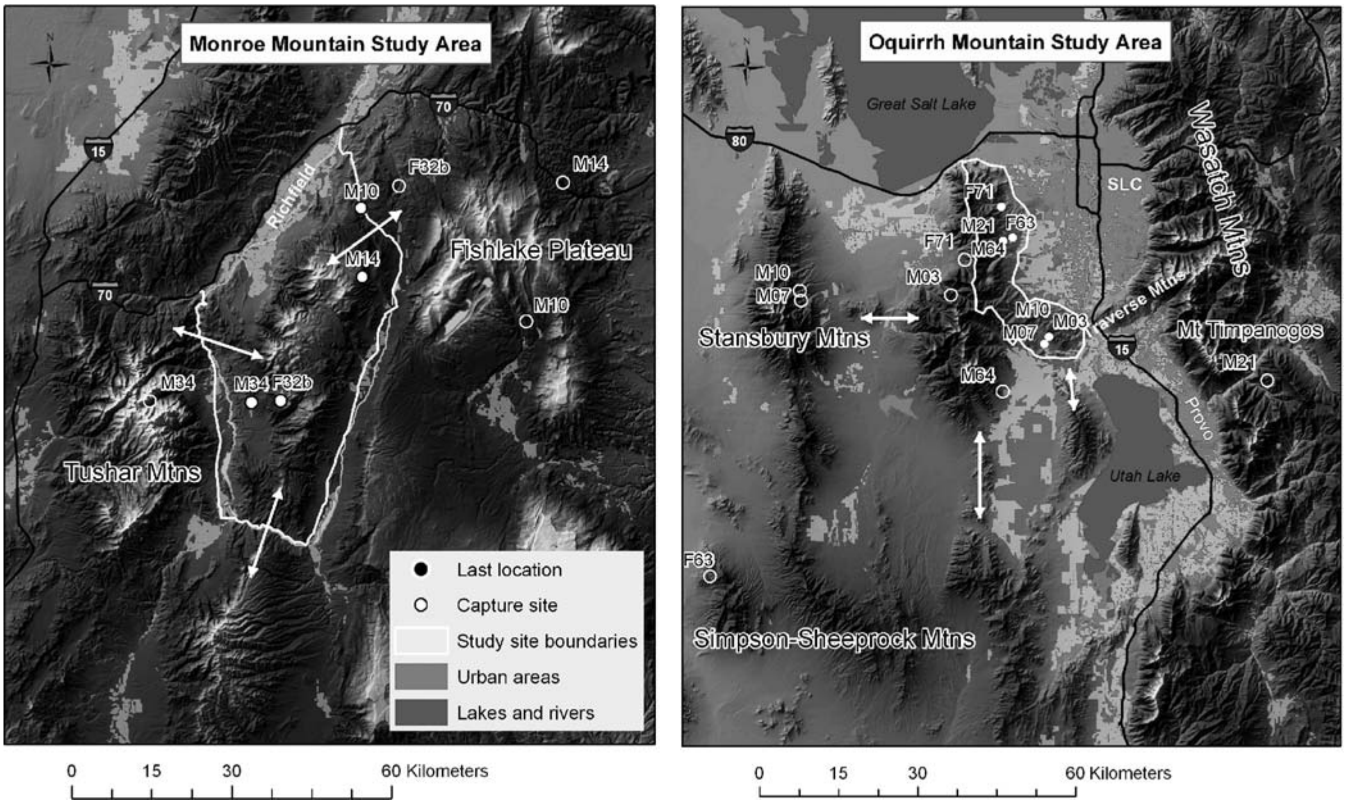

Figure 7. Dispersal patterns and landscape connectivity, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004. Arrows represent points of habitat connectivity.

Wasatch Mountains, crossing a 6-lane interstate and ≥5 km of city streets to get there.

Landscape Configuration

The study sites exhibited similar perimeter-area indices, but notable differences in connectivity and perimeter permeability (Table 3). During the study, no substantial movement barriers existed along the perimeter of Monroe Mountain, and in general, the unit was well connected to other habitats of similar quality within the Southern Mountains ecoregion (Fig. 7).

In contrast, only 5% of the Oquirrhs' perimeter was connected to neighboring habitat and approximately 40% was nearly impermeable to cougar movement. Movement barriers included the southern shore of the Great Salt Lake (7 km), the Salt Lake metro area (50 km), and a heavily traveled segment of Interstate 15 (2 km), which bisected the Traverse Mountains (Fig. 7). The remaining 55% graded into salt desert scrub communities offering little vegetative cover or surface water (West 1983). Additionally, residential development emanating from the Salt Lake–Provo metropolitan corridor was much greater around the Oquirrh site.

Overall, the Oquirrhs exhibited much thinner and more tenuous connectivity to neighboring patches of generally poorer quality (i.e., lower primary production), a pattern typical of basin and range topography (Fig. 1). This topographic fragmentation combined with anthropogenic fragmentation in the foothills and valleys around the site rendered this area susceptible to isolation (see Beier 1995).

Discussion

Influence of Harvest on Cougar Populations

Demographic differences between study populations reflected the prevailing management strategies. Cougar removal on Monroe Mountain ranged from 17.6–54.5% of the adult population exceeding 40% for 4 of the 5 years of high per-capita hunting pressure. Females comprised 32% of the harvest but 100% of depredation control and poaching mortality. Under this regime the population declined by >60%, whereas the Oquirrh Mountain population remained stationary. Moreover, the Oquirrh population had a significantly higher mean age among females and a smaller proportion of subadults. Age structure of males did not differ between sites, suggesting either: 1) males and females had a fundamentally different age distribution in the general population, or 2) the unhunted portion of the Oquirrhs was too small to adequately protect males. Density, survival, and fecundity were all negatively associated with sustained high per-capita hunting pressure on Monroe Mountain, whereas, with the exception of fecundity, these measures remained relatively constant over the same interval on the Oquirrh site. Though humans represented the single greatest source of mortality for animals traveling outside the Oquirrh study site, the absence of harvest within the study area suggests that the Camp Williams–Kennecott properties collectively acted as a functional refuge. Resident females were the primary beneficiaries of this protection. On the Monroe site, the prevalence

Table 3. Measures of landscape connectivity, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

Landscape metrics	Monroe	Oquirrhs
Perimeter (km)	178	150
Area (km^2)	1300	950
Perimeter:area	0.137	0.157
Greatest interpatch distance (km)	7	25
Perimeter impermeable (%)	0	40
Perimeter connected (%)	33	5
Width connective habitat (km)	7–21	2–4.5

of human-caused mortality, lack of starvation as a mortality cause, and moderately stable prey populations (UDWR, unpublished data) suggest that this level of mortality was largely additive. Annual harvests exceeding 30% of the adult population consisting of 42% females, carried out continuously for >3 years, can reduce density, fecundity, and skew age structure.

The consequences of sustained exploitation may not be limited to numeric population changes. Fecundity rates on Monroe tracked per-capita harvest pressure with a 1-year lag. We did not observe compensatory reproduction under increased harvest levels, as has been noted for some monogamous carnivores (Knowlton 1972, Frank and Woodroffe 2001). Smuts (1978), Knick (1990), and Wielgus and Bunnell (2000) reported analogous findings for hunted populations of African lions (*Panthera leo*), bobcats (*Lynx rufus*), and brown bears (*Ursus arctos*), respectively. One hypothesized function of male territoriality among polygynous carnivores is to increase offspring survival by excluding nonsire males from the natal range (Bertram 1975, Ross and Jalkotzy 1992), thereby reducing infanticide and optimizing fitness (Packer and Pusey 1984, Swenson 2003). Cougars are known to exhibit this behavior (Hornocker 1970, Hemker et al. 1986, Pierce et al. 1998) suggesting that hunted populations may experience increased levels of infanticide (Swenson 2003). On Monroe heavy harvest and subsequent social instability may have reduced the reproductive capacity of the population and therefore its ability to compensate losses.

Factors Influencing the Rate of Population Recovery

From 2002 to 2004 per capita hunting pressure on Monroe Mountain was reduced to <30%, during which survival and fecundity increased. Nevertheless, following 3 seasons of light harvest the population had only recovered to 52.4% of its 1997 levels, with nearly equal sex ratios and reproduction lagging behind resident replacement.

Lindzey et al. (1992) in Utah and Logan and Sweanor (2001) in New Mexico conducted controlled removals to examine the demographic mechanisms and time scales of population recovery. These authors noted that female recruitment was achieved via philopatric behavior or diffuse dispersal, whereas male recruitment was solely the product of immigration. Further, they suggested that recovery from 27–58% population reductions could be attained within 2–3 years under complete protection. However, those removals spanned only a single season and large sanctuaries (>1,000 km^2) buffered the treatment areas. In contrast, the Monroe population had only a 7-month annual reprieve from hunting pressure and was surrounded by units subjected to similar levels of exploitation.

The degree of landscape connectivity can mediate demographic connectivity, and is thus an important factor in population recovery or persistence (Beier 1993). Strong connectivity is the most likely reason we detected transients on Monroe each winter. These animals buffered population declines (Brown and Kodric-Brown 1977) but may have contributed to social instability. It has been hypothesized that the removal of resident males may induce a "vacuum effect" in which multiple transients vie for a vacant home range, potentially leading to an increase in population density (Shaw 1981, Logan et al. 1986). Our results lend only limited support to this argument. We observed an increase in the relative proportion of subadult males subsequent to removal of resident males, whereas the overall population declined. In general, males tend to disperse farther than females, remain transient longer, and are less tolerant of other males (Cunningham et al. 2001, Logan and Sweanor 2001, Maehr et al. 2002). Conversely, females often exhibit philopatric behavior, reproduce at an earlier age than males, and tolerate spatial overlap with other females (Murphy 1998, Pierce et al. 2000). Therefore, the transient segment of the cougar population is likely to be male biased (Hansson 1991). Removal of resident males provides territory vacancies that may be contested by multiple immigrants, thereby temporarily increasing the proportion of males in the population but not the overall density of males in the general population. Based on preliminary data from the post-treatment period, we hypothesize that following sustained disturbance, population recovery will proceed in 2 general phases: numerical and functional. Functional recovery implies not simply increases in absolute density but rather stabilization of social relationships and decreases in the variability of vital life-history rates. Female-biased sex ratios, low male turnover rates, and higher per-capita productivity may be used as relative indices of functional recovery.

Harvest Dynamics and the Regional Metapopulation

The metapopulation concept has been proposed as a framework for large-scale management of cougars (Beier 1996, Sweanor et al. 2000, Laundré and Clark 2003). In the strictest sense, a metapopulation is the composite of numerous spatially discrete subpopulations exhibiting independent behavior over time. The dynamics of the metapopulation are the net result of the shifting balance between local extinctions and recolonizations facilitated by intermittent dispersal events. The latter quality defines the classic metapopulation (Levins 1969, Hanski and Simberloff 1997).

The source–sink model provides a mechanism for metapopulation dynamics by emphasizing recruitment patterns within and among populations. The more general definition describes a sink as a net importer and a source as a net exporter of individuals over time (Pulliam 1988). Demographically, the Monroe and Oquirrh populations approximate the sink–source archetypes, respectively, albeit as a result of exploitation levels rather than habitat quality (e.g., Novaro et al. 2000). When harvest and its apparent impacts are considered, the Monroe population exhibited sink-like mortality. Notwithstanding low kitten production, each winter new animals, primarily subadult males, were captured on the site. Some of these individuals may have been resident progeny but mammalian dispersal patterns tend to be male-biased (Greenwood 1980). Low productivity and high immigration rates are the essence of a sink population.

In contrast, the Oquirrh population exhibited static density and emigration of resident progeny. No marked female kittens were detected as adults on the site. Indeed, 5 tattooed kittens (2 F, 3 M) were later killed elsewhere in the Oquirrhs or on neighboring mountain ranges up to 85 km distant. Solely based on age (4 yr) the female emigrants could have raised one litter to independence, whereas the males were killed immediately upon leaving their natal ranges, thereby subsidizing the harvest in adjacent units. On the Oquirrh site female dispersal appeared to be related to the saturation of available habitat, suggesting a source-like population structure.

When the prevailing harvest rate is considered a component of habitat quality, then a spatially clumped harvest distribution can promote source–sink dynamics. This may result in an immigration gradient directed toward patches such as Monroe Mountain, where strong connectivity coupled with low population density create an ecological trap (i.e., a productive habitat that displays sink-like mortality patterns, e.g., Bailey et al. 1986, Kokko and Sutherland 2001). These sites represent examples of populations exhibiting different dynamics simultaneously within a metapopulation. Importantly, source–sink characteristics may be dynamic and interchangeable depending on how prevailing management interacts with habitat productivity and connectivity. For example, the Monroe population illustrates the potential consequences of overharvest, yet is situated within a large semicontiguous tract of habitat spanning the state with extensions into Colorado, Idaho, and Arizona. Conversely, the Oquirrh population appears demographically stable, but lies within an ecoregion defined by weak connectivity among sparsely distributed desert ranges. Under different objectives, conservative management could render the Monroe population a source, whereas the Oquirrh population should be managed under the small population paradigm (Caughley 1994).

Management Implications

At the scale of the local population or management unit, annual harvests exceeding 40% of the nonjuvenile population for ≥4 years can not only reduce density but may also promote or maintain a demographic structure that is younger, less productive, and socially unstable. At an ecoregional scale the difficulties of reliably delineating discrete populations (Pierce and Bleich 2003) and their respective sizes (Choate et al. 2006) emphasize the importance of managing cougars in a metapopulation context. That said, source–sink characteristics may be more amenable to field evaluation than the extinction and recolonization events that define classic metapopulations. Numeric recovery of overexploited populations may initially depend more on immigration than in situ reproduction. Under moderate to heavy exploitation this tack may require: 1) an assessment of habitat connectivity between identified sources and sinks, and 2) the presence of truly functional source populations, most readily managed through the establishment of refugia.

Acknowledgments

A special thanks to our collaborators and sponsoring organizations, B. Blackwell, B. Bates, C. McLaughlin, A. Clark, and T. Becker from the Utah Division of Wildlife Resources; K. Rasmussen from the Fishlake National Forest; J. Crane, D. Johnson, and R. Dunton from the Utah Army National Guard; and to W. Adams, A. Neville, and M. Shoop from the Kennecott Utah Copper Corporation. This work could not have been accomplished without the hard work, dedication, and perspective of our houndsmen and pilots, C. Mecham, M. Mecham, C. Shaffer, C. Hunt, and S. Biggs. T. Kogianes, B. Bateman C. Hendrix, G. Jacobson, D. McQuillan and K. Christenson provided additional help in the field. T. DeLiberto, D. Carlson, and R. Skirpstunas assisted with capture protocols and necropsies; the Millville Predator Ecology Center supplied storage space and facilities for necropsies. Thanks also to G. Belovsky, S. Durham, D. Ramsey, M. Connor, L. Langs, W. Rieth, R. Johnson, A. Leidolf, and K. Bunnell for design, statistical, and GIS assistance. The authors extend their thanks to N. Frey, M. Ebinger, C. McLaughlin, and 2 anonymous reviewers for constructive criticism of the original manuscript. The Cougar Fund generously assumed all page charges associated with the publication of this manuscript.

Literature Cited

Anderson, A. E. 1983. A critical review of literature on puma (*Felis concolor*). Colorado Division of Wildlife, Special Report No. 54, Denver, USA.

Anderson, A. E., D. C. Bowden, and D. M. Kattner. 1992. The puma on the Uncompahgre Plateau, Colorado. Colorado Division of Wildlife, Technical Publication No. 40, Denver, USA.

Ashcroft, G. L., D. T. Jensen, and J. L. Brown. 1992. Utah climate. Utah Climate Center, Utah State University, Logan, USA.

Ashman, D. L., G. C. Christensen, M. L. Hess, G. K. Tsukamoto, and M. S. Wickersham. 1983. The mountain lion in Nevada. Nevada Department of Wildlife, Carson City, USA.

Bailey, T. N., E. E. Bangs, M. F. Portner, J. C. Malloy, and R. J. McAvinchey. 1986. An apparent overexploited lynx population on the Kenai Peninsula, Alaska. Journal of Wildlife Management 50:279–290.

Barnhurst, D. 1986. Vulnerability of cougars to hunting. Thesis, Utah State University, Logan, USA.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7:94–108.

Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. Journal of Wildlife Management 59:228–237.

Beier, P. 1996. Metapopulation models, tenacious tracking, and cougar conservation. Pages 293–323 *in* D. R. McCullough, editor. Metapopulations and wildlife conservation. Island, Covelo, California, USA.

Beier, P., and S. C. Cunningham. 1996. Power of track surveys to detect changes in cougar populations. Wildlife Society Bulletin 24: 540–546.

Bertram, B. C. R. 1975. Social factors influencing reproduction in wild lions. Journal of Zoology, London 177:463–482.

Bowyer, R. T., D. K. Person, and B. M. Pierce. 2005. Detecting top-down versus bottom up regulation of ungulates by large carnivores: implications for conservation of biodiversity. Pages 342–361 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island, Covelo, California, USA.

Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. American Naturalist 105:467–478.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Choate, D. M., M. L. Wolfe, and D. C. Stoner. 2006. Evaluation of cougar population estimators in Utah. Wildlife Society Bulletin 34: 782–799.

Cox, D. R., and D. Oakes. 1984. Analysis of survival data. Chapman & Hall, New York, USA.

Cunningham, S. C., W. B. Ballard, and H. A. Whitlaw. 2001. Age structure, survival, and mortality of mountain lions in southeastern Arizona. Southwestern Naturalist 46:76–80.

Edwards, T. C., C. G. Homer, S. D. Bassett, A. Falconer, R. D. Ramsey, and D. W. Wight. 1995. Utah gap analysis: an environmental information system. Utah Cooperative Fish and Wildlife Research Unit, Technical Report 95–1. Utah State University, Logan, USA.

Ernest, H. B., W. M. Boyce, V. C. Bleich, B. May, S. J. Stiver, and S. G. Torres. 2003. Genetic structure of mountain lion (*Puma concolor*) populations in California. Conservation Genetics 4:353–366.

Fjelline, D. P., and T. M. Mansfield. 1989. Method to standardize the procedure for measuring mountain lion tracks. Pages 49–51 *in* R. H. Smith, editor. Proceedings of the Third Mountain Lion Workshop. Arizona Game and Fish Department, Phoenix, USA.

Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. France, C. R. Goldman, K. Heanue, J. A. Jones, F. J. Swanson, T. Turrentine, and T. C. Winter. 2003. Road ecology—science and solutions. Island, Covelo, California, USA.

Frank, L. G., and R. Woodroffe. 2001. Behavior of carnivores in exploited and controlled populations. Pages 419–442 *in* J. L. Gittleman, S. M. Funk, D. MacDonald, and R. K. Wayne, editors. Carnivore conservation. University of Cambridge, United Kingdom.

Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Animal Behavior 28:1140–1162.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 *in* I. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics, and evolution. Academic, San Diego, California, USA.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42:89–103.

Hemker, T. P., F. G. Lindzey, and B. B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. Journal of Wildlife Management 48:1275–1284.

Hemker, T. P., F. G. Lindzey, B. B. Ackerman, and A. J. Button. 1986. Survival of cougar cubs in a non-hunted population. Pages 327–332 *in* S. D. Miller and D. D. Everett, editors. Cats of the world: biology, conservation, and management. National Wildlife Federation, Washington, D.C., USA.

Hill, H., and K. Bunnell. 2005. Utah Cougar harvest report, 2001–2002 to 2004–2005. Utah Department of Natural Resources, Publication No. 05-39. Salt Lake City, USA.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs 21:1–39.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildlife Monographs 108:1–42.

Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. Journal of Wildlife Management 36:369–382.

Kokko, H., and W. J. Sutherland. 2001. Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. Evolutionary Ecology Research 3:537–551.

Kreeger, T. J. 1996. Handbook of wildlife chemical immobilization. Wildlife Pharmaceuticals, Inc., Fort Collins, Colorado, USA.

Laing, S. P., and F. G. Lindzey. 1991. Cougar habitat selection in south-central Utah. Pages 27–37 *in* C. S. Braun, editor. Proceedings of the mountain lion–human interaction workshop. Colorado Division of Wildlife, Denver, USA.

Laundré, J., and T. W. Clark. 2003. Managing puma hunting in the western United States: through a metapopulation approach. Animal Conservation 6:159–170.

Laundré, J., L. Hernández, D. Streubel, K. Altendorf, and C. A. López-González. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963–966.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

Lindzey, F. G., W. D. Van Sickle, S. P. Laing, and C. S. Mecham. 1992. Cougar population response to manipulation in southern Utah. Wildlife Society Bulletin 20:224–227.

Logan, K. A., L. L. Irwin, and R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. Journal of Wildlife Management 50:648–654.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma—evolutionary ecology and conservation of an enduring carnivore. Island, Washington, D.C., USA.

Maehr, D. S., E. D. Land, D. B. Shindle, O. L. Bass, and T. S. Hoctor. 2002. Florida panther dispersal and conservation. Biological Conservation 106:187–197.

Mason, J., D. Peay, K. Robinson, R. Danvir, B. Bateman, M. Bodenchuk, M. Wolfe, L. Shirley, B. Bates, L. Cornicelli, B. Giunta, S. Cranney, J. Karpowitz, and J. Grandison. 1999. Utah cougar management plan. Utah Department of Natural Resources, Salt Lake City, USA.

Mech, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota, Minneapolis, USA.

Murphy, K. M. 1983. Relationships between a mountain lion population and hunting pressure in western Montana. Thesis, University of Montana, Missoula, USA.

Murphy, K. M. 1998. The ecology of the cougar (*Puma concolor*) in the northern Yellowstone ecosystem: interactions with prey, bears, and humans. Dissertation, University of Idaho, Moscow, USA.

Novaro, A. J., K. H. Redford, and R. Bodmer. 2000. Effect of hunting in source–sink systems in the neotropics. Conservation Biology 14:713–721.

Nowell, K., and P. Jackson, editors. 1996. Puma, *Puma concolor* (Linnaeus 1771). Pages 131–137 *in* Wild cats: status survey and conservation action plan. International Union for the Conservation of Nature. Burlington, Cambridge, United Kingdom.

Packer, C., and A. E. Pusey. 1984. Infanticide in carnivores. Pages 31–42 *in* G. Hausfater and S. B. Hrdy, editors. Infanticide—comparative and evolutionary perspectives. Aldine, New York, New York, USA.

Pierce, B. M., and V. C. Bleich. 2003. Mountain lion. Pages 744–757 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation.

Second edition. The Johns Hopkins University, Baltimore, Maryland, USA.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land tenure system regulate population size? Ecology 81:1533–1543.

Pierce, B. M., V. C. Bleich, C. B. Chetkiewicz, and J. D. Wehausen. 1998. Timing of feeding bouts of mountain lions. Journal of Mammalogy 79:222–226.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. Journal of Wildlife Management 56:417–426.

Ross, P. I., M. G. Jalkotzy, and J. R. Gunson. 1996. The quota system of cougar harvest management in Alberta. Wildlife Society Bulletin 24: 490–494.

Roylance, W. J. 1982. Utah: a guide to the state. Utah Arts Council, Salt Lake City, USA.

Shaw, H. G. 1981. Comparison of mountain lion predation on cattle on two study areas in Arizona. Pages 306–318 *in* L. Nelson Jr. and J. M. Peek, editors. Proceedings of the wildlife–livestock relationships symposium. Forest, Wildlife, & Range Experiment Station, University of Idaho, Moscow, USA.

Smuts, G. L. 1978. Effects of population reduction on the travels and reproduction of lions in Kruger National Park. Carnivore 2:61–72.

Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798–808.

Swenson, J. E. 2003. Implications of sexually selected infanticide for the hunting of large carnivores. Pages 171–189 *in* M. Festa-Bianchet and M. Apollonio, editors. Animal behavior and wildlife management. Island, Washington, D.C., USA.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571–573.

Van Sickle, W. D., and F. G. Lindzey. 1992. Evaluation of road track surveys for cougars (*Felis concolor*). Great Basin Naturalist 52:232–236.

West, N. E., editor. 1983. Intermountain salt-desert shrubland. Pages 375–397 *in* Temperate deserts and semi-deserts. Vol. 5: Ecosystems of the world. Elsevier, Amsterdam, Netherlands.

Wielgus, R. B., and F. L. Bunnell. 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. Biological Conservation 93:145–154.

Wolfe, M. L., D. M. Choate, and D. C. Stoner. 2004. USU/UDWR statewide cougar study—final report. Utah Division of Wildlife Resources, Salt Lake City.

Associate Editor: Ruggiero.

The Condor 112(1):65–78

COMMON RAVEN ACTIVITY IN RELATION TO LAND USE IN WESTERN WYOMING: IMPLICATIONS FOR GREATER SAGE-GROUSE REPRODUCTIVE SUCCESS

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Abstract. Anthropogenic changes in landscapes can favor generalist species adapted to human settlement, such as the Common Raven (*Corvus corax*), by providing new resources. Increased densities of predators can then negatively affect prey, especially rare or sensitive species. Jackson Hole and the upper Green River valley in western Wyoming are experiencing accelerated rates of human development due to tourism and natural gas development, respectively. Increased raven populations in these areas may negatively influence the Greater Sage-Grouse (*Centrocercus urophasianus*), a sensitive sagebrush specialist. We investigated landscape-level patterns in raven behavior and distribution and the correlation of the raven data with the grouse's reproductive success in western Wyoming. In our study areas towns provide ravens with supplemental food, water, and nest sites, leading to locally increased density but with apparently limited (<3 km) movement by ravens from towns to adjacent areas of undeveloped sagebrush. Raven density and occupancy were greatest in land covers with frequent human activity. In sagebrush with little human activity, raven density near incubating and brooding sage-grouse was elevated slightly relative to that expected and observed in sagebrush not known to hold grouse. Raven occupancy near sage-grouse nests and broods was more highly correlated with sage-grouse success than were raven density and behavior, suggesting that the majority of nest predation by ravens is most likely carried out by resident territorial individuals. Integrated region-wide improvement of sagebrush habitat, removal of anthropogenic subsidies, and perhaps removal or aversive conditioning of offending ravens might benefit sage-grouse populations in our study area.

Key words: anthropogenic subsidies, Centrocercus urophasianus, *Common Raven,* Corvus corax, *density and occupancy modeling, Greater Sage-Grouse, nest and brood predation*.

Actividad de *Corvus corax* en Relación al Uso del Suelo en el Oeste de Wyoming: Implicancias para el Éxito Reproductivo de *Centrocercus urophasianus*

Resumen. Los cambios en el paisaje de origen antropogénico pueden favorecer especies generalistas adaptadas a asentamientos humanos, como el cuervo *Corvus corax*, al proveer nuevos recursos. Luego, el aumento de la densidad de depredadores puede afectar negativamente a las presas, especialmente a las especies de presas raras o sensibles. Jackson Hole y la parte superior del valle del río Green en el oeste de Wyoming están experimentando tasas aceleradas de desarrollo humano debido a emprendimientos turísticos y de gas natural. El aumento de las poblaciones de *C. corax* en estas áreas puede influenciar de forma negativa a *Centrocercus urophasianus*, una especie sensible y especialista de matorrales de *Artemisia*. Investigamos patrones de comportamiento y distribución de *Corvus corax* a escala de paisaje y la correlación de los cuervos con el éxito reproductivo de *Centrocercus urophasianus* en el oeste de Wyoming. En nuestra área de estudio, las ciudades proveen alimento, agua y sitios de anidación suplementarios a los cuervos. Esto da como resultado el aumento de las densidades reproductivas locales pero con movimientos aparentemente limitados (<3 km) por parte de los cuervos desde las ciudades hacia las áreas no desarrolladas de matorrales de *Artemisia*. La mayor densidad y ocupación de *Corvus corax* fue observada en tipos de coberturas de suelo con actividades humanas frecuentes. En los matorrales de *Artemisia* con poca actividad humana, la densidad de cuervos fue levemente elevada cerca de las áreas de incubación y cría de *Centrocercus urophasianus*, comparada con la densidad esperada y observada en matorrales de *Artemisia* que no presentan individuos de *C. urophasianus*. La ocupación de cuervos en las proximidades de las áreas de cría de *C. urophasianus* tuvo una mejor correlación con el éxito de *C. urophasianus* que la densidad y el comportamiento de los cuervos. Esto sugiere que la mayor parte de la depredación por parte de los cuervos es realizada por individuos territoriales residentes. El mejoramiento integrado de los matorrales de *Artemisia* a nivel regional, la remoción de subsidios antropogénicos y quizás también la remoción o condicionamiento por aversión de los cuervos agresivos podrían beneficiar a las poblaciones de *C. urophasianus* en nuestra área de estudio.

Manuscript received 7 July 2009; accepted 10 November 2009.

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The Condor, Vol. 112, Number 1, pages 65–78. ISSN 0010-5422, electronic ISSN 1938-5422. DOI: 10.1525/cond.2010.090132

INTRODUCTION

The western United States is a land in transition. In only two centuries, a sparsely inhabited wilderness that first supplied minerals, food, and timber for an eastern population is now increasingly settled by the populus it helped grow (Hansen et al. 2002). As more people move to the West, ecosystem processes and biodiversity are altered (Theobald 2000, Robinson et al. 2005, Leu et al. 2008). Of importance to birds, the process of predation has been greatly modified by western people; large carnivores have been reduced or extirpated (Quammen 2004, Clark et al. 2005), while small generalists have been inadvertently aided by subsidies, enabling population growth and expansion (Restani et al. 2001, Kristan and Boarman 2003, Boarman et al. 2006). In landscapes where resource levels are naturally low, the inflation of densities of generalist predators caused by anthropogenic resources can be significant (Webb et al. 2004) and detrimental to sensitive prey (Sinclair et al. 1998).

The Common Raven (*Corvus corax*) benefits from human activity and has been implicated as a significant predator on other native species. Anthropogenic food sources can increase raven populations in lightly settled areas (Marzluff and Neatherlin 2006). As human populations increase in areas with few natural resources, human settlements become increasingly important for food and water subsidies for ravens and are responsible for recent regional increases in raven abundance (Boarman et al. 2006). Development of the landscape by humans can also provide ravens with artificial nesting and roosting structures, such as trees, poles, and buildings, thereby increasing local breeding density (Webb et al. 2004, Kristan and Boarman 2007). Roads, in particular, supplement the diets of ravens by providing a diversity of accessible, road-killed animals (Knight and Kawashima 1993, Boarman and Heinrich 1999). Furthermore, dispersing juveniles tend to concentrate around areas of human activity, which provide abundant, concentrated, and continually replenished food and water in an otherwise resource-poor environment (Webb et al. 2007). However, as ravens saturate high-quality habitat near human activity, they may spread into natural vegetation where they may prey upon the nests of other birds. As populations expand, breeding ravens may begin to colonize more natural habitats surrounding anthropogenic habitats (Kristan and Boarman 2007), where they can pose a threat to populations of prey (Kristan and Boarman 2003).

Jackson Hole and the upper Green River valley in western Wyoming are experiencing accelerated rates of human development. These areas encompass sagebrush steppe and grassland surrounded by the Wind River, Wyoming, Teton, and Gros Ventre mountain ranges. Until recently, these areas supported only light human settlement and cattle ranching. Today, however, settlements are expanding from tourism in Jackson Hole and natural gas development in the upper Green River valley. Jackson's local economy is largely dependent on tourism year round, as it is a major gateway for millions of tourists visiting Grand Teton and Yellowstone national parks in the summer and the Jackson Hole ski resorts in the winter. Oil and gas production in the upper Green River valley has grown rapidly as pressure to develop domestic energy supplies continues to escalate. Over 8500 wells have already been drilled in this region, and another 10 000 to 15 000 are forecast over the next decade (Berger 2004). The overall density of linear features, such as roads and pipelines, in the upper Green River valley is well above that in national forests (Thomson et al. 2005). Although the physical footprint of oil and gas infrastructure covers only a small portion of the valley, Weller et al. (2002) showed that the effects of this infrastructure on native wildlife can be extensive.

Human modification of Jackson Hole and the upper Green River valley may negatively influence sensitive sagebrush specialists, notably the Greater Sage-Grouse (*Centrocercus urophasianus*). These areas support important remaining populations of the sage-grouse (Braun 1998, Bureau of Land Management 2000), a species that is declining over most of its range (Connelly et al. 2004). Declines are due mostly to reduction and degradation of sagebrush habitat brought on by increases in human activity (Connelly et al. 2000, Schroeder and Baydack 2001), including subsidizing of known grouse predators, including the Common Raven (Coates and Delehanty 2008). Insulating traditional leks and nearby breeding areas from encroachment by human development so that the grouse's nesting success remains high is a key to maintaining a viable population (Aldridge et al. 2008). To do so likely will require extensive breeding habitat where nest density (Holloran and Anderson 2005) and predator effects (Coates and Delehanty 2008) are low.

We investigated landscape-level patterns in raven behavior and distribution and their correlation with sage-grouse reproduction in western Wyoming. Using point-count data from 2007 and 2008, we related raven occupancy and density to land cover, landscape pattern, and human activity. We predicted ravens would concentrate near areas of frequent human activity, such as cities and oil fields and that their density should decrease gradually with increasing distance from anthropogenic structures. We also expected raven abundance to be correlated positively with human population size, so that large towns, such as Jackson, Wyoming, should have the greatest raven densities. Because raven abundance may increase the risk of predation of sage-grouse nests (Coates and Delehanty, in press), we examined raven density, occupancy, and behavior at locations of sage-grouse nests and broods to determine if they were correlated with sage-grouse breeding success.

METHODS

STUDY AREA AND SITE SELECTION

We measured raven occupancy, density, and behavior as they relate to land cover and locations of nests and broods of the Greater Sage-Grouse in two separate areas of western Wyoming (Fig. 1). The Pinedale study area covered approximately

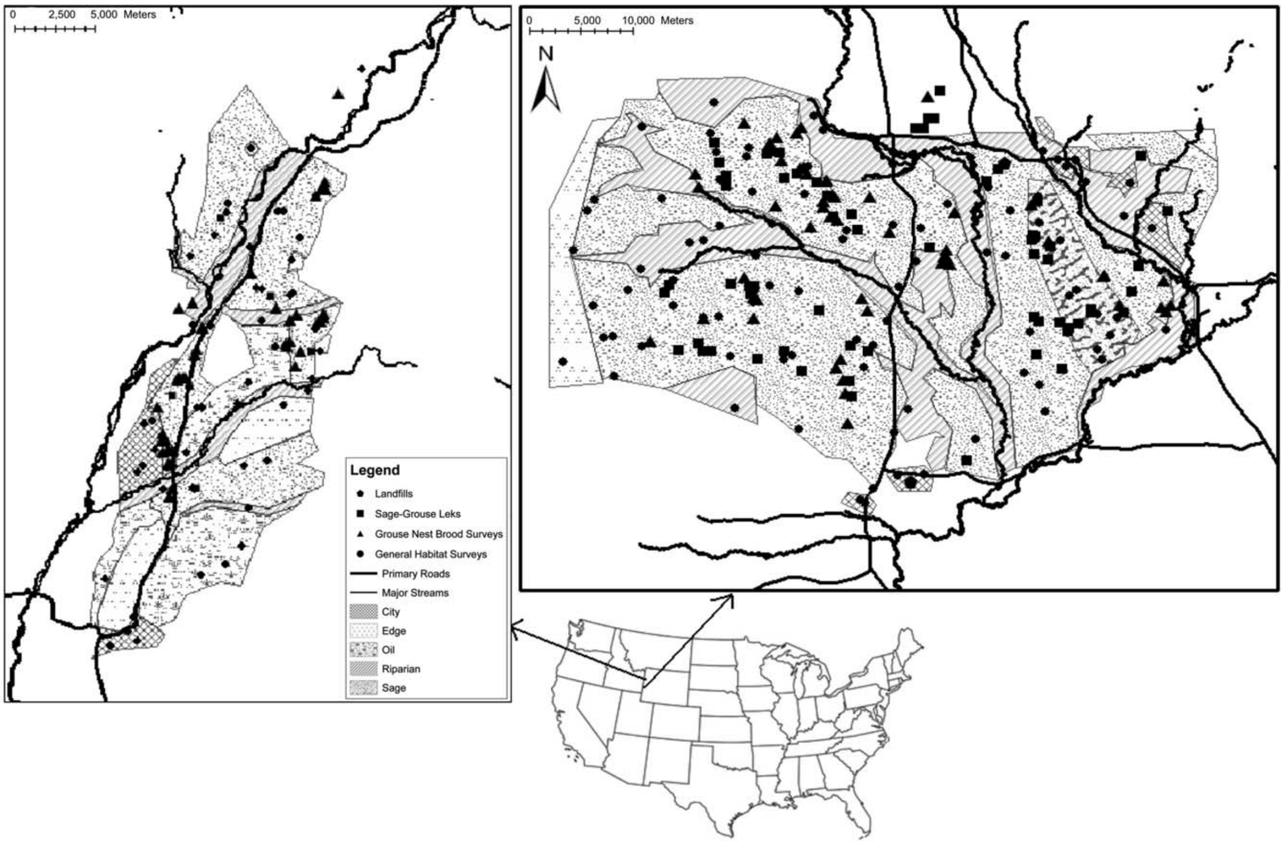

FIGURE 1. Locations of study areas in Wyoming, with magnified views of Pinedale (upper right) and Jackson study area (left) showing locations of raven survey points, sage-grouse leks, main roads, major streams, and land cover (sagebrush, riparian woodland, oil field, edge, city, hayfield). Filled pentagons represent landfills, filled squares represent sage-grouse leks, filled triangles represent surveys at sage-grouse nests and broods, filled circles represent general habitat surveys, and cross-hatching represents land cover.

6000 km^2 and encircled the area from approximately Pinedale (2007 population 2043; all population figures from U.S. Census Bureau 2009) in the north to Big Piney (2007 population 476) in the south and Boulder (2000 population 30) in the east. The study area was characterized by sagebrush, riparian woodland and surrounding agricultural land, oil fields, and human settlement. Areas dominated by sagebrush were dispersed among private property and parcels governed by the Bureau of Land Management; most riparian and all agricultural lands were privately owned. All oil fields were publicly owned. The Jackson study area encompassed the city of Jackson (2007 population 9631) and the National Elk Refuge to the south, the towns of Moose (2000 population 1439) and Kelly (population 242), and extended northward into Grand Teton National Park. The study area was characterized by sagebrush, riparian woodland, abandoned agricultural land, and human settlements. All lands, except for a small settlement, were publicly owned.

SAMPLING

To assess the correlation between raven abundance and land cover, we used stratified random sampling to select 166 survey points representing the types of land cover within each study area (sagebrush, riparian, oil field, edge, city, road, and hayfield; Fig. 1); a minimum distance of 1 km separated survey points. In 2007, we conducted general habitat surveys at 74 locations in the Pinedale area and at 45 locations in the Jackson area. In 2008, we surveyed at 28 and at 19 additional locations in the respective study areas; these surveys were randomly located in those sections of the study area not surveyed during the previous year. We surveyed at each location twice from 3 June to 1 August 2007 and from 16 May to 2 July 2008 to correspond with the sage-grouse's typical nesting and brood-rearing periods in these areas.

To assess the activity of ravens near sage-grouse nests and broods, we conducted 249 surveys in the vicinity of marked incubating or brooding sage-grouse hens (Fig. 1). We selected these survey locations by tracking radio-equipped sage-grouse hens ($n = 91$) throughout the reproductive season and included sage-grouse nests and broods of varying ages. The majority of surveys near sage-grouse nests and broods were in areas dominated by sagebrush, but some also contained riparian habitats or oil fields. In the two study areas, combined, we conducted 111 surveys around sage-grouse in 2007 (3 May–25 July) and 138 surveys in 2008 (6 May–23 July). Survey effort varied with the sage-grouse's breeding success and activity.

We conducted between one and five surveys at each sage-grouse nest (n = 169) and between one and four surveys at each sage-grouse with a brood (n = 80).

For each survey, we stood on top of a hill or other vantage point, listened for raven calls, and scanned with both unaided eyes and binoculars, alternating every 5 min for a total of 20 min (Luginbuhl et al. 2001). For surveys near sage-grouse nests and broods, we conducted the surveys with the observer located 200–300 m from the nest or brood, so as not to disturb the hen and her young or to attract predators to the location. Using a rangefinder, we measured the distance to ravens at first detection from the observer or from prominent landscape features of known distance previously measured on aerial photographs.

During surveys, we looked for any potential predators on sage-grouse nests and broods, including raptors and mammals, but report here only our observations of ravens. At each survey point, we recorded the following: date, observer's initials, start time, end time, observer's northing and easting (UTM NAD 83), cloud cover (percent), wind (in miles hr^{-1}), temperature (in °F), noise level (on a scale from 0 to 4, 0 being the lowest), habitat within a 400-m radius of the observer (by percentage), and any observation of predators. For the latter, this included time of observation, initial distance of predator from observer, lowest observed height of predator above ground, predator activity, habitat under predator, and any necessary comments. We mapped all observed predator activity onto a diagram of the survey point and its vicinity.

Sage-grouse nests were checked for survival at least twice weekly; sage-grouse broods were flushed at approximately 2 weeks and at 35 days after hatching (Schroeder et al. 1999, Walker et al. 2006). Nests were identified as successful if at least one egg hatched (Wallestad and Pyrah 1974); broods were identified as successful if at least one chick survived through the entire monitoring period. When possible, we documented the cause of nest failure; if the nest failed because of predation, we attempted to identify the predator as bird or mammal (Sargeant et al. 1998). We found no remains of broods following failure, so could not implicate specific predators in their loss. In our study area, the raven is one of many predators of grouse nests, and we assumed that our statistical analysis revealed the raven's potential contribution to nest and brood failure regardless of which predator actually ate a specific clutch or brood. This assumption overestimates the importance of the raven as a predator to the extent that other species are preying on the grouse simultaneously.

DETECTABILITY ANALYSIS

To estimate raven densities across the landscape, we first developed a detectability model to predict the probability of observing a raven. Detectability (the probability of observing an organism of interest at a survey location, given the organism is present at that location) can vary by distance from observer, observer ability, and environmental factors, creating biases in density estimates (Rosenstock et al. 2002). To examine our data for such bias, we tested for effects of land cover, study site, study year, and city/noncity categorization on the probability of detecting ravens at our survey locations. We used DISTANCE v.5.0 (Thomas et al. 2006) to fit detection-probability functions to our detections of ravens and to produce estimates of raven density in each land-cover type (sagebrush, riparian, oil field, edge, city, road, hayfield). Each land-cover type constituted a stratum, and each survey point included observations from both rounds of general habitat surveys conducted at that location. We assumed survey sites were located randomly with respect to the raven's distribution.

We used the multiple-covariates distance-sampling engine, with land-cover type, study site, and study year as covariates, to assess the fit of half-normal detection functions (with cosine, simple polynomial, and hermite polynomial series expansions) with values of Akaike's information criterion (AIC). Surveys conducted in edge category of land cover were too few to allow analysis by DISTANCE. We omitted surveys conducted in riparian habitat and along roads from detectability analyses because these land-cover types are linear, thus violating the assumption in DISTANCE analysis of uniform density. Inclusion of these surveys would have overestimated detectability-converted raven density and underestimated effective detection radius because the majority of detections in these habitats were close to the observer.

The null model that detectability was independent of covariates produced an AIC value lower than that of models considering study site, study year, land cover, and city/noncity categorization (Appendix 1: Table A1). Because we found most land covers to have no effect on the raven's detectability, and detectability-corrected density estimates were strongly correlated with unadjusted estimates (Appendix 1: Table A2), in further analyses we used estimates based on observed density instead of estimates corrected for detectability. We compared observed densities across land covers by using a one-factor (land cover), repeated-measures (two rounds of point counts per survey location) ANOVA (SPSS 2007).

MODELING RAVEN ABUNDANCE AND OCCURRENCE

We developed an occupancy model to predict the probability of raven presence or absence across our study areas. This involved assessing raven presence or absence at each survey location during successive counts and then investigating whether the probability of presence could be modeled as a function of characteristics (land cover, study site, study year, city/noncity categorization) measured at these locations (MacKenzie et al. 2006). We used RMARK (White 2008) and R for Windows 2.8.1 (R Development Core Team 2008) to assess the relative level of raven use and to estimate occupancy rates for each land-cover type. We considered the following models in our analysis: detectability and occupancy could vary by (1) any combination of land cover, (2) a more simplified categorization of land cover as city or noncity, (3) study site, or (4) study year. We expected land covers with high levels of human activity (i.e., city) to have greater occupancy, and perhaps reduced detectability, than those with less human use (i.e., noncity). We also tested for differences in occupancy rates between the two years of the study.

We then constructed a model to predict raven occupancy across the landscape. Using observed raven occupancy from our survey locations, we conducted a logistic regression analysis that considered the following variables: land cover at the survey point (undeveloped sagebrush, riparian, oil field [in Pinedale only], edge, city, road, hayfield [in Jackson only]), distance to nearest area of high human activity (road, city, landfill [in Pinedale only]), and various landscape-pattern metrics (Shannon diversity index, contagion, contrast-weighted edge density, patch richness). We used aerial photos to determine land cover at each survey location and distance to nearest area of high human activity. We used FRAGSTATS v.3.3 (McGarigal et al. 2002) to calculate landscape-pattern metrics within a 1-km circle (defined by sampling design to avoid overlap of circles) of each survey point. For contrast-weighted edge density, edges between a land cover with low human activity and another with high human activity received a weight of 1, whereas edges between two land covers with similar levels of human activity received a weight of 0. Because three of the four landscape-pattern metrics (Shannon diversity index, contagion, patch richness) were highly correlated ($r > 0.65$, $P < 0.01$), we included only contagion and contrast-weighted edge density in our regression model, as these were the least correlated of the landscape-pattern metrics ($r < 0.47$, $P > 0.5$). In predicting raven occupancy, we used SPSS v.11.1 to estimate coefficients of each independent variable. All coefficient estimates were calculated relative to cover catgory of sagebrush. Using ArcGIS v.9.3 (ESRI 2008), we extrapolated these coefficient estimates from our survey locations to our entire study area to produce a predictive map of raven occupancy across the landscape. Relative differences in predicted occupancy matched expectation, but absolute predicted occupancy was biased high (at 73 sample points in contiguous sagebrush we observed 20 ± 4% occupancy but predicted 40 ± 3%; $t_{72} = -5.5$, $P < 0.001$).

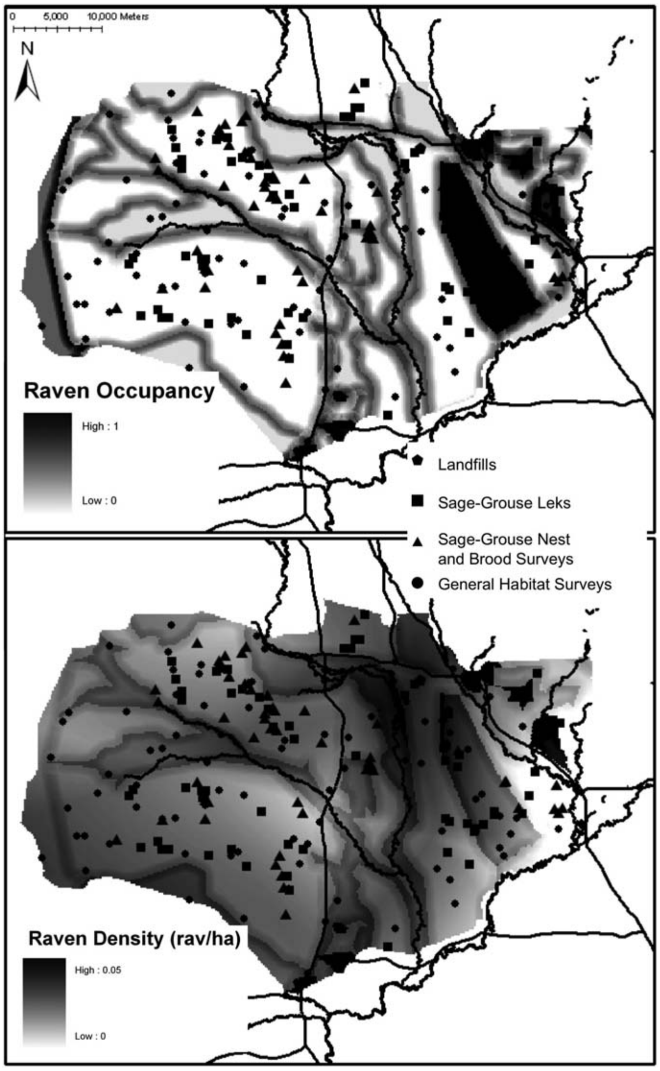

FIGURE 2. Major cities and landmarks, sage-grouse leks, expected raven occurrence (top), and expected raven density (ravens ha^{-1}) (bottom) in the Pinedale study area as predicted by our model. Filled pentagons represent landfills, filled squares represent sage-grouse leks, filled triangles represent surveys at sage-grouse nests and broods, filled circles represent general habitat surveys, cross-hatching represents land cover, and shading represents raven density and occurrence. Coefficients for occupancy model from Table 3. Coefficients for density model assumed normal error: 0.64 + 1.88(city) + 0.46(oil) + 0.26(riparian) + 0.04(edge) + 0.05(contrast edge density) + 0.01(road) − 0.003(contagion) + 0.00006(distance to road) − 0.00009(distance to landfill) + 0.00004(distance to city).

Because our logistic regression model indicated that ravens occupy the vast majority of our study area (Figs. 2, 3), we also constructed a model to predict variation in raven density. Using observed raven densities from our surveys, we conducted a linear regression analysis that considered the same independent variables as our logistic regression model. In the analysis of the Jackson observations we assumed errors were distributed normally because spatial autocorrelation of residuals was negligible (Moran's $I = -0.21$, $P = 0.62$). However, the residuals from the analysis of the Pinedale observations were spatially autocorrelated, especially along the north–south axis (Moran's $I = 0.45$, $P < 0.001$). Therefore, to evaluate the significance and relative importance of model coefficients, for this analysis we assumed a spatially autocorrelated error structure and estimated coefficients and standard errors with a maximum-likelihood estimator. We assumed estimated errors covaried with distance between points and accounted for

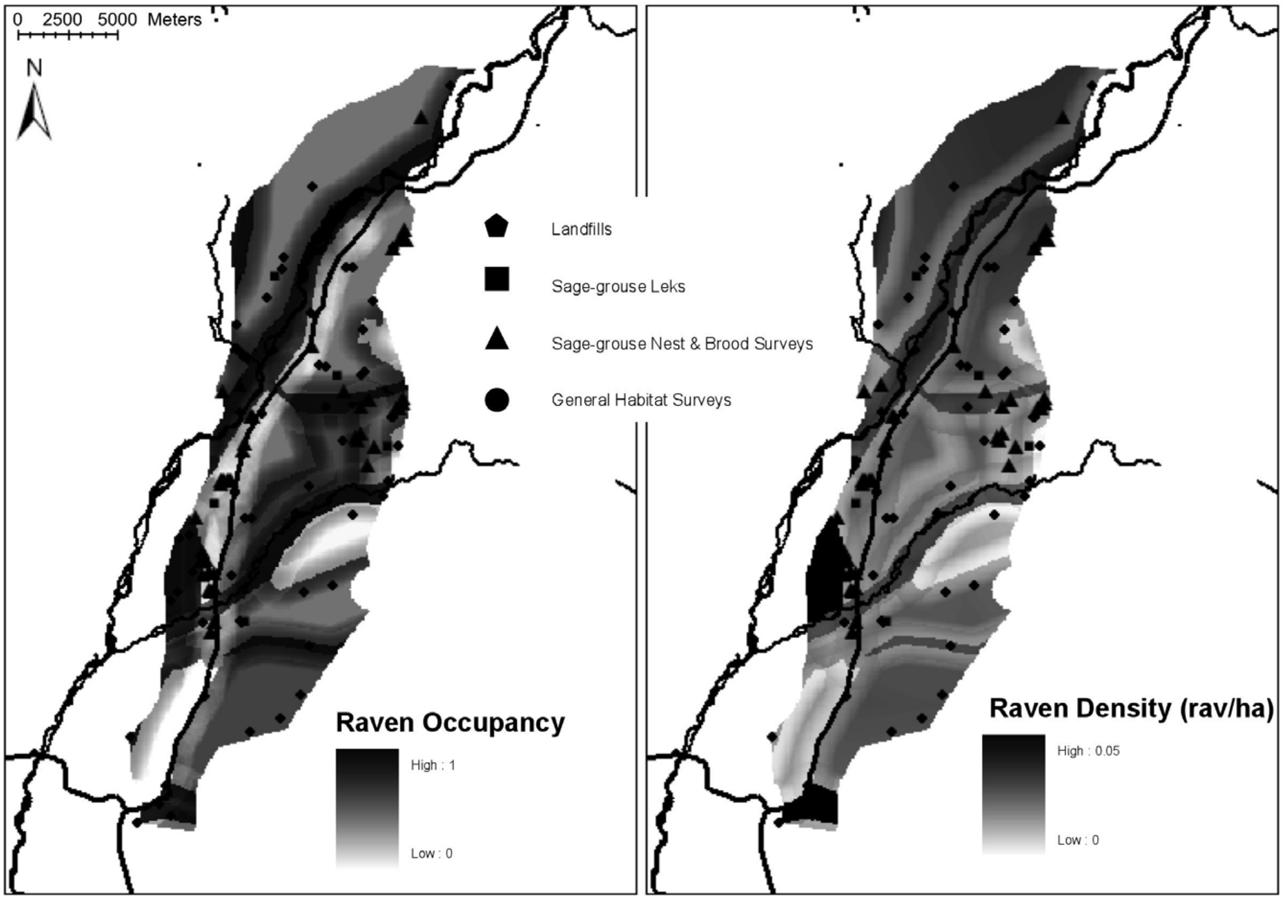

FIGURE 3. Major cities and landmarks, sage-grouse leks, expected raven occurrence (left), and expected raven density (ravens ha^{-1}; right) across the Jackson study area as predicted by our models (unstandardized coefficients in Table 3). Filled pentagons represent landfills, filled squares represent sage-grouse leks, filled triangles represent surveys at sage-grouse nests and broods, filled circles represent general habitat surveys, cross-hatching represents land cover, and shading represents raven density and occurrence.

this error structure by using maximum-likelihood, rather than least-squares, estimation of regression coefficients, doing this with "ruf.fit" v.1.3 (Handcock 2004) within the statistical software program R v.2.8 (2008). Using ArcGIS v.9.3 (ESRI 2008), we extrapolated the unstandardized regression coefficient estimate for each independent variable from our survey locations to our entire study area to produce a predictive map of raven abundance across the landscape. For consistency we based all predictions on coefficients assuming normal error. As expected (Nielsen et al. 2002, Marzluff et al. 2004), using standard least-squares estimates of coefficients did not influence predictions (raven densities in Pinedale predicted under the assumptions of normal and spatially autocorrelated errors were virtually identical; pixel-by-pixel comparison of model output: $r = 0.93$, $n = 54\,190$, $P < 0.001$). Predicted density also closely matched observation and was not biased (at 73 locations in contiguous sagebrush we observed a raven density of $0.007 \pm 0.002\ \text{ha}^{-1}$ and predicted 0.008 ± 0.002; $t_{72} = 0.05$, $P < 0.62$). All data are reported as means ± SE.

CORRELATING RAVEN ACTIVITY AND SAGE-GROUSE NEST AND BROOD SUCCESS

To evaluate potential attraction of ravens to areas where sage-grouse nest and rear broods, we using paired *t*-tests (SPSS v.11.1) to compare expected raven densities and occupancies, as predicted by our model of raven distribution, to observed values at random locations within contiguous sagebrush habitat (as a control measure) and at locations of sage-grouse nests and broods. We also directly compared observed counts in sagebrush where we did not know sage-grouse to be nesting or rearing broods to counts taken in sagebrush where sage-grouse were actively incubating or brooding.

We also developed a multinomial logistic regression model to assess the correlation of raven activity with the outcome of individual sage-grouse nests and broods. We considered all grouse nests and did not make assumptions about what predator caused each failure. The independent variables considered in our models were study site, percent sagebrush cover near the sage-grouse nest or brood, distance to nearest city, raven density, raven occupancy, and raven behavior. The dependent variable in our model was sage-grouse success, which fell into one of three categories: nest failure, brood failure, or survival throughout the entire reproductive season. We investigated models considering expected values of raven density and occupancy, as predicted by our model of raven distribution, observed values of raven density, occupancy, and behavior averaged over all surveys near a particular sage-grouse nest or brood throughout the season, and observed values of raven density, occupancy, and behavior from the survey conducted latest in the reproductive season near a particular sage-grouse nest or brood. We evaluated models' fit by calculating a Pearson goodness-of-fit coefficient for each model. For failed sage-grouse nests or broods, the "last" survey was the one conducted nearest in time to the failure (1 to 11 days, with an average of 5 days, prior to the failure). We scored raven behavior so that foraging received a higher score than nonpredatory behavior. Either flying at a height of >5 m and turning no more than once or perching >50 m from a sage-grouse nest or brood received a score of 1, flying at a height of <5 m and turning more than twice received a score of 2, and perching within 50 m of a sage-grouse nest or brood received a score of 3. It is possible that successful nests might be observed mostly late in the season, and if so this might bias our results if raven abundance were seasonal. Neither potential bias was evident. We observed successful and failed nests throughout the summer (nest failure occurred from 3 May to 23 June, brood failure from 12 to 24 June, and successful nesting from 8 May to 2 July). In each of these intervals raven abundance and occupancy in sagebrush were similar (nest-failure period: $n = 53$, density = 0.006 ± 0.002, occupancy = 0.15 ± 0.05; brood-failure period: $n = 33$, density = 0.004 ± 0.003, occupancy = 0.09 ± 0.05; successful-nesting period: $n = 68$, density = 0.005 ± 0.001, occupancy = 0.13 ± 0.04).

RESULTS

MODELING RAVEN ABUNDANCE AND OCCURRENCE

The density of ravens and modeled occupancy rates varied with land cover across both study areas (Table 1; $F_{1,159} = 5.9$, $P < 0.001$). Among the categories of land cover, city had the highest observed raven density and one of the highest occupancy rates (Table 1). Although raven density was not significantly correlated with the size of a town's human population ($r = 0.23$, $n = 6$, $P = 0.33$), the town with the largest human population, Jackson, had the greatest raven density of all towns surveyed. All other land-cover types had similarly low estimated raven densities, with hayfield having an observed density slightly higher than the others. Observed densities in both sagebrush and oil fields were low, but at the Pinedale study site, which contained both of these land covers, the relative occupancy rate in oil fields was higher than in sagebrush. Riparian habitat and roads, the two linearly oriented land-cover types we studied, had similarly low observed densities but occupancy was greater along roads than in riparian habitat. Edge habitat had the lowest observed density and occupancy rate, but the sample for this land cover was small. With the exception of oil fields, where the large effective detection radius can be explained by a high percentage (56%) of distant detections, the effective detection radii in the various land cover types were similar (Table 1), further supporting our conclusion of equal detectability across land covers (Appendix 1).

Study site, in addition to land cover, influenced occupancy (Table 2). There was some support (ΔAIC < 2) for models including varying detectability across all land covers, categorization as city or noncity, or study site. The four models that implicated detectability differences are different articulations of the influence of physical obstruction (vegetation, buildings, and noise) on our ability to see and hear

TABLE 1. Observed raven density, effective detection radius, and estimated relative occupancy rate for each land cover type. Occupancy rates are listed separately by study site whereas density estimates are combined across study sites because occupancy, not density, varied significantly between study sites. We used detections within 400 m of the observer in our analyses in order to have an area over which to calculate observed densities and because effective detection radii were approximately 400 m. See Appendix 1 for detectability-corrected densities.

Land cover	No. of counts	Detections within 400 m: Counts with detections	Detections within 400 m: No. of detections	Observed density (within 400 m; ravens ha^{-1})	Effective detection radius (m)	Estimated relative occupancy rate: Pinedale	Estimated relative occupancy rate: Jackson
Sagebrush	126	24	36	0.004 (0.001)	317.53 (40.48)	0.25 (0.07)	0.78 (0.11)
Riparian	64	16	26	0.005 (0.001)	N/A	0.57 (0.12)	0.93 (0.53)
Oil	20	6	8	0.005 (0.002)	916.29 (132.89)	0.93 (0.15)	N/A
Edge	12	1	1	0.001 (0.001)	N/A	0.05 (0.06)	0.34 (0.28)
City	56	30	82	0.015 (0.002)	280.87 (13.06)	0.78 (0.15)	0.97 (0.03)
Road	32	9	9	0.004 (0.001)	N/A	0.83 (0.16)	0.98 (0.02)
Hayfield	22	8	15	0.007 (0.002)	363.64 (53.45)	N/A	0.95 (0.14)

TABLE 2. Top-ranked models (out of 10 considered) of raven occupancy in relation to land cover, study site, and study year.

Occupancy model	ΔAIC	Akaike weight
Detectability constant; occupancy varies by land cover and study site[a]	0.0	0.37
Detectability varies by land cover; occupancy varies by land cover and study site	1.2	0.20
Detectability varies by city/noncity and study site; occupancy varies by land cover and study site	1.5	0.17
Detectability varies by land cover; occupancy varies by study site	2.1	0.13
Detectability varies by study site; occupancy varies by land cover and study site	2.2	0.12

[a] AIC = 403.3.

ravens. Therefore it is not surprising that each of these similar models was equally consistent with the data. Regardless of variability in detecting occupancy, all of the supported models indicated that occupancy varied considerably across land covers and between study sites. For land-cover types found in both study areas, occupancy was greater in Jackson than it was in Pinedale ($t_4 = 4.5$; $n = 5$ shared land covers; $P = 0.01$; Table 1), with probability of occupancy almost twice as high in Jackson (0.80 ± 0.12, $n = 5$) as it was in Pinedale (0.50 ± 0.15, $n = 5$). Although average raven density in Jackson (0.005 ± 0.003, $n = 5$) was about five times as great as in Pinedale (0.001 ± 0.0003, $n = 5$) in land covers found at both study sites, the difference in densities was not significant ($t_4 = 1.4$, $n = 5$, $P = 0.22$). All supported models indentified study site and land-cover effects, but not detectability, as important to raven occupancy, suggesting that despite differences in obstructions to observing it, the raven is strongly associated with some, and less strongly associated with other, aspects of the landscape.

Our models predicted the greatest levels of raven occupancy in the land covers of city, oil field, and edge but the highest raven densities in cities (Table 3; Figs. 2, 3). At both study sites, land cover was the variable most indicative of raven occupancy, followed by landscape metrics and finally by distance to areas of high human activity (Table 3). The raven population appears to be more uniformly distributed at Jackson than at Pinedale, as intermediate to high levels of occupancy were predicted over the majority of the Jackson study site, whereas the Pinedale study site was characterized by generally low levels of raven occupancy, with higher concentrations in cities. Contrast-weighted edge density and land cover were the most indicative of raven density, followed by contagion, and finally by distance to areas of high human activity (Table 3). In the Pinedale study area (Fig. 2), we predicted oil fields to have high levels of raven occupancy but only low to intermediate raven densities, suggesting constant but low

TABLE 3. Coefficients and SE for independent variables in linear and logistic regression analyses for predicting average raven density within 400 m and raven occupancy, respectively, where density = intercept + $\Sigma\beta_i x_i$ and $P(\text{occurrence}) = e^z/(1 + e^z)$, and $z = \text{intercept} + \Sigma\beta_i x_i$. Analyses assumed a normally distributed error structure, except in the Pinedale density analysis, where errors were adjusted for significant spatial autocorrelation. Standardized coefficients (linear regressions) and odds ratios (logistic regressions) are presented to allow comparison of relative importance of variables.

	Coefficients (SE) from linear regression on density				Coefficients (SE) from logistic regression on occupancy			
	Pinedale		Jackson		Pinedale		Jackson	
Variable	Unstandardized	Standardized	Unstandardized	Standardized	Unstandardized	Odds Ratio	Unstandardized	Odds Ratio
Intercept	0.66 (0.67)	N/A	0.20 (0.65)	N/A	−0.04	N/A	1.64	N/A
City	3.54 (0.36)	1.30	1.64 (0.45)	0.54	1.89 (0.87)	6.6	2.19 (1.09)	8.9
Oil field	0.63 (0.41)	0.18	N/A	N/A	2.33 (0.95)	10.3	N/A	N/A
Riparian	0.52 (0.30)	0.22	0.44 (0.40)	0.13	0.29 (0.79)	1.3	1.49 (0.98)	4.4
Edge	−0.13 (0.63)	−0.02	−0.32 (0.65)	−0.06	1.22 (1.41)	3.4	−1.24 (1.45)	0.29
Contrast-weighted edge density	0.06 (0.04)	0.21	−0.05 (0.05)	−0.17	0.03 (0.09)	1.0	−0.11 (0.10)	0.90
Road	0.12 (0.38)	0.04	0.04 (0.05)	0.01	0.88 (0.90)	2.4	1.07 (1.06)	2.9
Hayfield	N/A	N/A	0.03 (0.39)	0.01	N/A	N/A	0.52 (0.82)	1.7
Contagion	0.003 (0.006)	0.07	0.006 (0.006)	0.11	−0.02 (0.01)	0.98	−0.02 (0.01)	0.98
Distance to road	0.0001 (0.0)	1.00	−0.00002 (0.0)	−0.04	0.000 (0.0)	1.0	0.000 (0.0)	1.0
Distance to landfill	−0.0002 (0.0)	−1.90	N/A	N/A	0.000 (0.0)	1.0	N/A	N/A
Distance to city	0.0001 (0.0)	0.89	0.00002 (0.0)	0.09	0.000 (0.0)	1.0	0.000 (0.0)	1.0

TABLE 4. Multinomial logistic regression models, with ΔAIC, Akaike weight, degrees of freedom, and Pearson goodness-of-fit coefficient, used to test for the effects of raven abundance and behavior on the fate of sage-grouse nests and broods. Fate was classified into one of three states: failure to hatch, failure to survive brood rearing, or success of at least one chick to independence.

Model	ΔAIC	Akaike weight	df	Pearson	P
Study site, sagebrush cover, last observed raven occupancy[a]	0.00	0.95	30	33.09	0.32
Study site, sagebrush cover, last observed raven behavior	6.32	0.04	38	35.95	0.57
Study site, sagebrush cover, last observed raven density	8.83	0.01	40	46.09	0.23
Study site, sagebrush cover, average observed raven behavior	32.05	0.00	62	63.59	0.42
Study site, sagebrush cover, average observed raven occupancy	38.24	0.00	70	82.13	0.15
Study site, sagebrush cover, average observed raven density	47.26	0.00	76	94.56	0.07
Study site, sagebrush cover, predicted raven occupancy	51.55	0.00	98	93.11	0.62
Study site, sagebrush cover, distance to city	84.62	0.00	128	162.77	0.02
Study site, sagebrush cover, predicted raven density	101.87	0.00	158	171.43	0.22

[a] AIC = 69.32.

raven activity. In contrast, we predicted low occupancy and high density around the landfill in the town of Pinedale (Fig. 2), suggesting infrequent visits by large groups of ravens to this area.

We categorized each sampling point by its land cover as well as its distance to cities, roads, and landfills. This resulted in the models' incorporating dual measures of city and roads. These extra variables aided prediction but may confuse interpretation of a variable's relative importance. Ravens were consistently present and abundant in cities and consistently present along roads (Table 3). Including these direct associations in our models reduced the relative importance of the somewhat redundant variables measuring distances to cities and roads (Table 3).

RAVEN MOVEMENT INTO UNDEVELOPED SAGEBRUSH

In the Pinedale study area, although the raven's density was highest in cities, it was predicted to decrease sharply at distances beyond approximately 3 km from city boundaries, suggesting little movement by ravens from cities to adjacent areas of infrequent human activity (i.e., sagebrush). When ravens did move into undeveloped sagebrush, locations of raven nests and incidental sightings of ravens foraging implicated anthropogenic infrastructure in aiding their movement. In 2007, we recorded 34 incidental sightings of foraging by ravens throughout the Pinedale study area; of these, 18 were along roads, 17 in undeveloped sagebrush, and two in agricultural fields. When foraging near roads, ravens were often observed flying along the road network, suggesting they used roads in locating prey. Throughout the Pinedale study area, ravens also took advantage of anthropogenic infrastructure for nesting, especially in areas of undeveloped sagebrush. Between the two study seasons, we located 27 raven nests, 16 of which were on artificial structures including condensation tanks, windmills, solar panels, and telephone poles; the remaining 11 nests were in trees.

CORRELATION BETWEEN RAVEN ACTIVITY AND SAGE-GROUSE REPRODUCTIVE SUCCESS

During our study, predation on sage-grouse nests and broods was frequent; 51% of sage-grouse nests failed, of which 83% were lost to predation. The predators were not identified and certainly included a diversity of mammals and raptors as well as ravens. Forty-seven percent of sage-grouse broods failed, all presumably because of predation. An average of 1.34 and 1.56 juveniles fledged per sage-grouse hen in the Pinedale and Jackson study areas, respectively.

Ravens appeared to respond to the presence of sage-grouse nests and broods. Observed raven density (0.01 ± 0.002 ha^{-1}, n = 84) was significantly greater at locations near sage-grouse nests and broods than predicted (Figs. 2, 3) at these same locations (0.006 ± 0.001 ha^{-1}, $t_{83} = 2.89$, $P = 0.01$). This observed density was also marginally greater than the density we observed at other places in contiguous sagebrush where grouse were not known to be nesting (0.007 ± 0.002 ha^{-1}; $F_{1,156} = 2.1$; $P = 0.15$). Observed raven occupancy (0.29 ± 0.04) around grouse nests and broods was marginally greater than observed occupancy at locations within contiguous sagebrush where grouse were not known to be nesting (0.20 ± 0.04; $F_{1,156} = 3.4$, $P = 0.07$). Because of the bias in absolute values of modeled occupancy we did not formally compare observed raven occupancy around grouse to occupancy predicted for the same locations (it was higher).

The presence and behavior of ravens were associated with sage-grouse nest and brood success. Raven occupancy and, to a lesser extent, behavior observed near sage-grouse nests and broods were more highly correlated to sage-grouse fate than was raven density (Table 4). Raven occupancy observed on the "last" surveys was more highly correlated with the fate of sage-grouse nests and broods than was raven occupancy averaged over all surveys over the entire reproductive season, which, in turn, was more highly correlated with sage-grouse fate than were values of raven occupancy as predicted by our model of raven distribution.

There were no significant differences in the mean values of predicted or observed (averaged or "last") raven density, occupancy, or behavior among any of the three categories of sage-grouse nest failure, brood failure, or survival. However, for "last" surveys, mean raven density, mean occupancy, and behavior scores were slightly greater at failed sage-grouse nests and broods ($n = 62$, density = 0.01 ± 0.004, occupancy = 0.43 ± 0.11, behavior = 0.82 ± 0.27) than at those that survived the season ($n = 24$, density = 0.007 ± 0.004, occupancy = 0.26 ± 0.12, behavior = 0.25 ± 0.11). In addition, we observed more foraging behavior by ravens near failed than near successful sage-grouse nests and broods. A plurality (44%) of observations of raven behavior near failed sage-grouse nests and broods received a score of 3 (strongly indicating foraging), 38% received a score of 2, and only 18% received a score of 1 (slightly indicating foraging). In contrast, the majority (80%) of observations of raven behavior near successful sage-grouse nests and broods received a score of 1, 20% received a score of 2, and none received a score of 3. Furthermore, although adding distance to nearest city as a factor in our regression model of sage-grouse fate did not improve model fit (Table 4), failed sage-grouse nests and broods tended to be closer to cities (5339 ± 1236 m) than did successful nests and broods (37 608 ± 20 986 m).

DISCUSSION

MODELING THE RISK OF PREDATION

Recent increases in raven populations have been consistently linked with human activity (Restani et al. 2001, Marzluff and Neatherlin 2006, Kristan and Boarman 2007), which provides anthropogenic food, water, and nest sites (Boarman et al. 2006), increasing local raven density, productivity, and survival (Webb et al. 2004, Marzluff and Neatherlin 2006). Our results agree with these findings, as we estimated the raven's highest density and relative occupancy rate both to occur near cities, the land cover in our study area with the most frequent human activity. In our study areas, towns provide ravens with supplemental food, water, and nest sites, which may have led to locally increased density 3 km into undeveloped adjacent lands.

In oil fields, the raven's occupancy was high but its density was low, which is consistent with presence of territorial breeding pairs. The encroachment of oil fields upon undeveloped sagebrush appears to facilitate breeding ravens moving into the sagebrush, just as campgrounds facilitate the American Crow (*Corvus brachyrhynchos*) moving into forests it otherwise rarely visits (Neatherlin and Marzluff 2004). Incidental sightings of raven foraging during our study suggest ravens take advantage of the road networks associated with oil fields and undeveloped sagebrush, as found elsewhere (Knight and Kawashima 1993, Knight et al. 1995). Furthermore, artificial nesting substrates (i.e., telephone poles, windmills, buildings, and condensate-storage tanks), both within cities and in undeveloped sagebrush immediately surrounding cities and natural gas fields, may allow new breeding pairs to colonize sagebrush they rarely used previously, which may increase nest predation on sage-grouse (Manzer and Hannon 2005).

By modeling both raven density and occupancy, we were able to highlight areas with high occupancy but low density, like oil fields, which provided ravens with new nesting sites for pairs but not foraging sites for groups. We also were able to identify areas with high density and low occupancy of ravens, such as the area immediately surrounding the Pinedale landfill. This pattern suggested infrequent visits by large foraging groups of ravens, likely consisting mainly of juveniles and subadults, to the landfill, a prime location for anthropogenic food subsidies (Marzluff et al. 1996, Kristan and Boarman 2003) but not necessarily new nest sites. Although the Pinedale landfill attracted large numbers of ravens, their occupancy of this location was notably inconsistent, so overflow of ravens from the landfill into the surrounding sagebrush was minimal. No comparable locations with high raven density and low occupancy were predicted in the Jackson study area, not surprising because this study site contained no landfills or other similar areas of concentrated anthropogenic food subsidies.

Increased occupancy of areas with minimal human presence (like oil fields) by pairs of ravens rather than increased density associated with flocks of ravens in human-dominated areas like cities, towns, and landfills may affect locally breeding populations of sage-grouse negatively. Raven density was greater near sage-grouse nests and broods than at control locations, but it was still relatively low, which is consistent with foraging by territorial nesting pairs of ravens, not large congregations of nonbreeding individuals. The sage-grouse's patterns of incubation may have evolved to avoid visually cued diurnal predators such as ravens and other corvids (Angelstam 1984, Erikstad 1986; Coates and Delehanty, in press). Incubating sage-grouse hens typically leave their nests briefly to forage only at twilight; longer recesses that expose the nest in bright light may increase nest depredation by ravens (Coates and Delehanty 2008). Even in spite of such adaptations, increased occurrence of ravens in sagebrush can reduce the sage-grouse's nesting success. Our model of the grouse's reproductive fate suggested raven occupancy, rather than density, is important to the grouse's nesting success.

Local attraction of ravens to sage-grouse nesting habitat may be facilitated by the reduction, isolation, and fragmentation of native shrublands that is known to increase exposure of nests to potential predators (Lyon and Anderson 2003; Coates and Delehanty, in press) and ultimately lower reproduction (Vander Haegen et al. 2002, Aldridge and Boyce 2007). As more suitable sage-grouse habitat is converted to oil fields, agriculture, and other exurban development, sage-grouse nesting and brood rearing become increasingly spatially restricted. Where sage-grouse nests are more concentrated they are more easily detected, and increased nest densities could result in increased nest depredation (Holloran and Anderson 2005), especially when nests are clumped (Marzluff and Balda 1992).

Our model of sage-grouse fate implicated raven occupancy near sage-grouse nests and broods near the time of nest success or failure as the best predictor of the grouse's reproductive success, not raven density near nests or broods. This pattern suggests studies that measure only predator density (e.g., Manzer and Hannon 2005) near areas of sage-grouse nesting and brood rearing may not adequately quantify the potential effects of raven predation on the grouse's reproductive success. We suggest that the risk of predation of a particular sage-grouse nest or brood can be gauged by observing activity of predators nearby; a sudden increase in predator occupancy can be interpreted as an increase in probability of the depredation of the sage-grouse nest or brood. We also suggest that human-mediated increased occupancy of undeveloped sagebrush by ravens may affect sage-grouse populations negatively. This factor may be part of the reason that neither of the sage-grouse populations we studied reached the recommended level of productivity of 2.25 juveniles per hen surviving through the reproductive season to ensure long-term persistence (Connelly and Braun 1997).

There are several sources of potential bias in our methodology and analysis. First, we assumed all failures of sage-grouse broods to be due to predation, but environmental factors (i.e., exposure, starvation) could also contribute to brood mortality. Second, we could not determine how often ravens actually preyed upon sage-grouse eggs and chicks. Our models suggest the potential for raven predation is high, but it does not prove a causal link between raven occurrence and sage-grouse reproductive failure. Third, we likely underestimated successful brood rearing and underestimated absolute predation on eggs and chicks. We assumed all observations of brood failure were complete. Not accounting for the fact that some broods may have partially succeeded has the effect of overestimating the effect of predation on sage-grouse reproductive success. Therefore, our models estimate the maximum potential predation by ravens on sage-grouse broods. This bias may be balanced in part because we defined success as the hatching or rearing of at least one egg or chick. Therefore some sage-grouse nests or broods we categorized as successful may have been reduced by partial predation below their full potential. However, these potential biases may be negligible because monitoring studies have shown only a small proportion of instances of predation by ravens on sage-grouse nests are partial (Coates et al. 2008).

Our model of raven distribution overestimated absolute raven occupancy (but not density). This overestimation is most likely due to limited observations; we conducted only two surveys. Because raven abundance in contiguous sagebrush is lower than in other land covers, it is likely that ravens went undetected at some survey locations. Increasing the number of surveys at each location would decrease the incidence of false negatives and improve the absolute accuracy of resulting models. Although our model may not predict absolute rates of raven occupancy accurately, it clearly captures important relative differences in occupancy, such as those associated with differences in land cover.

MANAGING SUBSIDIZED NATIVE PREDATORS

Restoring viable populations of the Greater Sage-Grouse in increasingly human-dominated western landscapes will require conserving and restoring extensive tracts of sagebrush and, at least in the short-term, managing the factors that limit sage-grouse survival and reproduction within these lands. Humans (through recreational hunting) and a diversity of native species, including the Common Raven, prey upon grouse, limiting their survival and reproduction. Each of these factors—habitat availability and condition, predator populations, and direct harvest by humans—must be considered if the grouse is to be managed effectively. Our results can provide some guidance to managers seeking to minimize the potential and actual influence of expanding raven populations on the sage-grouse. The two species have coexisted for approximately two million years (Omland et al. 2000). Our results suggest that where myriad human factors reduce both grouse and their habitat, while simultaneously increasing generalist predators, this ancient coexistence may become unbalanced.

Managers attempting to reduce the potential effects of ravens on grouse reproduction should first reduce occupancy of important sage-grouse nesting habitat by ravens. This can be at least partially accomplished by education, regulation, and limiting anthropogenic subsidies far from cities and landfills. Anthropogenic nest sites should be managed to reduce raven use through retrofitting or the installation of deterrent fixtures (i.e., strips, netting, screening) on old structures, covering well heads, modifying future engineering of structures to avoid providing suitable nesting platforms, egg removal, nest destruction, and harassment of nesting pairs (Liebezeit and George 2000). Education about the effects of feeding wildlife should be widespread; this is especially important at tourist locations, such as the Jackson study area, where large groups of people congregate, many of whom are naïve to the effects their behavior can have on wildlife. Furthermore, corporations operating within sensitive sage-grouse nesting areas should consider policies of hiring, firing, and fining that strongly discourage their employees from purposefully or inadvertently providing supplemental food to ravens (USFWS 2003). Once subsidies are limited in habitats where sensitive grouse breed, additional measures of either direct removal of ravens or aversive conditioning of territorial ravens may be needed. Because direct removal of ravens may not be sufficient to benefit sage-grouse populations in the long term (new territorial pairs need simply colonize vacated areas), there may be additional benefits derived from discouraging predation through conditioned taste aversion while allowing the behaviorally modified predator to remain on the landscape (Avery et al. 1995). Modifying the raven's behavior to reduce its abundance near sage-grouse nests (Coates et al. 2007) or preference for sage-grouse eggs would result in decreased nest predation while leaving the resident pair of ravens to discourage intrusion by nonresident ravens by their territoriality.

A second strategy to lower the raven's effects on sage-grouse is to reduce the raven-carrying capacity of areas where the raven's density is high. This strategy is of secondary importance because raven density is low where sage-grouse nest. However, ravens may move from areas of high density as new subsidies are provided near sage-grouse or as resident territorial pairs die. Limiting the amount and availability of garbage to ravens in cities, towns, and landfills therefore could be an effective long-term strategy. In addition, access to sewage ponds and road kills should be reduced, perhaps by installing covers or wires (as deterrents) over dumpsters, incinerating garbage, removing animal carcasses from roads and burying them, and enforcing regulations concerning waste disposal, as they relate to wildlife (USFWS 2003). Once subsidies are limited, raven populations may disperse and decline on their own. Reducing the availability of resource subsidies may succeed in controlling raven abundance only when similar efforts are widespread in a region (Boarman 2003, Boarman et al. 2006).

Future management would also be aided by monitoring and additional research. The actual amount of predation by ravens on sage-grouse may vary by site and needs to be quantified. In our study, we assumed that observations of ravens reflected their habitat use; this assumption should be confirmed through utilization-distribution analysis of radio-equipped individuals (Marzluff et al. 2004). Although we measured raven abundance and occupancy in areas with both frequent (i.e., cities) and infrequent (i.e., sagebrush) human activity, it would be useful to compare raven density and presence in areas with towns (as was done in this study) to those in areas without towns or other locations with concentrated human activity. In addition, we did not investigate raven movement from cities into sagebrush in detail. This could be done through radio-tracking of ravens to pinpoint individuals most likely responsible for depredation of sage-grouse nests and broods. As management is implemented, the response of raven populations and sage-grouse nesting success should be monitored. Failure to do so and adapt management appropriately will help neither sage-grouse nor raven.

ACKNOWLEDGMENTS

This research was conducted through the academic and financial support of Craighead Beringia South and the College of Forest Resources, University of Washington. Additional financial support was provided by the Upper Green River Basin Local Sage-Grouse Working Group, the Wyoming Animal Damage Management Board, and the Tom Thorne Sage-Grouse Conservation Fund. Wyoming Wildlife Consultants LLC and Grand Teton National Park also provided significant in-kind support for this work. We would particularly like to recognize several individuals who promoted and encouraged our research, including J. Dahlke, M. Holloran, B. Barrett, T. Cleveland, D. Craighead, H. Quigley, T. Christiansen, G. Shedd, M. Szczepinski, S. Wolff, L. Dennis, J. Michalak, K. Blair, C. Chan, M. Noble, T. Haynam, V. Slabe, R. Crandall, A. Courtemanch, B. Oleson, K. Landau, S. Craighead, and M. Ruehmann. H. Quigley, J. Lawler, M. Holloran, D. Craighead, and the reviewing editors of the *Condor* provided perceptive comments on the manuscript.

LITERATURE CITED

ALDRIDGE, C. L., AND M. S. BOYCE. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered Greater Sage-Grouse. Ecological Applications 17:508–526.

ALDRIDGE, C. L., S. E. NIELSEN, H. L. BEYER, M. S. BOYCE, J. W. CONNELLY, S. T. KNICK, AND M. A. SCHROEDER. 2008. Range-wide patterns of Greater Sage-Grouse persistence. Diversity and Distributions 14:983–994.

ANGELSTAM, P. 1984. Sexual and seasonal differences in mortality of Black Grouse *Tetrao tetrix* in boreal Sweden. Ornis Scandinavica 15:123–124.

AVERY, M. L., M. A. PAVELKA, D. L. BERGMAN, D. G. DECKER, C. E. KNITTLE, AND G. M. LINZ. 1995. Aversive conditioning to reduce raven predation on California Least Tern eggs. Colonial Waterbirds 18:131–138.

BERGER, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology 18:320–329.

BOARMAN, W. I. 2003. Managing a subsidized predator population: reducing Common Raven predation on desert tortoises. Environmental Management 32:205–217.

BOARMAN, W. I., AND B. HEINRICH. 1999. Common Raven (*Corvus corax*), no. 476. *In* A. Poole and F. Gill [EDS.], The birds of North America. Birds of North America, Inc., Philadelphia.

BOARMAN, W. I., M. A. PATTEN, R. J. CAMP, AND S. J. COLLIS. 2006. Ecology of a population of subsidized predators: Common Ravens in the central Mojave Desert, California. Journal of Arid Environments 67: 248–261.

BRAUN, C.E. 1998. Sage Grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–156.

Bureau of Land Management. 2000. Record of decision and final EIS for the Pinedale Anticline oil and gas exploration and development project, Sublette County, WY. U.S. Department of the Interior, Bureau of Land Management, Pinedale Field Office, Pinedale, WY.

CLARK, T. W., M. B. RUTHERFORD, AND D. CASEY (EDS.). 2005. Coexisting with large carnivores. Island Press, Washington, DC.

COATES, P. S., J. W. CONNELLY, AND D. J. DELEHANTY. 2008. Predators of Greater Sage-Grouse nests identified by video monitoring. Journal of Field Ornithology 79:421–428.

COATES, P. S., AND D. J. DELEHANTY. 2008. Effects of environmental factors on incubation patterns of Greater Sage-Grouse. Condor 110:627–638.

COATES, P. S., AND D. J. DELEHANTY. In press. Nest predation of Greater Sage-Grouse in relation to microhabitat factors and predators. Journal of Wildlife Management.

COATES, P. S., J. O. SPENCER JR., AND D. J. DELEHANTY. 2007. Efficacy of CPTH-treated egg baits for removing ravens. Human–Wildlife Conflicts 1:224–234.

CONNELLY, J. W., AND C. E. BRAUN. 1997. Long-term changes in Sage Grouse *Centrocercus urophasianus* populations in western North America. Wildlife Biology 3/4: 123–128.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage Sage Grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Environmental Systems Research Institute. 2008. ArcGIS 9.3. Environmental Systems Research Institute, Redlands, CA.

Erikstad, K. E. 1986. Relationship between weather, body condition, and incubation rhythm in Willow Grouse. Cinclus 9:7–12.

Handcock, M. S. [online]. 2004. Ruf: An R package for the estimation of the resource utilization function. <http://csde.washington.edu/~handcock/ruf> (1 October 2006).

Hansen, A. J., R. L. Knight, J. M. Marzluff, S. Powell, K. Brown, P. Hernandez, and K. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, research needs. Ecological Applications 15:1893–1905.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of Greater Sage-Grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

Jiménez, J. E., and M. R. Conover. 2001. Ecological approaches to reduce predation on ground-nesting gamebirds and their nests. Wildlife Society Bulletin 29:62–69.

Knight, R. L., and J. Y. Kawashima. 1993. Responses of raven and Red-tailed Hawk populations to linear right-of-ways. Journal of Wildlife Management 57:266–271.

Knight, R. L., H. A. L. Knight, and R. J. Camp. 1995. Common Ravens and number and type of linear rights-of-way. Biological Conservation 74:65–67.

Kristan, W. B. III, and W. I. Boarman. 2003. Spatial pattern of risk of Common Raven predation on desert tortoises. Ecology 84:2432–2442.

Kristan, W. B. III, and W. I. Boarman. 2007. Effects of anthropogenic developments on Common Raven nesting biology in the west Mojave Desert. Ecological Applications 17:1703–1713.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Liebezeit, J. R., and T. L George. 2000. A summary of predation by corvids on threatened and endangered species in California and management recommendations to reduce corvid predation. Humboldt State University, Arcata, CA.

Luginbuhl, J. M., J. M. Marzluff, J. E. Bradley, M. G. Raphael, and D. E. Varland. 2001. Corvid survey techniques and the relationship between corvid relative abundance and nest predation. Journal of Field Ornithology 72:556–572.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on Sage Grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, San Diego.

Manzer, D. L., and S. J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. Journal of Wildlife Management 69:110–123.

Marzluff, J. M., and R. P. Balda. 1992. The Pinyon Jay: behavioral ecology of a colonial and cooperative corvid. Academic Press, San Diego.

Marzluff, J. M., B. Heinrich, and C. S. Marzluff. 1996. Raven roosts are mobile information centres. Animal Behaviour 51: 89–103.

Marzluff, J. M., and E. Neatherlin. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. Biological Conservation 130: 301–314.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. A. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. Ecology 85: 1411–1427.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene [online]. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst. <http://www.umass.edu/landeco/research/fragstats/fragstats.html> (1 September 2007).

Neatherlin, E. A., and J. M. Marzluff. 2004. Campgrounds enable American Crows to colonize remote native forests. Journal of Wildlife Management 68:708–718.

Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2002. Modeling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. Ursus 13: 45–56.

Omland, K. E., C. L. Tarr, W. I. Boarman, J. M. Marzluff, and R. C. Fleischer. 2000. Cryptic genetic variation and paraphyly in ravens. Proceedings of the Royal Society of London B 267: 2475–2482.

Quammen, D. 2004. Monster of God: the man-eating predator in the jungles of history and the mind. Norton, New York.

R Development Core Team. 2008. R for Windows 2.8. Release 1. R Foundation for Statistical Computing, Vienna, Austria.

Restani, M., J. M. Marzluff, and R. E. Yates. 2001. Effects of anthropogenic food sources on movements, survivorship, and sociality of Common Ravens in the Arctic. Condor 103: 399–404.

Robinson, L., J. P. Newell, and J. M. Marzluff. 2005. Twenty-five years of sprawl in the Seattle region: growth management responses and implications for conservation. Landscape and Urban Planning 71:51–72.

Rosenstock, S. S., D. R. Anderson, K. M. Giesen, T. Leukering, and M. F. Carter. 2002. Landbird counting techniques: current practices and an alternative. Auk 119:46–53.

Sargeant, A. B., M. A. Sovada, and R. J. Greenwood. 1998. Interpreting evidence of depredation of duck nests in the prairie potholes region. U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND.

Schroeder, M. A., and R. K. Baydack. 2001. Predation and the management of prairie grouse. Wildlife Society Bulletin 29:24–32.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage Grouse (*Centrocercus urophasianus*), no. 425. *In* A. Poole and F. Gill [eds.], The birds of North America. Birds of North American, Inc., Philadelphia.

Sinclair, A. R. E., R. P. Pech, C. R. Dickman, D. Hik, P. Mahon, and A. E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. Conservation Biology 12:546–575.

SPSS. 2007. SPSS for Windows, Release 11.1. SPSS Inc., Chicago.

Theobald, D. M. 2000. Fragmentation by inholdings and exurban development, p. 155–174. *In* R. L. Knight, F. W. Smith, S. W. Buskirk, W. H. Romme, and W. L. Baker [eds.], Fragmentation in the central Rocky Mountains. University Press of Colorado, Boulder, CO.

Thomas, L., J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, J. R. B. Bishop, and T. A. Marques [online]. 2006. Distance 5.0. Release 1. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. <http://www.ruwpa.st-and.ac.uk/distance> (1 September 2007).

THOMSON, J. L., T. S. SCHAUB, N. WOLFF CULVER, AND P. C. AENGST. 2005. Wildlife at a crossroads: energy development in western Wyoming. Effects of roads on habitat in the upper Green River valley. The Wilderness Society, Washington, DC.

UNITED STATES CENSUS BUREAU. 2009. <http://www.censusgov.com> (1 May 2009).

UNITED STATES FISH AND WILDLIFE SERVICE. 2003. Human influences on predators of nesting birds on the North Slope of Alaska. Proceedings of a public workshop held 17–18 April 2003 in Anchorage, AK. U.S. Fish and Wildlife Service, Fairbanks, AK.

VANDER HAEGEN, W. M., M. A. SCHROEDER, AND R. M. DEGRAAF. 2002. Predation on real and artificial nests in shrubsteppe landscapes fragmented by agriculture. Condor 104:496–506.

WALKER, B. L., K. E. DOHERTY, AND D. E. NAUGLE. 2006. Spotlight counts: a new method for assessing chick survival in Greater Sage-Grouse. University of Montana, Missoula, MT.

WALLESTAD, R. O., AND D. B. PYRAH. 1974. Movement and nesting of Sage Grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

WEBB, W. C., W. I. BOARMAN, AND J. T. ROTENBERRY. 2004. Common Raven juvenile survival in a human-augmented landscape. Condor 106:517–528.

WEBB, W. C., W. I. BOARMAN, AND J. T. ROTENBERRY. 2007. Movements of juvenile Common Ravens in an arid landscape. Journal of Wildlife Management 73:72–81.

WELLER, C., J. THOMSON, P. MORTON, AND G. APLET. 2002. Fragmenting our lands: the ecological footprint from oil and gas development. A spatial analysis of a Wyoming gas field. The Wilderness Society, Washington, DC.

WHITE, G. C. 2008. Mark and recapture parameter estimation 5.0 release 1. Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO.

APPENDIX 1. SELECTION OF DETECTABILITY MODEL

We considered the following models when fitting detectability probability functions to our observed raven detections and to produce estimates of raven density in each land-cover type: null (detectability is independent of all covariates considered), study site, study year, study site and year, land cover (sagebrush, riparian, oil, edge, city, road, hayfield), and city/noncity categorization. The null model that detectability is independent of covariates (study site, study year, land cover, city/non-city) had the lowest AIC value of all models considered (Table A1), indicating detectability did not vary among the land covers of interest in our study. Because detectability-corrected density estimates (Table A2) did not vary greatly from observed estimates and were strongly correlated with unadjusted density estimates ($r = 0.97$, $n = 4$, $P = 0.03$), we used observed estimates in our analyses. Observed raven densities within towns were not strongly correlated with human populations of those towns ($r = 0.23$, $n = 6$, $P = 0.33$).

TABLE A1. Values of ΔAIC for each detectability model.

Detectability model	Covariates considered	ΔAIC
Null model half-normal cosine[a]	none	0.00
Land cover half-normal cosine	land cover	10.22
City/noncity half-normal cosine	city	14.92
Site year half-normal cosine	study site and year	25.86
Site half-normal cosine	study site	27.98
Year half-normal cosine	study year	33.71

[a] AIC = 2667.42.

TABLE A2. Detectability-corrected density for each land cover according to the null model that detectability is independent of covariates.

Land cover	Detectability-corrected density (ravens ha^{-1})
Sagebrush	0.037 (0.013)
Riparian	N/A
Oil field	0.007 (0.002)
Edge	N/A
City	0.17 (0.035)
Road	N/A
Hayfield	0.064 (0.027)

Environmental Management (2017) 59:189–203
DOI 10.1007/s00267-016-0789-9

Effectiveness of Wyoming's Sage-Grouse Core Areas: Influences on Energy Development and Male Lek Attendance

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Received: 12 November 2015 / Accepted: 22 October 2016 / Published online: 8 November 2016

Abstract Greater sage-grouse (*Centrocercus urophasianus*) populations have declined across their range due to human-assisted factors driving large-scale habitat change. In response, the state of Wyoming implemented the Sage-grouse Executive Order protection policy in 2008 as a voluntary regulatory mechanism to minimize anthropogenic disturbance within defined sage-grouse core population areas. Our objectives were to evaluate areas designated as Sage-grouse Executive Order Core Areas on: (1) oil and gas well pad development, and (2) peak male lek attendance in core and non-core sage-grouse populations. We conducted our evaluations at statewide and Western Association of Fish and Wildlife Agencies management zone (MZ I and MZ II) scales. We used Analysis of Covariance modeling to evaluate change in well pad development from 1986–2014 and peak male lek attendance from 958 leks with consistent lek counts within increasing (1996–2006) and decreasing (2006–2013) timeframes for Core and non-core sage-grouse populations. Oil and gas well pad development was restricted in Core Areas. Trends in peak male sage-grouse lek attendance were greater in Core Areas compared to non-core areas at the statewide scale and in MZ II, but not in MZ I, during population increase. Trends in peak male lek attendance did not differ statistically between Core and non-core population areas statewide, in MZ I, or MZ II during population decrease. Our results provide support for the effectiveness of Core Areas in maintaining sage-grouse populations in Wyoming, but also indicate the need for increased conservation actions to improve sage-grouse population response in MZ.

Keywords *Centrocercus urophasianus* · Greater sage-grouse · Core area · Impact assessment · Natural resource policy · Population monitoring · Wyoming Sage-grouse executive order

Introduction

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) have declined from historical numbers across the western United States and Canada (Garton et al. 2011). Declines include an overall annual rate of 2 % from 1965–2003 (Connelly et al. 2004) and a 56 % decline in males counted on 10,060 leks (i.e., spring breeding grounds) in 11 western states from 2007 (109,990) to 2013 (48,641; Garton et al. 2015). However, sage-grouse populations are cyclic (Fedy and Doherty 2011; Fedy and Aldridge 2011) and counts indicate range-wide increases in 2014 and 2015 (Nielson et al. 2015). Coincidentally, the distribution of sage-grouse has contracted approximately half from historical range (Schroeder et al. 2004) primarily due to degradation and loss of sagebrush (*Artemisia* spp.) habitat (Connelly et al. 2004; U. S. Fish and Wildlife Service 2010). Infrastructure and activities associated with natural resource extraction, which are most prominent in the eastern portion of sage-grouse range, adversely impact sage-grouse (Braun et al. 2002; Holloran and Anderson 2005; Walker et al. 2007; Harju et al. 2010; Holloran et al. 2010;

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USFWS 2010; LeBeau et al. 2014). Energy development has been shown to specifically impact male sage-grouse lek attendance (Walker et al. 2007; Harju et al. 2010; Gregory and Beck 2014), lek persistence (Walker et al. 2007; Hess and Beck 2012), recruitment of yearling male and female grouse to leks (Holloran et al. 2010), nest initiation and site selection (Lyon and Anderson 2003), nest survival (Dzialak et al. 2011; LeBeau et al. 2014), chick survival (Aldridge and Boyce 2007), brood survival (LeBeau et al. 2014; Kirol et al. 2015a), summer survival of adult females (Dinkins et al. 2014a), early brood-rearing habitat selection (Dinkins et al. 2014b), adult female summer habitat selection (Fedy et al. 2014; Kirol et al. 2015a), and adult female winter habitat selection (Doherty et al. 2008; Carpenter et al. 2010; Dzialak et al. 2013; Smith et al. 2014; Holloran et al. 2015).

The cumulative effects of energy-related impacts in the eastern range, and other impacts such as invasive plant species and altered fire regimes in the western portion of sage-grouse range, have led to consideration of the sage-grouse for threatened or endangered species listing under the Endangered Species Act of 1973 by the United States Fish and Wildlife Service ([USFWS] 2010, 2015). The March 2010 USFWS listing decision designated the greater sage-grouse as a candidate species, warranted for listing, but precluded from listing at that time because other species were under severe threat of extinction (USFWS 2010—sage-grouse were subsequently found unwarranted for listing [USFWS 2015]). In response to anticipated threatened or endangered species listing, the State of Wyoming developed a strategy through an executive order issued by the Governor of Wyoming to conserve sage-grouse. The Wyoming Governor's Executive Order for Sage-Grouse (SGEO) was first implemented in late 2008 and provides a voluntary regulatory mechanism designed to limit and/or minimize anthropogenic disturbance within defined boundaries identified as sage-grouse population areas (State of Wyoming 2008; Doherty et al. 2010, 2011[Fig. 1]). A major component of this mechanism is the establishment of

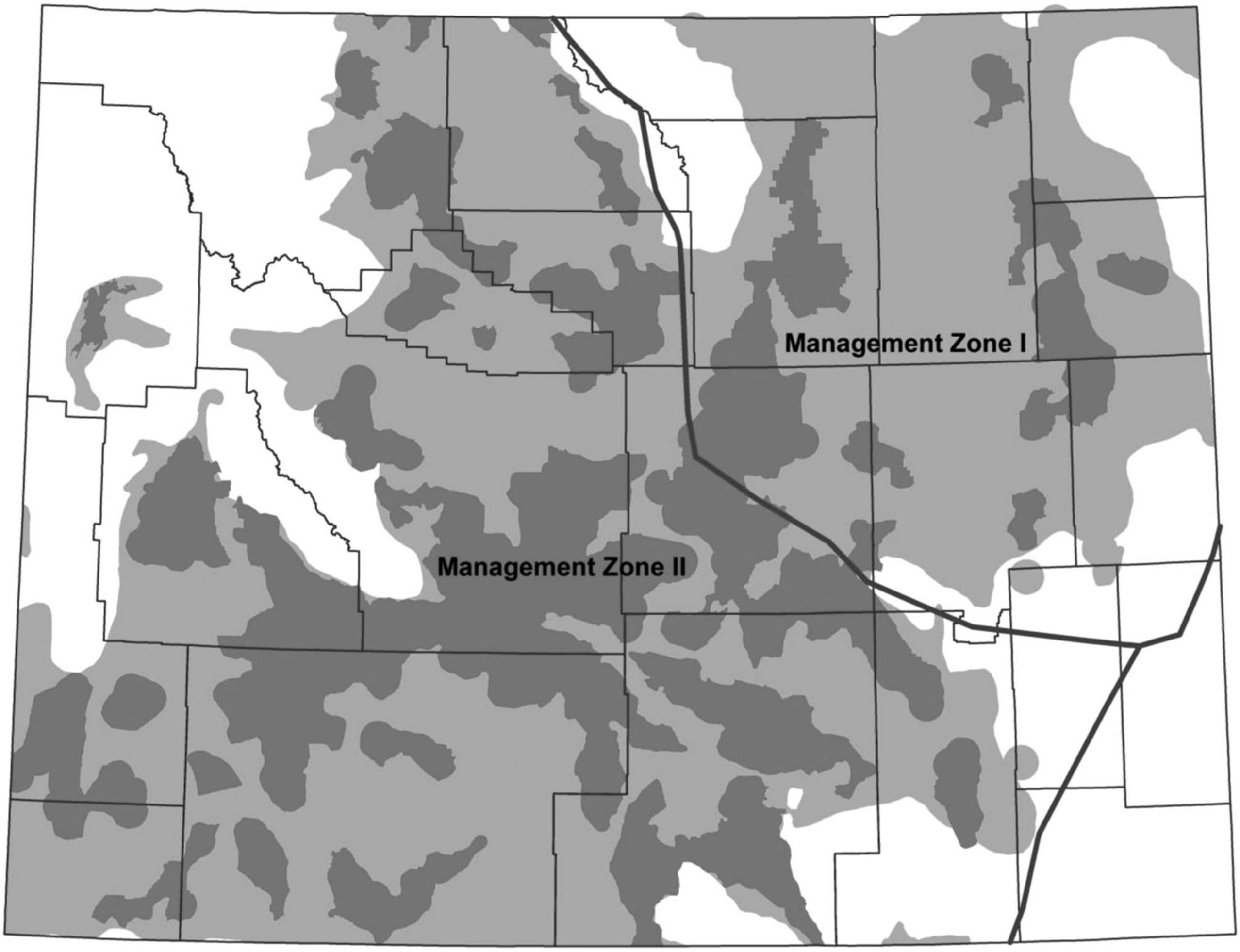


Fig. 1 Location map of 31 core population areas (*dark gray-shaded* areas; *light gray-shaded* areas represent sage-grouse range where non-core sage-grouse populations occur) within current sage-grouse range and Western association of Fish and Wildlife agencies management zones I and II in Wyoming, USA

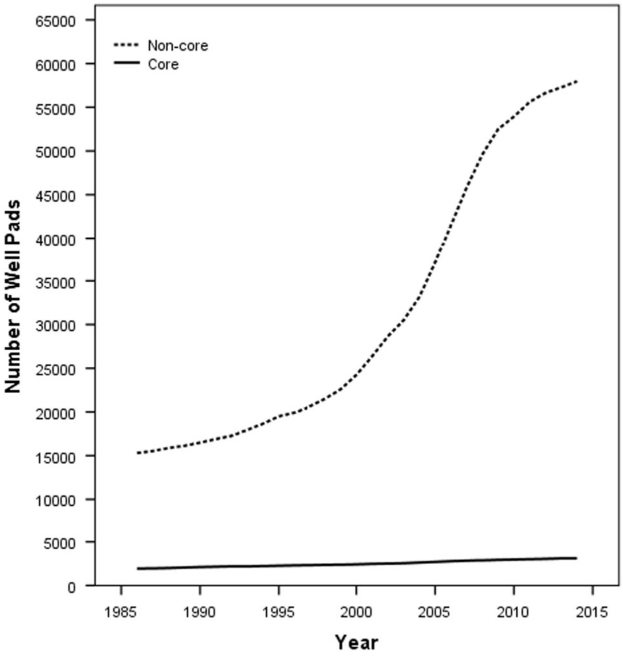


Fig. 2 Number of well pads in core and non-core areas from 1986–2014, Wyoming, USA

defined conservation areas for sage-grouse termed Core Area.

The SGEO, as a state-driven regulatory mechanism, was designed to conserve and maintain sage-grouse populations and habitat through a detailed process of planning and managing energy development and other surface disturbing activities within the boundaries of sage-grouse Core Areas. The goal was to protect two-thirds of the sage-grouse population within the state as identified by peak male lek attendance (B. Budd, Wyoming Sage-Grouse Implementation Team [SGIT], personal communication). This effort assimilated the highest sage-grouse density areas identified by Doherty et al. (2010) as they were identified as the most productive habitats for sage-grouse in Wyoming. In addition, the mapping of Core Areas considered current and potential energy development and encapsulated areas historically low in production (Gamo 2016; Fig. 2). The end result included approximately 82 % of Wyoming's total male sage-grouse population as measured by peak male lek attendance (unpublished data, Wyoming Game and Fish Department [WGFD]). By design, the SGEO process minimizes surface disturbance size and densities at a landscape scale within Core Area boundaries. Policymakers utilized research evaluating the impacts of energy extraction on sage-grouse to develop the specifics of the SGEO. Three parameters were adopted forming the basis for conservation measures within the SGEO: 1) disturbances should not occur within 1 km (0.60 mi) of occupied leks, 2) disturbance density should not exceed 1 per 2.6 km^2 (640 ac) within the analysis area (e.g., Holloran 2005; Doherty 2008), and 3) total disturbance acreage should not exceed 5 % of the analysis area (State of Wyoming 2011). In contrast, sage-grouse populations outside of Core Areas (i.e., non-core areas) are not subject to these conservation measures. Prescribed stipulations for breeding habitat in non-core areas include maintaining a 0.40 km (0.25 mi) buffer of controlled surface use around leks, and a 3.33 km (2.0 mi) buffer with a seasonal timing stipulation (15 Mar-30 Jun) around leks. Both of these stipulations are subject to potential modification or waiver (State of Wyoming 2011).

Wyoming's governor requested a review of the progress and effectiveness of the SGEO to occur every 5 years (State of Wyoming 2011). In addition, the USFWS conducts 5-year status reviews of candidate species including sage-grouse (USFWS 2010). Thus, the State of Wyoming has a need to provide an accurate and accountable examination of the effectiveness of the SGEO in maintaining sage-grouse populations in Wyoming. The effectiveness of the SGEO is dependent upon multiple factors. First, whether the lands encompassed by Core Area benefit sage-grouse. Second, how well have the parameters been applied. This is particularly tenuous as the SGEO is a Governor's order, not a rule of legislated law. And, finally, are the parameters, which are based on science, truly effective when applied at a landscape scale. The success of the SGEO has greater ramifications than just for Wyoming. Other western states are also implementing approaches to sage-grouse conservation within their jurisdictions (e.g., Oregon Department of Fish and Wildlife 2011; State of Idaho 2012a, 2012b; State of Montana 2014; State of Nevada 2014; Stiver 2011). The Bureau of Land Management also recently incorporated additional protections for sage-grouse into their current and updated land management plans (BLM 2012, 2015).

Since it was initiated in 2008, there has not been an evaluation of whether Core Areas designated by the SGEO are effective in conserving sage-grouse in light of continued energy development. The designation of Core Areas is the major component of the SGEO as Core Areas delineate the habitat across the state where SGEO conservation measures are applied. Further, lands encompassed by Core Area likely served as functional Core Area even prior to policy designation as evidenced by historically high densities of sage-grouse (Doherty et al. 2010, WGFD unpublished data) and minimal development through time (Gamo 2016). In addition, disturbance was minimal around Core Area leks prior to 2008 policy implementation. For instance, 4 of 674 (<0.01 %) Core Area leks we evaluated occurred within 1.0 km of a well pad (Gamo, unpublished data). Therefore, the focus of our study was on assessing whether Wyoming Core Areas benefit sage-grouse populations. Our objectives included: (1) evaluating oil and gas well pad development within Core Area, and (2) comparing total peak male sage-grouse lek attendance in Core Area and non-core areas. In line with existing habitat quality at time of SGEO implementation, we predicted that rate of energy development within sage-grouse Core Area would be lower compared to non-core areas. We further predicted oil and gas development in the Core Areas would exhibit less expansion after SGEO implementation compared to non-core area. We also predicted that sage-grouse populations within Core Area would exhibit more robust male lek attendance than non-core area grouse populations. To test these predictions, we evaluated well pad numbers and male sage-grouse lek attendances between core and non-core population areas at statewide and management zone scales. Finally, we provide initial information related to disturbances within Core Area to assess short-term progress of SGEO implementation. Our paper provides an assessment of the measured effectiveness of the Wyoming's Core Area designations for breeding sage-grouse (see Smith et al. 2016 for an evaluation of winter habitat protections afforded by SGEO), which should be of great value to managers and scientists considering implementing other landscape-scale species conservation programs.

Materials and Methods

Study Area

Our study area encompassed the range of sage-grouse across Wyoming. Within this delineated range, 31 Core Areas have been designated and mapped (State of Wyoming 2011; Fig. 2). Core Areas occupy approximately 24 % of the land area of Wyoming and generally reside in the major basins found between mountain ranges including the Wyoming Basins (Rowland and Leu 2011) in the western and central portions of the state and the Powder River Basin in the northeast (Knight et al. (2014). Sage-grouse Core Areas vary in size from a minimum of 41 km^2 to a maximum of 18,587 km^2. The Western Association of Fish and Wildlife Agencies (WAFWA) mapped the entire sage-grouse range into 7 sage-grouse management zones based on ecological conditions (MZ; Stiver et al. 2006). The Great Plains-Management Zone-MZ I and the Wyoming Basin-MZ II occur in Wyoming. The northeastern portion of Wyoming, including the Powder River Basin and the plains extending east and north from the northern Laramie Mountains to the state line bordering South Dakota lie within MZ I. The remainder of the state (excluding the southeastern plains, which are not inhabited by sage-grouse) including the sagebrush dominated basins west of the Laramie and Bighorn Mountain Ranges fall within MZ II (Rowland and Leu 2011). From 2010–2014, MZ II included 36.8 % of range-wide breeding male sage-grouse (compared to 12.4 % in MZ I; Doherty et al. 2015) and the second largest area of suitable habitat range-wide (Wisdom et al. 2011).

Northeastern Wyoming rangelands, including the Powder River Basin, consist of sagebrush dominated shrub steppe integrating with mixed grass prairie toward the South Dakota border (Knight et al. 2014). Sagebrush steppe vegetation consists of Wyoming big sagebrush (*A. tridentata wyomingensis*, silver sagebrush (*A. cana*). and a diverse understory of herbaceous plants. Common native grasses include blue grama (*Bouteloua gracilis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and non-native grasses include crested wheatgrass (*Agropyron cristatum*) and cheatgrass (*Bromus tectorum*; Thilenius et al. 1994). Rocky Mountain juniper (*Juniperus scopulorum*) and ponderosa pine (*Pinus ponderosa*) occur on rocky uplifts and in river drainages.

The Wyoming Basins in the western part of the state consist of multiple basins between mountain ranges. Major basins include the Bighorn, Great Divide, Green River, and Shirley. Vegetation in these basins is much more dominated by sagebrush than northeast Wyoming and consist of sagebrush steppe dominated by Wyoming big sagebrush with areas of black (*A. nova*) and low sagebrush (*A. arbuscula*; Rowland and Leu 2011; Knight et al. 2014). Common grasses include bluebunch wheatgrass, and needle and thread (*Hesperostipa comata*). Invasive grass species such as cheatgrass are becoming more common in the Wyoming Basins (Knight et al. 2014).

Methods

Wells Pads

We obtained data on numbers of wells from the Wyoming Oil and Gas Conservation Commission (WOGCC) oil and gas well database dating from 1986 through 2014 (WOGCC 2014). Higher well numbers have been previously correlated to higher levels of infrastructure (Walker et al. 2007). Similar to Harju et al. (2010), we used well pads as a more easily measureable surrogate for energy impacts. We tabulated wells located within sage-grouse range and only included active wells; wells that were plugged, abandoned, or not active were removed from further analysis (e.g., Holloran 2005). Wells were also assigned to Core Area or non-core area. We calculated average well pad size based upon the average size of 100 randomly chosen well pads digitized in GIS. Based upon the average well pad size we calculated an average well pad diameter of 120 m. We thus computed the number of well pads by placing a 60 m radius circle around each well head. Using GIS, anywhere a 60 m radius touched or overlapped another 60 m radius that intersection was merged into one well pad. Finally, we determined the number of well pads at a statewide level, within MZ I and II for each year 1986 through 2014.

Male Sage-Grouse Lek Attendance

Our analyses used total (i.e., sum of all lek counts in each analysis scale per year) annual peak male counts, which is the statistic used to monitor sage-grouse populations per the Wyoming SGEO (B. Budd, Wyoming SGIT, personal communication). We calculated annual peak male lek attendance using the WGFD sage-grouse lek count database from 1996 through 2014. Our analyses did not rely on average males per lek, which is a common statistic used to monitor trends in sage-grouse populations (e.g., Walker et al. 2007; Harju et al. 2010; Gregory and Beck 2014). However, for comparison we also calculated and report average males per lek from 1996 through 2014 among our sampled leks. Lek count procedures were standardized in 1996 and protocols consisted of three separate counts for each lek spaced at least 7 days apart from March through May (Connelly et al. 2003, 2004). The peak count was the maximum recorded number of males of the three counts. We only included leks considered active by WGFD definition (e.g., documented attendance of 2 or more individuals within a 10-year timeframe). Leks were identified as Core Area leks or non-core leks according to their location within a Core Area or outside of those areas as described in the SGEO. We evaluated total peak male sage-grouse lek attendance statewide and for WAFWA MZs I and II. These designations were chosen as they correspond to state policy (statewide) and potential regulatory decisions at the federal level (MZs). We summed total peak male lek attendance in Core Area and non-core area at the statewide and WAFWA MZ scales. Statewide estimates included leks aggregated from all 31 individual core population areas.

Recognizing the strong cyclic nature of sage-grouse populations in Wyoming (Fedy and Doherty 2011; Fedy and Aldridge 2011), we chose to evaluate differences between Core Area and non-core area birds separately during periods of population increase (1996–2006) and decline (2006–2013). Core Areas were originally identified based upon high lek densities with abundant grouse populations, high quality habitat (Doherty et al. 2010), and relative exclusion from development (B. Budd, pers. comm., Gamo 2016). Fedy and Aldridge (2011) noted sage-grouse populations in Wyoming experienced a period of increase from 1996 through 2006. Correspondingly, a downward trend was observed from 2006 through 2013 (unpublished data, WGFD, Nielson et al. 2015). Therefore, our evaluation of Core Area influence on grouse includes years prior to the SGEO policy designation and allows the opportunity to evaluate implications of the chosen landscape during both increasing and decreasing phases of a sage-grouse population cycle.

To provide insight on the effectiveness of the Wyoming SGEO policy, we report data provided by the WGFD in response to the 2014 USFWS greater sage-grouse data call as part of their Endangered Species Act listing determination. These data provide a short-term description of SGEO-related features obtained from site-specific impact analyses conducted by development proponents, and state and federal agencies that were reviewed for SGEO policy conformance by the WGFD. Data were available only for the years 2012 through 2014 which correspond to the implementation of a statewide SGEO database system.

Statistical Analysis

We utilized Analysis of Covariance (ANCOVA; PROC REG, SAS 9.4, SAS Institute, Cary, NC) to compare trends in well pad development between Core Area and non-core area at statewide and management zone scales. We compared the main effects of study area (i.e., Core Area or non-core area) with time being the covariate in each ANCOVA. In our design, well pads in Core Area constructed after 2009 constituted the treatment whereas non-core well pads after 2009 served as the control. Well pads within Core Areas from 1986 through 2008 served as before or pre-treatment data. We compared trends in numbers of active well pads between Core Areas and non-core areas (control) from 2009–2014 coinciding with SGEO implementation. We then compared trends in numbers of active well pads from 1986 through 2008 prior to SGEO policy with trends from 2009 through 2014 representing impacts post policy implementation.

We also utilized ANCOVA to evaluate differences in sage-grouse population trends between Core and non-core areas during an increasing population cycle (1996–2006) and a decreasing population cycle (2006–2013) both statewide and within MZs. As some leks occurred within relative close proximity to each other and count data were collected at essentially the same time each year on an annual basis, there was potential for spatial and temporal autocorrelation, respectively, among the data. We tested for temporal autocorrelation among sage-grouse count data using a Durbin-Watson test. If tests for autocorrelation were significant ($\alpha \leq 0.05$), we transformed the data using differencing to remove the temporal autocorrelation prior to employing the regressions within the ANCOVA (Box et al. 1994). Differencing is a technique that simply subtracts the previous year count from the current year count in sequence through the progression of years of data. By doing so, differencing removes the temporal trend but retains the mean across the data.

The ANCOVA procedure we employed used a suite of four models and systematically compared among models to determine the best fit for the comparison among the two trend lines (i.e., core and non-core) from linear regressions (Weisberg 1985). The models were as follows:

Model 1. $\hat{y} = b_{0,1}W_1 + b_{0,2}W_2 + b_{1,1}Z_1 + b_{1,2}Z_2$

Model 2. $\hat{y} = b_{0,1}W_1 + b_{0,2}W_2 + b_1X_1$

Model 3. $\hat{y} = b_0 + b_{1,1}Z_1 + b_{1,2}Z_2$

Model 4. $\hat{y} = b_0 + b_1X$

Where b_0 was the y-intercept, b_1 was the slope estimate, W was a label term, Z was the value associated with the corresponding W, and X was time. We first tested Model 1 against Model 2 to test the null hypothesis that the slopes of Core and non-core area sage-grouse trends were identical vs. the alternate that they were different ($\alpha = 0.05$). If the null hypothesis was accepted, we then tested Model 2 against Model 4 to test the null hypothesis that the slopes were identical between core and non-core areas as well as the y-intercepts being identical between the two areas vs. the alternate that the slopes were identical but the y-intercepts were different. In addition, if upon visual inspection of the plots of the compared slopes, the y-intercepts were clearly distinct we first tested model 1 against model 3 to test the null hypothesis that the y-intercepts were identical between core and non-core areas vs. the alternate that they were different. If the null hypothesis was accepted, we then tested model 3 against model 4 to test the null hypothesis that the y-intercepts were identical between Core and non-core areas as well as the slopes being identical between the two areas vs. the alternate that the y-intercepts were identical but the slopes were different. We tested for normal probabilities and used Ordinary Least Squares assuming residuals were normally distributed. Model significance testing was accomplished using an F-test.

We calculated coefficients of variation (CV) for each year's average peak male lek attendance by MZ and statewide to obtain a measure of the variation around the mean of each year's lek attendance. We considered populations that exhibited smaller CVs to be more stable and resilient to changing environmental conditions (Harrison 1979).

Results

Well Pads

Well pads within statewide sage-grouse range increased from 1946 in Core Area and 15,304 in non-core area in 1986 to 3112 and 57,970, respectively, in 2014 (Table 1). Well pads in MZ I increased from 866 in Core and 8244 in non-core in 1986 to 1174 in Core and 34,178 in non-core in 2014 (Table 1). During this same time frame, well pads in MZ II increased from 1080 in core and 7060 in non-core to 1938 in core and 23,792 in non-core in 2014. Comparing non-core to Core Area at the statewide scale, well pads increased at a ratio of 29 to 1 per year, 48 to 1 in MZ I, and 15 to 1 in MZ II (Table 1).

Core Area vs. Non-core Population Areas (2009–2014: post SGEO policy implementation)

Rate of increase in active well pads differed ($F_{1,8} = 97.77$, $p < 0.01$, $r^2 = 1.00$; Fig. 3a) as Core ($\hat{\beta}_1 = 37.43$,

Table 1 Numbers of well pads by year statewide and within Western association of fish and wildlife agencies management zones I and II (MZ I and MZ II) in Wyoming, USA, 1986–2014

Year	Number of active well pads					
	Statewide		MZ I		MZ II	
	Core	Non-core	Core	Non-core	Core	Non-core
1986	1946	15,304	866	8244	1080	7060
1987	1958	15,538	870	8386	1088	7152
1988	2000	15,878	880	8562	1120	7316
1989	2052	16,128	904	8646	1148	7482
1990	2102	16,498	922	8746	1180	7752
1991	2152	16,900	938	8874	1214	8026
1992	2178	17,270	946	8988	1232	8282
1993	2194	17,952	950	9096	1244	8856
1994	2228	18,664	956	9258	1272	9406
1995	2266	19,508	958	9428	1308	10,080
1996	2300	19,918	966	9494	1334	10,424
1997	2324	20,614	970	9688	1354	10,926
1998	2364	21,510	974	9968	1390	11,542
1999	2386	22,588	976	10,406	1410	12,182
2000	2420	24,234	980	11,446	1440	12,788
2001	2466	26,366	994	12,772	1472	13,594
2002	2510	28,656	1002	14,096	1508	14,560
2003	2550	30,500	1004	15,234	1546	15,266
2004	2622	33,158	1016	16,936	1606	16,222
2005	2708	37,142	1032	19,822	1676	17,320
2006	2774	41,490	1056	23,074	1718	18,416
2007	2836	45,846	1074	26,134	1762	19,712
2008	2878	49,624	1086	28,590	1792	21,034
2009	2940	52,514	1096	30,352	1844	22,162
2010	2964	53,944	1102	31,316	1862	22,628
2011	3014	55,614	1120	32,558	1894	23,056
2012	3050	56,646	1132	33,240	1918	23,406
2013	3102	57,276	1160	33,686	1942	23,590
2014	3112	57,970	1174	34,178	1938	23,792

$SE = 75.59$, $DF_{error} = 8$, $p = 0.63$) was less compared to non-core ($\hat{\beta}_1 = 1094.51$, $SE = 75.59$, $DF_{error} = 8$, $p < 0.01$) areas at the statewide level. Within MZ I, rate of increase of well pads differed ($F_{1,8} = 95.16$, $p < 0.01$, $r^2 = 1.00$; Fig. 3b) as Core ($\hat{\beta}_1 = 16.46$, $SE = 54.56$, $DF_{error} = 8$, $p = 0.77$) was less than in non-core areas ($\hat{\beta}_1 = 769.2$, $SE = 54.56$, $DF_{error} = 8$, $p < 0.01$). Rate of increase in active well pads differed ($F_{1,8} = 99.13$, $p < 0.01$, $r^2 = 1.00$;Fig. 3c) in MZ II as Core ($\hat{\beta}_1 = 20.97$, $SE = 21.61$, $DF_{error} = 8$, $p = 0.36$) was lower compared to non-core ($\hat{\beta}_1 = 325.31$, $SE = 21.61$, $DF_{error} = 8$, $p < 0.01$) sage-grouse population areas.

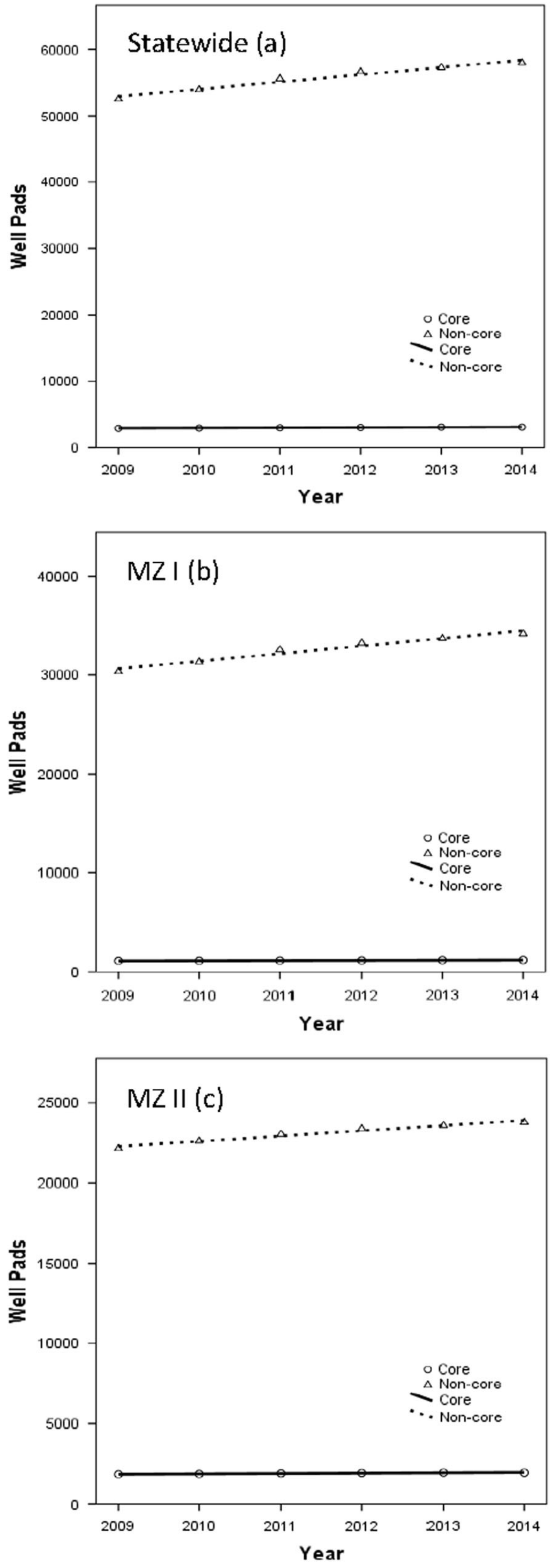


Fig. 3 Well pad comparison between core and non-core areas in Wyoming, USA, 2009–2014. Data are reported at statewide **a** and management zone (MZ I **b** and MZ II **c**) scales

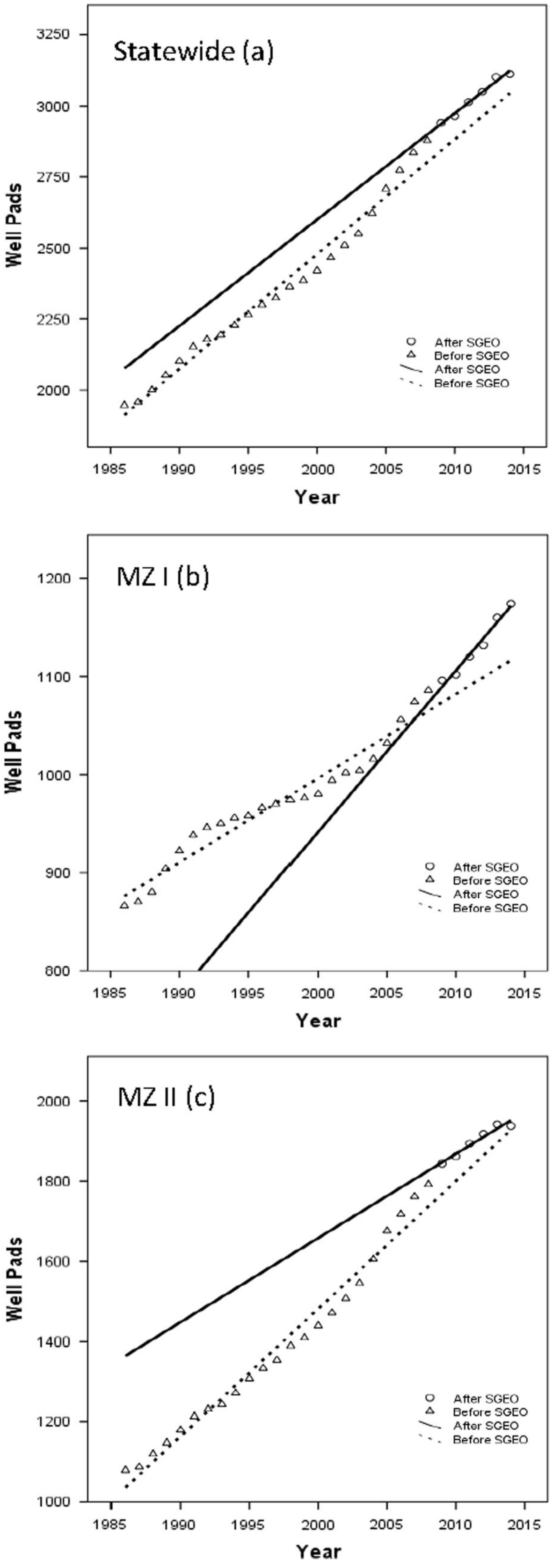
Before (1986–2008)–After (2009–2014) Impact (SGEO Policy Implementation)

Trends in the rate of increase of number of active well pads were the same ($F_{1,25} = 0.11$, $p = 0.75$, $r^2 = 1.00$) within Core Area before (1986–2008; $\hat{\beta}_1 = 40.42$, $SE = 1.20$, $DF_{error} = 25$, $p < 0.01$) and after (2009–2014; $\hat{\beta}_1 = 37.42$, $SE = 9.13$, $DF_{error} = 25$, $p < 0.01$; Fig. 4a) Core Area designation at the statewide level. In MZ I, the rate of increase in the number of active well pads differed ($F_{1,25} = 6.8$, $p < 0.02$, $r^2 = 1.00$) as the rate before ($\hat{\beta}_1 = 8.59$, $SE = 0.39$, $DF_{error} = 25$, $p = 0.01$) was less than after ($\hat{\beta}_1 = 16.45$, $SE = 2.99$, $DF_{error} = 25$, $p < 0.01$) Core Area designation (Fig. 4b). In MZ II, the rate of increase in the number of active well pads in Core Areas was similar ($F_{1,25} = 2.09$, $p = 0.16$, $r^2 = 1.00$) before ($\hat{\beta}_1 = 31.83$, $SE = 0.98$, $DF_{error} = 251$, $p = 0.0$) and after ($\hat{\beta}_1 = 20.97$, $SE = 7.44$, $DF_{error} = 25$, $p < 0.01$) Core Area designation (Fig. 4c).

Male Sage-Grouse Lek Attendance

We identified 958 active leks (674 Core Area leks and 284 non-core leks) statewide that were consistently surveyed each year from 1996 through 2014. Surveyed leks in MZ I and II included 63 and 611 in Core Areas, and 110 and 174 in non-core areas, respectively. Lek counts increased from 1996 through 2006 and decreased from 2006 through 2013 (Table 2).

Male lek attendance for Core Area grouse populations exhibited smaller CVs as compared to non-core CVs (Table 3). Specifically, both MZ II and statewide CVs were consistently lower in Core than in non-core population areas across years. For MZ I, CVs were also lower in Core than in non-core population areas except in 1998 and 2004, when they were higher in Core. In addition, CVs in MZ II Core Area were lower than CVs in MZ I Core Area in 16 out of 18 years (Table 3).



◀ **Fig. 4** Oil and gas well pad comparison between before (1986–2008) and after (2009–2014) SGEO implementation in core areas in Wyoming, USA. Data are reported at statewide **a** and management zone (MZ I **a** and MZ II **c**) scales. Extended linear trend lines (solid *black* lines) for after SGEO implementation (2009–2014) are provided for slope comparisons among landscape scales

Table 2 Peak male sage-grouse counted from annual lek counts statewide and within Western association of fish and wildlife agencies management zones I and II (MZ I and MZ II) based on 958 active leks in Wyoming, USA, with consistent lek counts, 1996–2013

Year	Peak total male sage-grouse counted					
	Statewide		MZ I		MZ II	
	Core	Non-core	Core	Non-core	Core	Non-core
Period of increase						
1996	3516	784	204	150	3312	634
1997	4103	1096	185	212	3918	884
1998	6384	1386	288	335	6096	1051
1999	9127	1861	558	288	8569	1573
2000	11,068	2475	842	658	10,226	1817
2001	9021	1976	520	497	8501	1479
2002	8062	1639	367	248	7695	1391
2003	9709	1765	555	320	9154	1445
2004	10,715	1518	508	265	10,207	1253
2005	17,686	2728	1177	503	16,509	2225
2006	20,893	2763	1364	588	19,529	2175
Period of decrease						
2006	20,893	2763	1364	588	19,529	2175
2007	18,544	2496	1137	608	17,407	1888
2008	14,613	2379	853	473	13,760	1906
2009	13,444	1993	550	367	12,894	1626
2010	10,966	1761	647	297	10,319	1464
2011	8621	1275	463	210	8158	1065
2012	7684	1299	379	204	7305	1095
2013	6526	1520	283	148	6243	1372

Note: 2006 lek attendance is reported for periods of increase and decrease because these data were used in calculations for each period

Period of Increase (1996–2006)

During the 1996–2006 population increase, average lek size (males per lek) in Core Areas was 14.9 (range: 5.2–31.0) statewide, 9.5 (range: 2.9–21.7) in MZ I, and 15.4 (range: 5.4–32.0) in MZ II (Table 4). Non-core lek averages during 1996–2006 were 6.4 (range: 2.8–9.7) statewide, 3.4 (range: 1.4–6.0) in MZ I, and 8.3 (range: 3.6–12.8) in MZ II (Table 4). Our 1996–2006 ANCOVA models considered an average of 10,259 (range: 3516–20,893) peak male sage-grouse in Core Areas and 1817 (range: 784–2763) peak males in non-core areas at the statewide scale (Table 2). Our

Table 3 Coefficients of variation for core and non-core peak male populations in Western association of fish and wildlife agencies management zones I and II (MZ I and MZ II), and statewide in Wyoming, USA, 1997–2014

Year	Coefficient of variation					
	Statewide		MZ I		MZ II	
	Core	Non-core	Core	Non-core	Core	Non-core
Period of increase						
1997	219.3	272.6	252.7	321.6	214.9	243.5
1998	202.7	242.4	263.9	259.5	197.7	225.8
1999	173.5	233.2	183.0	301.5	171.7	199.9
2000	155.2	199.4	174.0	229.2	153.6	183.7
2001	162.1	206.7	164.3	212.8	160.3	194.7
2002	157.0	258.2	185.3	242.9	153.3	227.7
2003	145.4	211.7	199.4	241.0	141.4	186.9
2004	157.8	232.8	218.4	210.0	153.3	209.8
2005	152.4	226.8	175.4	229.1	150.2	204.1
2006	143.0	222.2	178.9	218.6	140.1	205.2
Period of decrease						
2006	143.0	222.2	178.9	218.6	140.1	205.2
2007	137.9	225.6	153.6	211.3	135.9	215.4
2008	156.8	227.6	162.0	219.7	155.0	208.4
2009	149.7	235.7	179.7	207.8	145.6	214.8
2010	142.7	218.3	168.3	278.5	140.1	188.5
2011	156.2	239.2	158.8	277.0	154.1	209.3
2012	163.0	238.8	154.5	263.9	160.7	208.7
2013	163.2	227.1	161.5	326.6	159.9	185.1
2014	170.3	232.5	143.9	361.4	167.6	189.1

Table 4 Average annual peak per lek attendance of male sage-grouse obtained from annual lek counts statewide and within Western association of fish and wildlife agencies management zones I and II (MZ I and MZ II) based on 958 active leks with consistent counts in Wyoming, USA, 1996–2013

Year	Average peak male sage-grouse per lek					
	Statewide		MZ I		MZ II	
	Core	Non-core	Core	Non-core	Core	Non-core
Period of increase						
1996	5.2	2.8	3.2	1.4	5.4	3.6
1997	6.1	3.9	2.9	1.9	6.4	5.1
1998	9.5	4.9	4.6	3.1	10.0	6.0
1999	13.5	6.6	8.9	2.6	14.0	9.0
2000	16.4	8.7	13.4	6.0	16.7	10.4
2001	13.4	7.0	8.3	4.5	13.9	8.5
2002	12.0	5.8	5.8	2.3	12.6	8.0
2003	14.4	6.2	8.8	2.9	15.0	8.3
2004	15.9	5.4	8.1	2.4	16.7	7.2
2005	26.2	9.6	18.7	4.6	27.0	12.8
2006	31.0	9.7	21.7	5.4	32.0	12.5
Period of decrease						
2006	31.0	9.7	21.7	5.4	32.0	12.5
2007	27.5	8.8	18.1	5.5	28.5	10.9
2008	25.5	8.4	13.5	4.3	22.5	11.0
2009	20.0	7.0	8.7	3.3	21.1	9.3
2010	16.3	6.2	10.3	2.7	16.9	8.4
2011	12.8	4.5	7.4	1.9	13.4	6.1
2012	11.4	4.6	6.0	1.9	12.0	6.3
2013	9.7	5.4	4.5	1.4	10.2	7.9

Note: 2006 lek attendance is reported for periods of increase and decrease because these data were used in calculations for each period

ANCOVA models also considered an average of 597 (range: 204–1364) peak male sage-grouse in Core Areas and 369 (range: 150–658) in non-core areas in MZ I and 9429 (range: 3312–19,529) and 1448 (range: 634–2225) males in Core and non-core areas, respectively in MZ II (Table 2).

Our test for autocorrelation confirmed sage-grouse count data were temporally correlated ($p < 0.001$) so we transformed these data using the differencing technique and utilized the transformed count data (BIRDTRANS) for analysis. Differencing sacrifices the first year of data (1996) so transformed analyses began with 1997. At the statewide scale, trends in BIRDTRANS differed ($F_{1,17} = 5.29$, $p = 0.034$, $r^2 = 0.27$) as the rate in Core ($\hat{\beta}_1 = 284.06$, SE = 146.68, $\mathrm{DF}_{\mathrm{error}} = 17$, $p = 0.07$) was greater than non-core ($\hat{\beta}_1 = 0.58$, SE = 146.68, $\mathrm{DF}_{\mathrm{error}} = 17$, $p = 0.99$) population areas during 1997–2006 (Fig. 5a). In MZ I, trends in BIRDTRANS were not different ($F_{1,17} = 0.46$, $p = 0.37$, $r^2 = 0.18$) between Core ($\hat{\beta}_1 = -0.06$, SE = 26.47, $\mathrm{DF}_{\mathrm{error}} = 18$, $p = 0.99$) and non-core ($\hat{\beta}_1 = 24.92$, SE = 24.47, $\mathrm{DF}_{\mathrm{error}} = 18$, $p = 0.36$) population areas during 1997–2006 (Fig. 5b). In MZ II, trends in BIRDTRANS differed ($F_{1,17} = 6.04$, $p = 0.03$, $r^2 = 0.30$) as the rate in Core ($\hat{\beta}_1 = 263.79$, SE = 129.68, $\mathrm{DF}_{\mathrm{error}} = 17$, $p = 0.06$) was greater than non-core ($\hat{\beta}_1 = -4.01$, SE = 129.68, $\mathrm{DF}_{\mathrm{error}} = 17$, $p = 0.98$) areas during 1997–2006 (Fig. 5c).

Period of Decrease (2006–2013)

During the 2006–2013 population decrease, average lek size in Core Area was 19.3 (range: 9.7–31.0) statewide, 11.3 (range: 4.5–21.7) in MZ I, and 19.6 (range: 10.2–32.0) in MZ II (Table 4). Non-core lek size during 2006–2013 averaged 6.8 (range: 4.5–9.7) statewide, 3.3 (range: 1.4–5.5) in MZ I, and 9.0 (range: 6.1–12.5) in MZ II (Table 4).

Our ANCOVA models during 2006–2013 at the statewide scale considered average peak males in Core Area of 12,661 (range: 6526–20,893), and 1936 (range: 1275–2763) in non-core areas (Table 2). Peak males considered in MZ I averaged 710 (283–1363) and 362 (range: 148–608) in Core

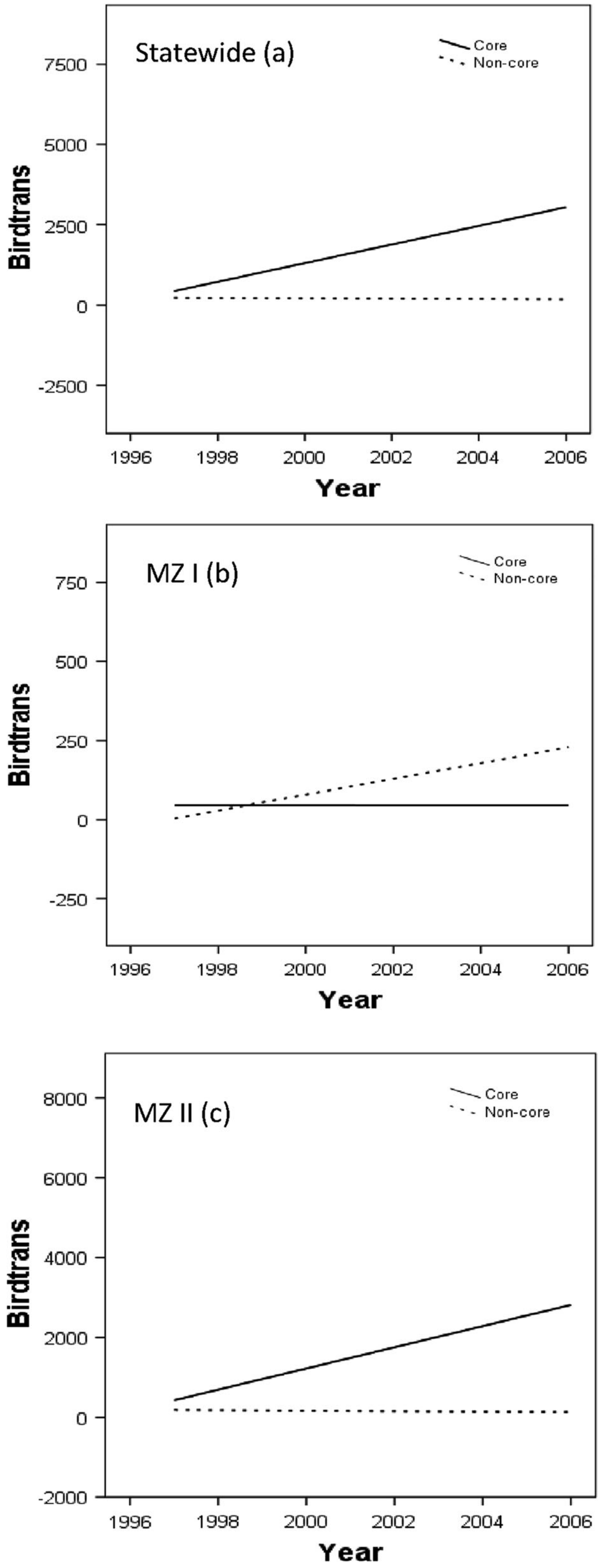


Fig. 5 Linear trend comparison of BIRDTRANS (differenced peak male sage-grouse numbers) between core and non-core areas in Wyoming, USA during period of population increase (1997–2006; *note—differencing removed the year 1996*). Data are reported at statewide **a** and management zone (MZ I **b** and MZ II **c**) scales

and non-core areas, respectively. Peak males considered in MZ II averaged 11,952 (range: 6243–19,529) and 1574 (range: 1065–2175) in Core and non-core population areas, respectively (Table 2).

Trends in BIRDTRANS were not different ($F_{1,12} = 3.42$, $p = 0.09$, $r^2 = 0.23$) between statewide Core ($\hat{\beta}_1 = -245.13$, $\mathrm{SE} = 178.64$, $\mathrm{DF}_{\mathrm{error}} = 13$, $p = 0.19$) and non-core ($\hat{\beta}_1 = -27.95$, $\mathrm{SE} = 178.64$, $\mathrm{DF}_{\mathrm{error}} = 12$, $p = 0.88$) population areas during 2006–2013 (Fig. 6a). In MZ I, trends in differenced transformed counts did not differ ($F_{1,12} = 0.02$, $p = 0.89$, $r^2 = 0.33$) between Core ($\hat{\beta}_1 = -11.15$, $\mathrm{SE} = 15.07$, $\mathrm{DF}_{\mathrm{error}} = 12$, $p = 0.62$) and non-core ($\hat{\beta}_1 = -6.74$, $\mathrm{SE} = 15.07$, $\mathrm{DF}_{\mathrm{error}} = 12$, $p = 0.77$) population areas. In MZ II, trends in BIRDTRANS were not statistically different ($F_{1,13} = 3.54$, $p = 0.08$, $r^2 = 0.24$) between Core ($\hat{\beta}_1 = -230.69$, $\mathrm{SE} = 168.43$, $\mathrm{DF}_{\mathrm{error}} = 13$, $p = 0.19$) and non-core ($\hat{\beta}_1 = 31.41$, $\mathrm{SE} = 168.43$, $\mathrm{DF}_{\mathrm{error}} = 13$, $p = 0.85$) population areas during 2006–2013 (Fig. 6c).

Policy Application

We found from 2012 through 2014, the average level of surface disturbance incurred from projects ranged from 0.7 to 18.7 % per analysis area within a Core Area (Table 5). Project densities averaged 0.0 per 2.6 km^2 (640 ac)–1.65 per 2.6 km^2. During this period, 174 projects occurred in Core Area with 126 (72.4 %) initially conforming to SGEO stipulations. The remaining 27.6 % of projects went through further review and mitigation practices including co-location on previously disturbed sites, site-specific avoidance of sage-grouse habitat, habitat restoration and reclamation projects, and creation of habitat management plans to minimize disturbance and provide consistency with the SGEO (WGFD 2014). There were 26 (15 %) instances where disturbances exceeded the 5 % threshold. These exceedances were resultant of landscapes that included existing permit rights prior to 2008 (WGFD 2014). Such existing rights are recognized in the SGEO and are not subject to thresholds, but are considered disturbance in some situations whether developed or not (State of Wyoming 2011).

Discussion

An important aspect of implementing natural resource policy is determining whether it is effective in achieving the desired outcome. In the case of Wyoming's SGEO, Core Areas as identified in the policy were intended to provide for the maintenance or increase of sage-grouse populations across the state (State of Wyoming 2008, 2011). We predicted a lesser rate of development within sage-grouse Core Area compared to non-core areas. Well pads did increase at a lesser rate statewide and in MZ's I and II post SGEO

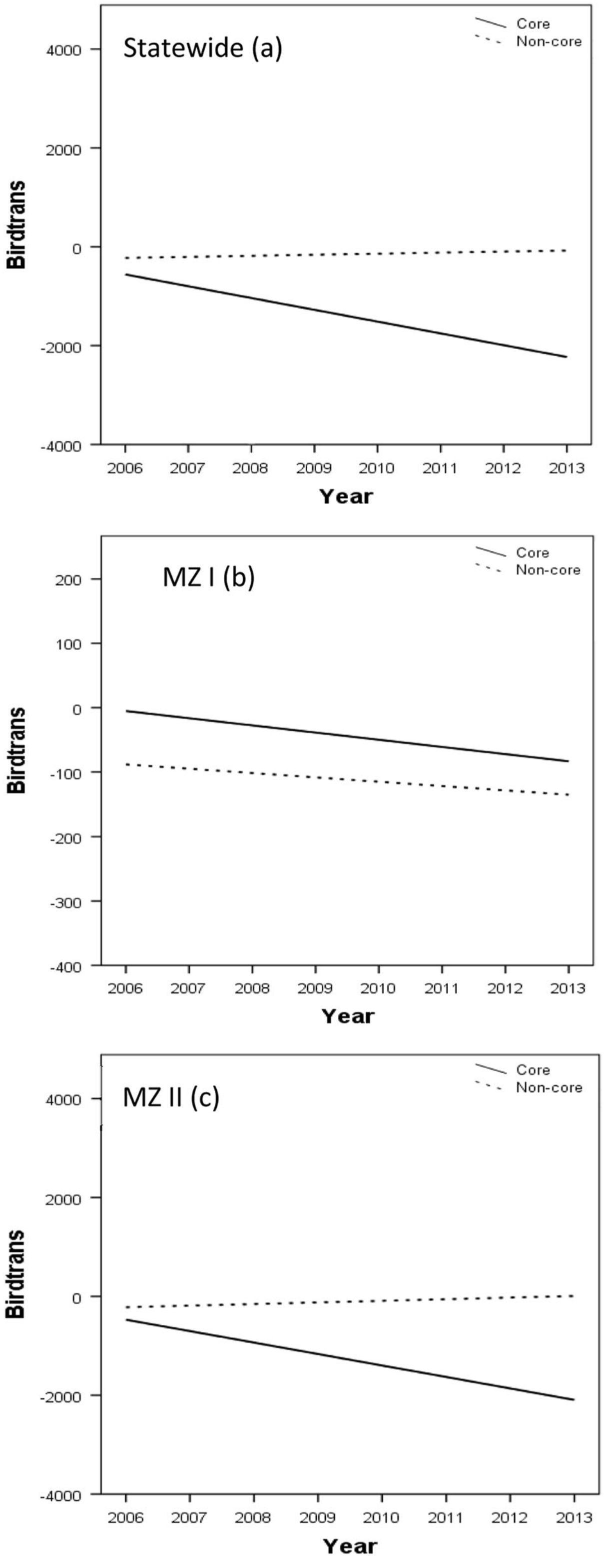


Fig. 6 Linear trend comparison of BIRDTRANS (differenced peak male sage-grouse numbers) comparison between core and non-core areas in Wyoming, USA during period of population decrease (2006–2013; *note—differencing removed the year 2005*). Data are reported at statewide **a** and management zone (MZ I **b** and MZ II **c**) scales

implementation (2009–2014) in Core Area as compared to non-core areas. This finding was not surprising as well pad development has historically been higher in non-core areas. In addition, during the mapping of Core Area, locations of existing development influenced placement of Core Area boundaries as policymakers constrained boundaries to avoid heavily developed areas and protect undeveloped areas (B. Budd, Wyoming SGIT, personal communication). Nonetheless, our analysis showed well pads in non-core area continued to increase at a higher rate than in Core Area. Although not definitive, these findings suggest the implementation of the Core Area policy pertaining to oil and gas development was being met during the timeframe we analyzed.

Our before-after SGEO policy comparisons provide further evidence of the role Core Area plays within the SGEO policy in relation to development statewide and in MZ II. In both instances, the rate of development remained the same throughout 1986–2014. Thus, the SGEO may have been influential at maintaining the slow pace of development that has historically occurred in areas now designated as Core Area. Alternatively, the slow development pace may simply be the result of continued low interest in resource development within areas mapped as Core Area. Interestingly, we did not find this in MZ I. Rather, the rate of development in Core Areas in MZ I actually was higher post SGEO implementation compared to long-term development. This trend began around the early 2000s. We suspect this trend may be at least in part due to coalbed methane gas development (Stilwell et al. 2012) and the more recent interest in oil production maintaining well pad development in the area as evidenced by an increase in WOGCC permits since a low in 2009 (Applegate and Owens 2014).

We predicted male sage-grouse lek attendance would be higher in Core Areas before and after implementation of the SGEO. We found mixed results in male lek attendance, depending on the spatial scale and timeframe. Total male sage-grouse lek attendance was greater in Core Area compared to non-core area at the statewide scale and in MZ II, but not in MZ I, during 1996–2006, when sage-grouse populations in Wyoming were notably increasing. Trends in male sage-grouse lek attendance did not differ between Core and non-core population areas statewide, in MZ I, or MZ II during 2006–2013, when sage-grouse were declining across Wyoming. However, from a biologically significant standpoint, Core Area populations in MZ II appeared to decrease at a greater rate than non-core area birds during the period of decline. This decline was likely mathematically related to loss of relatively more males from Core Areas, which had higher absolute numbers of grouse prior to the period of decline compared to non-core leks. Our findings on trends and numbers of well pads, and male lek

Table 5 Average surface disturbance and density of projects within Wyoming's 31 Sage-grouse core areas including core area size, percentage surface disturbance, and disturbance density (No./2.66 km^2), 2012–2014 (WGFD 2014)

Core area	MZ	km^2	Percentage disturbance (range)		No./2.66 km^2 (range)	
Buffalo	I	1974	4.1	(1.5–6.8)	0.2	(0.1–0.3)
Douglas	I	356	18.7	(4.1–42.9)	0.6	(0.3–0.8)
North Gillette	I	493	3.1	(2.4–3.9)	0.4	(0.1–0.7)
Newcastle	I	481	7.0	(2.5–10.2)	1.1	(0.6–1.3)
North Glenrock	I	556	11.2	(N/A)	0.8	(N/A)
North Laramie	I	890	4.3	(2.8–5. 8)	0.1	(0.0–0.1)
Thunder Basin	I	3119	4.9	(0.9–25.7)	0.2	(0.1–1.0)
Natrona	I, II	10,011	5.3	(0.5–11.9)	0.2	(0.1–1.5)
Black's Fork	II	753	n/a		n/a	
Continental Divide	II	697	1.4	(1.3–1.6)	0.3	(0.3–0.3)
Crowheart	II	1259	10.6	n/a	1.7	n/a
Daniel	II	2069	1.9	(1.7–2.2)	0.0	(0.0–0.0)
Elk Basin East	II	144	No projects		No projects	
Elk Basin West	II	41	No projects		No projects	
Fontenelle	II	608	No Projects		No projects	
Grass Creek	II	660	No projects		No projects	
Greater South Pass	II	18,587	4.6	(0.2–53.4)	0.0	(0.0–2.1)
Hanna	II	2958	5.6	(0.6–12.5)	0.1	(0.0–0.3)
Heart Mountain	II	487	No projects		No projects	
Hyattville	II	585	No projects		No projects	
Jackson	II	342	No projects		No projects	
Little Mountain	II	199	No projects		No projects	
Oregon Basin	II	2462	11.5	(3.6–26.1)	0.2	(0.0–0.5)
Sage	II	2566	1.2	(0.8–1.8)	0.0	(0.0–0.0)
Salt Wells	II	1595	No projects		No projects	
Seedskadee	II	352	4.6	(2.1–9.3)	0.4	(0.1–0.7)
Shell	II	147	No projects		No projects	
South Rawlins	II	3694	14.6	(0.4–31.4)	0.2	(0.0–1.3)
Thermopolis	II	105	No projects		No projects	
Uinta	II	950	5.5	(1.5–16.8)	0.1	(0.0–0.1)
Washakie	II	2599	0.7	(0.6–0.9)	0.1	(0.0–0.1)

attendance suggest that Core Areas in general were well delineated to capture productive sage-grouse populations in areas of less energy disturbance.

When conditions are favorable, sage-grouse populations can increase after a period of decrease (Garton et al. 2011). During the 1996 through 2006 recent peak, our data, in agreement with Fedy and Aldridge (2011), demonstrated Wyoming sage-grouse populations increased dramatically both in Core and non-core areas statewide and in MZ II. And, within these area designations, we found increases within Core Area were significantly higher than those observed in non-core area. We also found population variation was less in MZ II Core than in non-core areas indicating stability and resilience within Core Area sage-grouse populations in this management zone. Populations exhibiting higher variability may be more prone to significant decline as opposed to those with lower variability (Pimm 1991; Vucetich et al. 2000). Thus, in Core Area in MZ II, it appears that trends in sage-grouse populations here were able to remain more consistent due to slow rate of energy development likely combined with favorable habitats. Comparatively, in MZ I, while total male lek attendance also increased during population increase, increases in Core did not out pace those in non-core. Conditions within Core Area in MZ I, may not be more favorable to sage-grouse populations than those in non-core areas or certainly not to the degree found in MZ II. This result may be due a combination of factors including degree of development, habitat condition, or relative lower population levels.

Regardless of timeframe, we found no statistical differences between total male lek attendance in Core and non-core populations in MZ I. However, CVs indicated population numbers were more stable in Core Area vs. non-core in MZ I for most years (Harrison 1979). Regardless, MZ I habitats have been described as being less favorable to sage-grouse, in general, as MZ I includes the interface of sagebrush with the Great Plains (Knight et al. 2014) resulting in patchier sagebrush habitats across only 14 % of the area compared to 45 % in MZ II (Knick 2011). In addition, the region encompassed in MZ I has experienced historical land treatments aimed at reducing or removing sagebrush, further exacerbating the fragmentation of naturally occurring vegetation (BLM 2010). From a development perspective, MZ I experienced tremendous growth from natural gas development (primarily coalbed methane) during the 1990s through the early 2000s (Stilwell et al. 2012) and our well pad data reflect this. One study conducted in MZ I found that by 2005, male lek attendance within coalbed methane fields was 46 % less than at leks outside of these areas (Walker et al. 2007). Doherty et al. (2008) also found sage-grouse were 1.3 times more likely to occupy winter habitats that had not been developed for energy. They found a density of well spacing at12.3 well pads per 4 km^2 resulted in a decrease in odds of sage-grouse use by 0.30 compared to the average landscape (odds 0.57 vs. 0.87) in MZ I. In addition, lower numbers of males attending leks in MZ I compared to MZ II suggest MZ I leks have difficulty in recovering from energy development impacts, which occur immediately (1 year) after development in MZ I (Gregory and Beck 2014). Disease also likely contributed negatively to sage-grouse populations in MZ I. For example, Taylor et al. (2013) found after West Nile virus outbreaks in 2003 and 2007, lek inactivity rates in MZ I doubled. All of these factors likely contributed to Core Area performance not exceeding non-core in MZ I.

The majority of project development from 2012–2014 within Core Area fell within the 5 % surface disturbance thresholds of the SGEO. Yet, over 25 % of the projects did not initially meet all of the threshold requirements. It is our understanding the impacts associated with these remaining projects were minimized through further guidance with the WGFD and land management agencies (WGFD 2014). An unquantifiable aspect of the SGEO is the effort and practice of agencies applying the components of the SGEO across the Core Areas.

Conclusion

While difficult to ascertain the effects of the Wyoming SGEO policy so soon after implementation, it appears Core Area designations combined higher quality habitats with low paced levels of oil and gas development, which contribute to conserving sage-grouse. We suggest these areas contributed to the sustainability of sage-grouse populations at the statewide level and within MZ II enabling sage-grouse to continue to fluctuate and exhibit population cycles. However, despite implementation of the SGEO, we are concerned with the relatively poorer performance of sage-grouse populations in MZ I. Garton et al. (2011) developed a predictive model suggesting continued declines in MZ I potentially leading to extinction in 2107 if projected trends continue. Perhaps the current slowdown in natural gas development and increased use of horizontal drilling, which places multiple wells per pad (Applegate and Owens 2014), concurrently reducing numbers of well pads, combined with increased reclamation, restoration, and protection of habitats through easement (Copeland et al. 2013) may help provide conditions for birds to respond more favorably. In addition, a recent study reported nesting success in MZ I was higher in areas with fewer reservoirs and higher sagebrush cover, suggesting two critical issues to focus energy development mitigation in this management zone to benefit sage-grouse (Kirol et al. 2015b). Perhaps greater focus on future mitigation efforts will improve sage-grouse population response during periods of decline. Success may ultimately rest on whether the state of Wyoming maintains the political fortitude to keep this experiment in landscape conservation operating into the future.

Acknowledgments Our research would not have been possible without the efforts of biologists from Wyoming Game and Fish Department (WGFD), USDI-Bureau of Land Management, other agencies, and consulting firms in collecting lek attendance data we used to frame our analyses. The authors thank Tom Christiansen from WGFD for providing access to the Wyoming sage-grouse lek database. The authors especially acknowledge David Legg, University of Wyoming, for his critical assistance with statistical analyses. Matthew Kauffman, Roger Coupal, and Peter Stahl, University of Wyoming, and Joshua Millspaugh, University of Missouri-Columbia, all provided helpful insights in regard to study design and analyses. They also thank Mary Flanderka, John Emmerich, John Kennedy, and Troy Gerhardt from WGFD for their insights. Mark Rumble, U.S. Forest Service Research Ecologist, provided an outside review of an earlier draft, and Brian Brokling processed spatial data for use in analyses. The authors' research was supported by WGFD Grant Number 0020011.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no competing interests.

References

Aldridge CL, Boyce MS (2007) Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecol Appl 117:508–526

Applegate DH, Owens NL (2014) Oil and gas impacts on Wyoming's sage-grouse: summarizing the past and predicting the foreseeable future. Hum Wildlife Interact 8:284–290

Box GEP, Jenkins GM, Reinsel GC (1994) Time Series Analysis, Forecasting and Control, 3rd edn. Prentice Hall, Englewood Cliffs, NJ

Braun CE, Oedekoven OO, Aldridge CL (2002) Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage-grouse. Transactions of the North American Wildlife and Natural Resources Conference 67:337–349

Bureau of Land Management (2010) Draft Resource Management Plan and Final Environmental Impact Statement for the Buffalo Field Office Planning Area. U.S. Department of the Interior, Bureau of Land Management, Wyoming State Office, Cheyenne, WY

Bureau of Land Management (2012) Greater sage-grouse habitat management policy on Wyoming Bureau of Land Management (BLM) administered public lands including the Federal Mineral Estate. Instruction Memorandum No. WY-2012-019, Cheyenne, WY

Bureau of Land Management (2015) Record of Decision and Approved Resource Management Plan Amendments for the Rocky Mountain Region, Including the Greater Sage-Grouse Sub-Regions of Lewistown, North Dakota, Northwest Colorado, Wyoming, and the Approved Resource Management Plans for Billings, Buffalo, Cody, HiLine, Miles City, Pompeys Pillar National Monument, South Dakota, Worland. US Department of the Interior, Bureau of Land Management, Washington, DC

Carpenter J, Aldridge CL, Boyce MS (2010) Sage-grouse habitat selection during winter in Alberta. J Wildl Manage 74:1806–1814

Connelly JW, Knick ST, Schroeder MA, Stiver SJ (2004) Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, WY

Connelly JW, Reese KP, Schroeder MA (2003) Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station Bulletin, Vol. 80, Moscow, ID

Copeland HE, Pocewicz A, Naugle DE, Griffiths T, Keinath D, Evans J, Platt J (2013) Measuring the effectiveness of conservation: a novel framework to quantify the benefits of sage-grouse conservation policy and easements in Wyoming. PLoS ONE 8(6): e67261. doi:10.1371/journal.pone.0067261

Dinkins JB, Conover MR, Kirol CP, Beck JL, Frey SN (2014a) Greater sage-grouse hen survival: effects of raptors, anthropogenic and landscape features, and hen behavior. Can J Zool 92:319–330

Dinkins JB, Conover MR, Kirol CP, Beck JL, Frey SN (2014b) Greater sage-grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features. The Condor 116:629–642

Doherty KE (2008) Sage-grouse and energy development: integrating science with conservation planning to reduce impacts. Dissertation, University of Montana, Missoula

Doherty KE, Evans JS, Coates PS, Juliusson L, Fedy BC (2015) Importance of regional variation in conservation planning and defining thresholds for a declining species: A range-wide example of the Greater Sage-Grouse. USGS, Technical Report, p 51

Doherty KE, Naugle DE, Copeland HE, Pocewicz A, Kiesecker JM (2011) Energy development and conservation trade-offs: systematic planning for greater sage-grouse in their eastern range. In: Knick ST, Connelly JW (eds) Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38, University of California Press, Berkeley, CA, pp 505–516

Doherty KE, Naugle DE, Walker BL, Graham JM (2008) Greater sage-grouse winter habitat selection and energy development. J Wildl Manage 72:187–195

Doherty KE, Tack JD, Evans JS, Naugle DE (2010) Breeding densities of greater sage grouse: a tool for range wide conservation. BLM Completion Report: Interagency Agreement No. L10PG00911, p 30

Dzialak MR, Olson CV, Harju SM, Webb SL, Mudd JP, Winstead JB, Hayden-Wing LD (2011) Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PLoS ONE 6:e26273

Dzialak MR, Webb SL, Harju SM, Olson CV, Winstead JB, Hayden-Wing LD (2013) Greater sage-grouse and severe winter conditions: Identifying habitat for conservation. Rangeland Ecol and Manage 66:10–18

Fedy BC, Aldridge CL (2011) The importance of within-year repeated counts and the influence of scale on long-term monitoring of sage-grouse. J Wildl Manage 75:1022–1033

Fedy BC, Doherty KE (2011) Population cycles are highly correlated over long time series and large spatial scales in two unrelated species: greater sage-grouse and cottontail rabbits. Oecologia 165:915–924

Fedy BC, Doherty KE, Aldridge CL, O'Donnell M, Beck JL, Bedrosian B, Holloran MJ, Johnson GD, Kaczor NW, Kirol CP, Mandich CA, Marshall D, McKee G, Olson C, Pratt AC, Swanson CC, Walker BL (2014) Habitat prioritization across large landscapes, multiple seasons, and novel areas: an example using greater sage-grouse in Wyoming. Wildl Monographs 190:1–39

Gamo RS (2016) Effectiveness of Wyoming's sage-grouse core areas in conserving greater sage-grouse and mule deer and influence of energy development on big game harvest. Dissertation, University of Wyoming, Laramie, WY

Garton EO, Connelly JW, Horne JS, Hagen CA, Moser A, Schroeder MA (2011) Greater sage-grouse population dynamics and probability of persistence. In: Knick ST, Connelly JW (eds) Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38, University of California Press, Berkeley, CA, pp 293–382

Garton EO, Wells AG, Baumgardt JA, Connelly JW (2015) Greater sage-grouse population dynamics and probability of persistence. Final Report to The Pew Charitable Trusts, Washington, DC

Gregory AJ, Beck JL (2014) Spatial heterogeneity in response of male greater sage-grouse lek attendance to energy development. PLoS ONE 9(6):e97132

Harju SM, Dzialak MR, Taylor RC, Hayden-Wing LD, Winstead JB (2010) Thresholds and time lags in effects of energy development on greater sage-grouse populations. J Wildl Manage 74:437–448

Harrison GW (1979) Stability under environmental-stress—resistance, resilience, persistence, and variability. Am Nat 113:659–669

Hess JE, Beck JL (2012) Disturbance factors influencing greater sage-grouse lek abandonment in north-central, Wyoming. J Wildl Manage 76:1625–1634

Holloran MJ (2005) Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, WY

Holloran, MJ, SH Anderson SH (2005) Greater sage-grouse population response to natural gas development in western Wyoming: are regional populations affected by relatively localized disturbances. Trans North American Wildl and Nat Res Conf 70:160–170

Holloran MJ, Fedy BC, Dahlke J (2015) Winter habitat use of greater sage-grouse relative to activity levels at natural gas well pads. J Wildl Manage 79:630–640

Holloran MJ, Kaiser RC, Hubert WA (2010) Yearling greater sage grouse response to energy development in Wyoming. J Wildl Manage 74:65–72

Kirol CP, Beck JL, Huzurbazar SV, Holloran MJ, Miller SN (2015a) Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. Ecol Apps 25:968–990

Kirol CP, Sutphin AL, Bond L, Fuller MR, Maechtle TL (2015b) Mitigation effectiveness for improving nesting success of greater sage-grouse influenced by energy development. Wildl Biol 21:98–109

Knick ST (2011) Historical development, principal federal legislation, and current management of sagebrush habitats. In: Knick ST, Connelly JW (eds) Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38, University of California Press, Berkeley, CA, pp 13–31

Knight DH, Jones GP, Reiners WA, Romme WH (2014) Mountains and plains: the ecology of Wyoming landscapes, 2nd edn. Yale University Press, New Haven, CT

LeBeau CW, Beck JL, Johnson GD, Holloran MJ (2014) Short-term impacts of wind energy development on greater sage-grouse fitness. J Wildl Manage 78:522–530

Lyon AG, Anderson SH (2003) Potential gas development impacts on sage grouse nest initiation and movement. Wildl Soc Bull 31:486–491

Nielson RM, McDonald LL, Mitchell J, Howlin S, LeBeau C (2015) Analysis of greater sage-grouse lek data: Trends in peak male counts 1965-2015. West. EcoSys. Tech., Inc., Cheyenne, WY

Oregon Department of Fish and Wildlife (2011) Greater sage-grouse conservation assessment and strategy for Oregon: a plan to maintain and enhance populations and habitat, p 221

Pimm SL (1991) The balance of nature. University of Chicago Press, Chicago, IL

Rowland MM, Leu M (2011) Study area description. In: Hanser SE, Leu M, Knick ST, Aldridge CL (eds) Sagebrush ecosystem conservation and management: Ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, KS, pp 10–45

Schroeder MA, Aldridge CL, Apa AD, Bohne JR, Braun CE, Bunnell SD, Connelly JW, Deibert PA, Gardner SC, Hilliard MA, Kobriger GD, McAdam SM, McCarthey CW, McCarthy JJ, Mitchell DL, Rickerson EV, Stiver SJ (2004) Distribution of sage-grouse in North America. Condor 106:363–376

Smith KT, Beck JL, Pratt AC (2016) Does Wyoming's core area policy protect winter habitats for greater sage-grouse? Environ Manage 58:585–596

Smith KT, Kirol CP, Beck JL, Blomquist FC (2014) Prioritizing winter habitat quality for greater sage-grouse in a landscape influenced by energy development. Ecosphere 5:15

State of Idaho (2012a) Governor C. L. Butch Otter. Establishing the Governor's sage-grouse task force. Executive Order 2012–02

State of Idaho (2012b) Federal alternative of Governor C. L. Butch Otter for greater sage-grouse management in Idaho, p 54

State of Montana (2014) Office of Steve Bullock. State of Montana Executive Order No. 10-2014. Executive Order Creating the Sage Grouse Oversight Team and the Montana Sage Grouse Habitat Conservation Plan, p 29

State of Nevada (2014) Nevada greater sage-grouse conservation plan. Sagebrush Ecosystem Program, Carson City, NV, p 214

State of Wyoming (2008) Office of Governor Freudenthal. State of Wyoming Executive Department Executive Order. Greater Sage Grouse Area Protection, 2008–02

State of Wyoming (2011) Office of Governor Mead. State of Wyoming Executive Department Executive Order. Greater Sage Grouse Area Protection, 2011–05

Stilwell DP, Elser AM, Crockett FJ (2012) Reasonable Foreseeable Development Scenario for Oil and Gas Buffalo Field Office Planning Area, Wyoming. U.S. Department of the Interior, Bureau of Land Management, Buffalo, WY

Stiver SJ, Apa AD, Bohne JR, Bunnell SD, Deibert PA, Gardner SC, Hilliard MA, McCarthy CW, Schroeder MA (2006) Greater sage-grouse: comprehensive conservation strategy. Western Association of Fish and Wildlife Agencies, Cheyenne, WY, USA

Stiver SJ (2011) The legal status of greater sage-grouse: organizational structure of planning efforts. In: Knick ST, Connelly JW (eds) Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38, University of California Press, Berkeley, CA, pp 33–52

Taylor RL, Tack JD, Naugle DE, Mills LS (2013) Combined effects of energy development and disease on greater sage-grouse. PLoS ONE 8(8):e71256

Thilenius JF, Brown GR, Medina AL (1994) Vegetation on semi-arid rangelands, Cheyenne River Basin, Wyoming. General Technical Report RM-GTR-263. Fort Collins, CO. U. S. Dept. of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, p 60

U. S. Fish and Wildlife Service [USFWS] (2010) Endangered and Threatened Wildlife and Plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Fed Reg 75:13909–14014

U.S. Fish and Wildlife Service [USFWS] (2015) Endangered and Threatened Wildlife and Plants; 12-Month Finding on a Petition to list Greater Sage-Grouse (*Centrocercus urophasianus*) as an Endangered or Threatened Species; Proposed Rule. Fed Reg 80:59858–59942

Vucetich JA, Waite TA, Qvarnemark L, Ibarguen S (2000) Population variability and extinction risk. Cons Biol 14:1704–1714

Walker BL, Naugle DE, Doherty KE (2007) Greater sage-grouse population response to energy development and habitat loss. J Wildl Manage 71:2644–2654

Weisberg S (1985) Applied linear regression. John Wiley and Sons, New York and Chichester, UK

Wisdom MJ, Meinke CW, Knick ST, Schroeder MA (2011) Factors associated with extirpation of sage-grouse. In: Knick ST, Connelly JW (eds) Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38, University of California Press, Berkeley, CA, pp 451–474

Wyoming Game and Fish [WGFD] (2014) US Fish and Wildlife Service Greater Sage-Grouse (*Centrocercus urophasianus*) 2014 Data Call. Wyoming Game and Fish Department October 31, p 258

Wyoming Oil and Gas Conservation Commission (2014) WOGCC homepage. http://www.wogcc.wyo.gov/ Accessed Dec 2014

Grancel Fitz measuring the circumference of the main beam of an Alaska-Yukon moose. Fitz and Dr. James L. Clark were key members of a committee formed by the Boone and Crockett Club to develop an equitable, objective measurement system for big game of North America. Photo courtesy Boone and Crockett Club.

Wildlife Monographs 183:1–26; 2013; DOI: 10.1002/wmon.1007

Effects of Harvest, Culture, and Climate on Trends in Size of Horn-Like Structures in Trophy Ungulates

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ABSTRACT Hunting remains the cornerstone of the North American model of wildlife conservation and management. Nevertheless, research has indicated the potential for hunting to adversely influence size of horn-like structures of some ungulates. In polygynous ungulates, mating success of males is strongly correlated with body size and size of horn-like structures; consequently, sexual selection has favored the development of large horns and antlers. Horn-like structures are biologically important and are of great cultural interest, both of which highlight the need to identify long-term trends in size of those structures, and understand the underlying mechanisms responsible for such trends. We evaluated trends in horn and antler size of trophy males (individuals exhibiting exceptionally large horns or antlers) recorded from 1900 to 2008 in Records of North American Big Game, which comprised >22,000 records among 25 trophy categories encompassing the geographic extent of species occupying North America. The long-term and broad-scale nature of those data neutralized localized effects of climate and population dynamics, making it possible to detect meaningful changes in size of horn-like structures among trophy males over the past century; however, ages of individual specimens were not available, which prevented us from evaluating age-class specific changes in size. Therefore, we used a weight-of-evidence approach based on differences among trophy categories in life-history characteristics, geographic distribution, morphological attributes, and harvest regimes to discriminate among competing hypotheses for explaining long-term trends in horn and antler size of trophy ungulates, and provide directions for future research. These hypotheses were young male age structure caused by intensive harvest of males (H1), genetic change as a result of selective male harvest (H2), a sociological effect (H3), effects of climate (H4), and habitat alteration (H5). Although the number of entries per decade has increased for most trophy categories, trends in size of horn-like structures were negative and significant for 11 of 17 antlered categories and 3 of 8 horned categories. Mean predicted declines during 1950–2008 were 1.87% and 0.68% for categories of trophy antlers and horns, respectively. Our results were not consistent with a sociological effect (H3), nutritional limitation imposed by climate (H4), or habitat alteration (H5) as potential explanations for long-term trends in size of trophies. In contrast, our results were consistent with a harvest-based explanation. Two of the 3 species that experienced the most conservative harvest regimes in North America (i.e., bighorn sheep [*Ovis canadensis*] and bison [*Bison bison*]) did not exhibit a significant, long-term trend in horn size. In addition, horn size of pronghorn (*Antilocapra americana*), which are capable of attaining peak horn size by 2–3 years of age, increased significantly over the past century. Both of those results provide support for the intensive-harvest hypothesis, which predicts that harvest of males has gradually shifted age structure towards younger, and thus smaller, males. The absence of a significant trend for mountain goats (*Oreamnos americanus*), which are difficult to accurately judge size of horns in the field, provided some support for the selective-harvest hypothesis. One other prediction that followed from the selective-harvest hypothesis was not supported; horned game were not more susceptible to reductions in size. A harvest-induced reduction in age structure can increase the number of males that are harvested prior to attaining peak horn or antler size, whereas genetic change imposed by selective harvest may be less likely to occur in free-ranging populations when other factors, such as age and nutrition, can override genetic potential for size. Long-term trends in the size of trophy horn-like structures provide the incentive to evaluate the appropriateness of the current harvest paradigm, wherein harvest is focused largely on males; although the lack of information on age of specimens prevented us from rigorously differentiating among causal mechanisms. Disentangling potential mechanisms underpinning long-term trends in horn and antler size is a daunting task, but one that is worthy of additional research focused on elucidating the relative influence of nutrition and effects (both demographic and genetic) of harvest. © 2013 The Wildlife Society.

Received: 10 November 2011; Accepted: 11 October 2012.

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Los Efectos De La Explotación, La Cultura Y El Clima En El Tamaño De Estructuras Corniformes En Los Ungulados Tipo “Trofeo”

RESUMEN La caza sigue siendo el fundamento del modelo norteamericano de conservación y mantenimiento de la fauna y la flora. Sin embargo, las investigaciones evidencian la posibilidad de que la caza pueda tener un impacto negativo en el tamaño de las estructuras corniformes de algunos ungulados. En el caso de los ungulados poligínicos, el apareamiento exitoso de los machos tiene una estrecha correlación con el tamaño del individuo y de las estructuras corniformes; por lo que la selección sexual ha favorecido el desarrollo de cuernos y de astas de gran tamaño. Las estructuras corniformes tienen importancia desde el punto de vista biológico y cultural, lo que destaca la necesidad de identificar tendencias a largo plazo en el tamaño de dichas estructuras, así como de entender los mecanismos subyacentes responsables de tales tendencias. Hemos evaluado tendencias en tamaño de los cuernos y astas de machos tipo “trofeo” (individuos que presentan cuernos o astas de tamaño excepcional) documentadas desde 1900 hasta 2008, en el Registro sobre la caza mayor en América del Norte (*Records of North American Big Game*), que comprende más de 22.000 registros que abarcan 25 categorías distintas de “trofeos,” comprendiendo el total de las especies que habitan en la extensión geográfica de América del Norte. La circunstancia de que estos datos son de largo plazo y gran escala, neutraliza los efectos localizados del clima y la dinámica demográfica, haciendo posible detectar cambios significativos en el tamaño de las estructuras corniformes entre machos “trofeo” a lo largo del siglo pasado; sin embargo, no tuvimos disponible la edad de cada uno de los especímenes, lo cual nos impidió evaluar cambios en el tamaño de grupos separados por edades. Es por ello que, para discriminar entre las hipótesis alternativas que explican las tendencias en el largo plazo del tamaño de los cuernos y astas de los ungulados tipo “trofeo,” ponderamos la evidencia, basándonos en las diferencias entre categorías de individuos “trofeo” con fundamento en características del ciclo vital, la distribución geográfica, atributos morfológicos y sistemas de explotación, proporcionando así orientación para las investigaciones futuras. Las mencionadas hipótesis son: estructura de edad en los machos jóvenes causada por la explotación intensiva de los mismos (H1), el cambio genético resultante de la explotación selectiva de machos (H2), el efecto sociológico (H3), los efectos del clima (H4) y la modificación del hábitat (H5). Aunque para la mayoría de las categorías “trofeo” ha habido un incremento en el número de registros por década, las tendencias de tamaño en las estructuras corniformes fueron significativamente negativas para 11 de las 17 categorías con astas, y para 3 de las 8 categorías con cuernos. Desde 1950 hasta 2008, la disminución prevista de los promedios para las categorías con astas y las categorías con cuernos fue de 1,87% y de 0,68%, respectivamente. Nuestros resultados no fueron congruentes con el efecto sociológico (H3), la limitación alimenticia impuesta por el clima (H4), ni con la modificación del hábitat (H5), como posibles explicaciones de las tendencias a largo plazo en el tamaño de los trofeos, pero sí concordaron con la explicación basada en la explotación. Dos de las 3 especies en América del Norte que experimentaron los regímenes más conservadores de explotación (a saber, el carnero de las rocosas o muflón montañés, *Ovis canadensis* y el bisonte americano, *Bison bison*) no mostraron una tendencia significativa en el largo plazo en el tamaño de los cuernos. Adicionalmente, el tamaño de los cuernos entre los antílopes americanos (*Antilocapra americana*), cuyos cuernos pueden alcanzar el máximo tamaño a los 2 ó 3 años de edad, aumentó considerablemente a lo largo del siglo pasado. Los resultados anteriores apoyan la hipótesis de la explotación intensiva; lo cual, indica que la explotación cuantiosa de machos a través del tiempo ha desplazado gradualmente las estructuras de edad hacia machos más jóvenes, y en consecuencia, más pequeños. La falta de una tendencia significativa en el caso de la cabra montesa o cabra blanca (*Oreamnos americanus*), el tamaño de cuyos cuernos es difícil de evaluar en su hábitat natural, proporciona apoyo a la hipótesis de la explotación selectiva. Otra proyección que se deriva de la anterior hipótesis no se pudo apoyar. La reducción en estructuras de edad, inducida por la explotación, puede incrementar el número de machos explotados antes de alcanzar el máximo tamaño de cuernos o astas, mientras que el cambio genético impuesto por la explotación selectiva tiene menor probabilidad de ocurrir entre poblaciones silvestres cuando existe la posibilidad de que otros factores, tales como la edad y la nutrición, resten valor al potencial genético de tamaño. Las tendencias a largo plazo en el tamaño de estructuras corniformes tipo “trofeo” son un incentivo para el análisis de la adecuación del patrón de explotación actual, el cual está enfocado principalmente en los machos; no obstante, la falta de información sobre la edad de los ejemplares nos impidió distinguir con precisión entre los mecanismos de causalidad. Dilucidar los posibles mecanismos que respaldan las tendencias a largo plazo en el tamaño de los cuernos y astas es una tarea ardua, pero merecedora de investigación adicional con énfasis en la aclaratoria de la influencia relativa de la alimentación y los efectos (tanto demográficos como genéticos) de la explotación.

Effets de la récolte, de la culture, et du climat sur les tendances de la taille des ornements chez Les ongulés à trophée

RÉSUMÉ La chasse demeure la pierre angulaire des modèles de conservation et d'aménagement de la faune en Amérique du Nord. De récentes recherches ont toutefois révélé que la chasse avait le potentiel d'affecter négativement la structure de la taille des ornements (i.e., cornes ou bois) chez certains ongulés. Chez les ongulés polygynes, le succès d'accouplement des mâles est fortement corrélé à la taille corporelle et à la taille des ornements; par conséquent, la sélection sexuelle tend à favoriser le développement de bois ou de cornes de fortes dimensions. L'importance biologique et le grand intérêt culturel relié aux ornements mettent, tous deux, en évidence la nécessité d'identifier les tendances à long terme dans la taille de ces structures et de comprendre les mécanismes responsables ces tendances. Nous avons évalué les tendances dans la taille des cornes et des bois de mâles trophées (individus présentant des cornes et bois de taille exceptionnelle) enregistrés, entre 1900 et 2008, dans le «Records of North American Big Game» qui comprenait >22,000 enregistrements répartis dans 25 catégories de trophées couvrant la répartition géographique des espèces occupant l'Amérique du Nord. Le fait que les données soient disponibles à long terme et à large échelle spatiale a permis de compenser pour les effets localisés du climat et de la dynamique de population, rendant possible la détection de changements significatifs dans la taille des ornements parmi les mâles trophées récoltés au cours de la dernière décennie; l'âge des individus n'était toutefois pas disponible, ce qui nous a empêché d'évaluer les changements de la taille des ornements entre les classes d'âge. Par conséquent, nous avons utilisé l'approche du poids de la preuve basée sur les différences entre les catégories de trophées au niveau des traits bio-démographiques, de la répartition géographique, des caractéristiques morphologiques, et du taux de récolte afin de discriminer entre les hypothèses concurrentes visant à expliquer les tendances à long terme dans la taille des cornes et des bois des trophées chez les ongulés et d'orienter de futures recherches. Les hypothèses concurrentes étaient que: la jeune structure d'âge des mâles découle de la récolte intensive des mâles (H1), du changement génétique résultant de la sélectivité des mâles récoltés (H2), d'un effet sociologique (H3), et des effets du climat (H4) et d'une altération de l'habitat (H5). Malgré l'augmentation du nombre de données récoltées par décennie pour la plupart des catégories de trophée, les tendances dans la taille des ornements étaient négatives et significatives pour 11 des 17 catégories de bois et 3 des 8 catégories de cornes. Entre 1950–2008, le déclin moyen prédit pour les catégories de trophées de bois et de cornes était, respectivement, de 1.87% et 0.68%. Nos résultats ne concordaient pas avec un effet sociologique (H3), une contrainte nutritionnelle imposée par le climat (H4), ou une altération de l'habitat (H5) comme explications potentielles des tendances à long terme de la taille des trophées. À l'opposé, nos résultats concordaient avec une explication basée sur la récolte. Deux des 3 espèces ayant connu les niveaux de récolte les plus conservateurs en Amérique du Nord (i.e., le mouflon d'Amérique, *Ovis canadensis* et le bison, *Ovis canadensis*) ne présentaient pas de tendance à long terme dans la taille de cornes. De plus, la taille des cornes chez l'antilope d'Amérique (*Antilocapra americana*), qui peut atteindre une taille asymptotique vers l'âge de 2–3 ans, a augmenté significativement au cours du siècle dernier. Ces résultats appuient, tous deux, l'hypothèse d'une récolte intensive prédisant que la forte récolte de mâles peut déplacer graduellement la structure d'âge vers les jeunes et, conséquemment, plus petits individus. L'absence d'une tendance significative pour les chèvres de montagne (*Oreamnos americanus*), dont la taille des cornes est difficile d'évaluer précisément sur le terrain, fourni un certain support à l'hypothèse de la récolte sélective. Une autre prédiction découlant de cette hypothèse n'était pas supportée. Une réduction de la structure d'âge induite par la récolte peut augmenter le nombre de mâles qui sont récoltés avant l'atteinte de la taille asymptotique de leurs bois ou cornes, alors qu'un changement génétique résultant de la sélectivité de la récolte est moins susceptible de se produire chez des populations sauvages lorsque d'autres facteurs, tels que l'âge et la nutrition, prévalent au potentiel génétique pour la taille des ornements. Les tendances à long terme de la taille des trophées incitent à évaluer la pertinence du paradigme actuel suggérant que la récolte cible principalement les mâles; toutefois le manque d'information sur l'âge des individus récoltés nous a empêché de distinguer rigoureusement entre les mécanismes causaux suggérés. Distinguer les mécanismes potentiels sous-jacents aux tendances à long terme de la taille des cornes et des bois est une tâche ardue, mais qui mérite d'être sujette à des efforts de recherche supplémentaires portant sur l'influence relative de la nutrition et des effets, tant démographiques que génétiques, de la récolte.

KEY WORDS antlers, Artiodactyla, Bovidae, Cervidae, climate, exploitation, horns, North America, selective harvest, trophy hunting.

Contents

INTRODUCTION

Horn-like structures of Cervidae and Bovidae are among the most spectacular examples of secondary sexual characteristics (Geist 1966*a*, Gould 1974, Wilson and Mittermeier 2011), and likely evolved primarily for male-male combat, including display related to such interactions (Geist 1966*b*, 1971; Clutton-Brock 1982; Goss 1983; Bubenik and Bubenik 1990). Antlers typically are branched structures composed of bone that are grown and shed on an annual basis, whereas true horns are permanent structures with sheaths composed of cornified epidermal cells usually arranged around a bony core (Goss 1983). Pronghorn (*Antilocapra americana*) are the sole member of Antilocapridae, and possess branched, deciduous horns (Byers 1997, O'Gara and Yoakum 2004).

Size of horn-like structures is influenced by age, nutrition, and genetics (Harmel 1982, Brown 1983, Goss 1983, Bubenik and Bubenik 1990, Hartl et al. 1995). Antler size in cervids typically increases with age, peaks only after asymptotic body mass has been reached, and then often exhibits declines with senescence (Brown 1983, Goss 1983, Stewart et al. 2000, Bowyer et al. 2001, Monteith et al. 2009). In bovids, growth rate of horns declines with age, yet horn size typically continues to increase over the lifetime of an animal (Bergeron et al. 2008). Brooming (i.e., the wearing of horn tips) is an exception to this pattern, because it results in the loss of the distal portion of horns (Geist 1971, Shackleton and Hutton 1971, Bubenik and Bubenik 1990). Annual horn growth in later life may not be adequate to compensate for horn loss associated with brooming. Pronghorn are unique among North American artiodactyls because they exhibit advanced horn development at a young age; peak horn size can occur as early as 2–3 years of age (Mitchell and Maher 2001, 2006).

In contrast to natural sources of mortality, which may affect young-of-the-year and senescent individuals disproportionately, human harvest causes high mortality among prime-aged (after attaining asymptotic body mass, but prior to senescence) and young adults (Gaillard et al. 1998, Festa-Bianchet 2003, Berger 2005). Further, wildlife-management agencies in North America often restrict harvest to mostly males, thereby protecting females that, in polygynous species, represent the primary reproductive component of the population (McCullough 1979); such regimes are possible because a single male can inseminate numerous females (Noyes et al. 1996, 2002; Mysterud et al. 2003; Bowyer et al. 2007). Results of such a harvest regime include sex ratios skewed towards females and a young age structure for males (Ginsberg and Millner-Gulland 1994, Berger and Gompper 1999, Whitten 2001, Jenks et al. 2002, Keyser et al. 2006). Skewed sex ratios and a young male age structure reduces the proportion of prime-aged males, which may cause increased reproductive effort by young males and an associated reduction in their growth (Stevenson and Bancroft 1995, Laurian et al. 2000, Singer and Zeigenfuss 2002, Garel et al. 2006, Milner et al. 2007).

Allocation of resources to size of horn-like structures comes secondary to growth and maintenance of somatic tissues (Jorgenson et al. 1998, Stewart et al. 2000, Kruuk et al. 2002, Festa-Bianchet et al. 2004, Mysterud et al. 2005). Horns and antlers are phenotypic characters that are genetically based but, because they are costly to produce, their growth is influenced strongly by nutrition (Harmel 1982, Geist 1986, Lukefahr and Jacobson 1998, Festa-Bianchet et al. 2004, Monteith et al. 2009). Nutritional effects on growth of horns and antlers may be manifested through mechanisms that are determined by variation in climate and density dependence. For example, large-scale climatic regimes influence local and regional patterns of temperature and precipitation, both of which strongly affect quality and abundance of forage (Post et al. 1997, Post and Stenseth 1999, Marshal et al. 2002, Forchhammer and Post 2004, Forchhammer et al. 2005). As a result, climate-mediated variation in annual forage quality and availability in relation to population density affects net nutritional gain and the capacity of males to allocate resources to growth of horns or antlers (Schmidt et al. 2001, Kruuk et al. 2002, Mysterud et al. 2005, Loehr et al. 2010).

Size and symmetry of horn-like structures are heritable (Hartl et al. 1991, 1995; Williams et al. 1994; Lukefahr and Jacobson 1998; Kruuk et al. 2002), are considered to be honest signals of phenotypic quality (Solberg and Sæther 1993, Ditchkoff et al. 2001, Malo et al. 2005, Vanpé et al. 2007, Bonenfant et al. 2009*b*), including increased sperm production (Preston et al. 2003, Malo et al. 2005, Gomendio et al. 2007) and parasite resistance (Ezenwa and Jolles 2008), and often are positively correlated with body size (Clutton-Brock et al. 1982, Bowyer 1986, Stewart et al. 2000, Monteith et al. 2009). For many species of large herbivores, big males with large horn-like structures frequently enjoy high reproductive success (Clutton-Brock 1982, Coltman et al. 2002, Kruuk et al. 2002, Preston et al. 2003, Mainguy et al. 2008). As a result, sexual selection has favored development of large horn-like structures in many artiodactyls (Vanpé et al. 2010). In harvested populations, however, natural mating systems may be disrupted by the selective removal of large males (Coltman et al. 2003, Garel et al. 2007, Rasmussen et al. 2008, Bonenfant et al. 2009*b*) or heavy harvest of males (Bowyer et al. 1999, Langvatn and Loison 1999, Laurian et al. 2000, Solberg et al. 2000, Milner et al. 2007).

Among polygynous ungulates, large horns and antlers can enhance reproductive success, but they also are favored by trophy hunters (Festa-Bianchet and Lee 2009, Messner 2011). Although effects of hunting on demographics of ungulate populations are well recognized (Bowyer et al. 1999, Langvatn and Loison 1999, Solberg et al. 2000, Milner et al. 2007, Hengeveld and Festa-Bianchet 2011), the consequence of selection against heritable traits remain a contentious issue (Darimont et al. 2009, Festa-Bianchet and Lee 2009). The primary empirical evidence supporting effects of trophy hunting on growth of secondary sexual characters is for wild sheep (*Ovis* spp.), wherein intensive harvest of males with superior secondary sexual characteristics has led to decreased size or altered conformation of horns (Coltman et al. 2003, Garel et al. 2007). Long-term consequences of human harvest on targeted phenotypes continue to be debated (Mysterud and Bischof 2010, Hedrick 2011, Mysterud 2011, Pérez et al. 2011), in part because the applicability of these unique studies to other populations occupying a variety of habitats with wide geographic ranges, and different harvest pressure, is uncertain.

Despite the importance of hunting as a tool for conservation and management (Whitfield 2003, Lindsey et al. 2007, Festa-Bianchet and Lee 2009, Groves and Leslie 2011, Becker et al. 2013), heavy harvest of males could reduce mean size of horn-like structures through changes in age at harvest (Stewart et al. 2000, Loehr et al. 2007, Bonenfant et al. 2009*b*, Monteith et al. 2009, Servanty et al. 2011), sex ratios (Laurian et al. 2000, Garel et al. 2006, Milner et al. 2007), or via genetic changes caused by selective removal of large or rapidly growing males (Coltman et al. 2003, Garel et al. 2007). As a result, questions related to effects of harvest on size of horn-like structures remain controversial (Fenberg and Roy 2008). A major difficulty in addressing those questions is the near absence of data that span a sufficiently long time frame for harvested populations (Proaktor et al. 2007, Tiilikainen et al. 2010, Servanty et al. 2011). Effects of harvest may require decades to manifest themselves (Hundertmark et al. 1998), and studies conducted at the population level must account for effects of nutritional limitation via density dependence, habitat loss, or other factors, which are more likely to be diluted and less influential when analyses are conducted at a broad geographic scale, such as the geographic range of a species.

The importance of trophy hunting as an economic activity and conservation tool for multiple species in many countries (Harris and Pletscher 2002, Whitfield 2003, Lindsey et al. 2007, Groves and Leslie 2011, Becker et al. 2013) reinforces the need to understand long-term relationships between harvest regimes and horn and antler size. The Records of North American Big Game, which was established by the Boone and Crockett Club in 1932, contains data on horn and antler size of trophy ungulates spanning more than a century and includes the entire geographic range of most native species (Reneau and Buckner 2005). Data available in Records of North American Big Game represent a unique resource for evaluating long-term patterns of horn and antler size among trophy ungulates in North America. Although these data do not represent a random sample of ungulates across North America, they should be representative of the size of large, trophy ungulates, most of which will already have attained asymptotic body mass (Monteith et al. 2009). Moreover, if changes in the size of large, horn-like structures occur, they should be manifested in the size of these trophy males.

Weight-of-Evidence Approach

The broad-scale nature of Records of North American Big Game precluded testing some hypotheses that could explain temporal trends in those data at a smaller spatial scale (i.e., regional). In addition, ages of individual specimens were not available, which prevented us from evaluating age-class specific changes in size of horns and antlers. Consequently, after identifying temporal trends in size of horn-like structures, we used a weight-of-evidence approach (Bowyer et al. 2003, Pierce et al. 2012) that was based on a series of category-specific predictions for explaining those trends that followed directly from 5 primary hypotheses. We identified differences among trophy categories in life-history characteristics, geographic distribution, morphological attributes, harvest regimes, and anthropogenic disturbance that helped to infer potential mechanisms underpinning observed trends.

Intensive-harvest hypothesis (H1).—The intensive-harvest hypothesis is based on the premise that as harvest intensity increases, age distribution shifts towards younger age classes (Jenks et al. 2002). Harvest intensity of large ungulates varies greatly both among and within species across their geographic ranges (Demarais and Krausman 2000). Given the difficulty in estimating population size and harvest rates of large ungulates accurately, reliable estimates of harvest intensity generally were not available (Walker 2011). Consequently, we limited our interpretation of relationships between harvest intensity and trends in horn or antler size to a categorical comparison of bighorn sheep (*Ovis canadensis canadensis*), desert sheep (*Ovis canadensis nelsoni*), and bison (*Bison bison*) with all other trophy categories. Although harvest of some populations of wild sheep are still regulated by size restrictions, most populations of bighorn sheep, desert sheep, and bison are harvested based on very conservative quotas compared with other species where males are more heavily exploited (Winkler 1987, Douglas and Leslie 1999, Krausman and Shackleton 2000, Festa-Bianchet and Lee 2009). Among jurisdictions responsible for managing bighorn and desert sheep in North America, harvest rates of male sheep as of 2007 averaged 2.5 males per 100 sheep (range 1.3–3.5), which represented an estimated 7–12% of all males within the population, with 51% of the harvest ≥8 years old (Wild Sheep Foundation Professional Biologist Meeting Attendees 2008). Similarly, because of their restricted range, which often is limited to national and state parks or preserves, bison were not typically managed to provide a sustained harvest, but were harvested by small opportunistic hunts with limited trophy harvest (Shaw and Meagher 2000). Although, for other trophy categories, some hunt units are more conservatively managed to allow for increased trophy potential, the more common management scenario increases hunter opportunity by allowing harvest of a much larger proportion of the male segment of the population (Jenks et al. 2002). For example, an estimated 14.3% of deer (*Odocoileus* spp.) and 15.5% of elk (*Cervus* spp.) across 19 western states and provinces were harvested in 2009 (Walker 2011), which typically results in a lower age distribution of the male harvest. Indeed, for 26 states with available age data, 68% of male white-tailed deer harvested in 2010 were ≤2.5 years old (Adams et al. 2012).

Conservative male harvest yields a higher relative abundance of prime-aged males with large horns or antlers (Milner et al. 2007, Fenberg and Roy 2008), compared with other species where males are more heavily exploited. If intensive harvest of males has progressively shifted age structure toward younger males with fewer individuals surviving to old ages and reaching large sizes, then horn size of bighorn sheep, desert sheep, and bison should be less likely to decline through time, because male harvest regimes for those trophy categories generally were highly conservative (i.e., limited harvest of males; P1a). Additionally, pronghorn should be less prone to declines in horn size caused by a downward shift in age structure by heavy harvest (P1b), because pronghorn can attain peak horn size by 2–3 years old (Mitchell and Maher 2001, 2006).

Selective-harvest hypothesis (H2).—We assessed 2 predictions that were based on the hypothesis that trophy hunting has selected against genes for large horn-like structures. Species that are difficult to field judge should be less likely to exhibit a negative trend than species for which hunters can more easily assess size in the field, and thus selectively remove the largest individuals (P2a). For example, mountain goats (*Oreamnos americanus*) should be less prone to selective harvest because size of their small, cylindrical horns is difficult to assess in the field (Festa-Bianchet and Côté 2008).

Once a horned animal becomes large enough to be considered a trophy, it will remain a trophy throughout its lifetime regardless of environmental conditions or age, unless substantial brooming occurs. In contrast, antlers are cast and regrown each year, and size varies as a curvilinear function of age and can be influenced strongly by interannual variation in environmental conditions. Consequently, an individual cervid may be a trophy in 1 year and not in subsequent years. Based on those differential patterns of growth and morphology, we predicted that if selective harvest was the primary cause of declines in size of horn-like structures, then declines would be more apparent for horned than antlered game (P2b); trophy hunters may be more effective at removing trophy males with large horns, because those phenotypic characters are expressed more consistently through time than are those of antlers.

Sociological effect hypothesis (H3).—We evaluated 2 specific predictions that followed from the hypothesis that an increased desire to submit smaller, yet eligible, trophies to the Boone and Crockett Club record book (i.e., sociological hypothesis; Messner 2011) has biased observed trends in size of horn-like structures downward through time. First, assuming that annual number of entries recorded partially reflects interest in submitting trophies, number of entries (number of trophies entered per year for each trophy category) should be negatively related to size of horn-like structures (P3a). Second, negative trends in size of trophy horn-like structures should be less apparent among the largest specimens compared with the entire dataset, because the sociological hypothesis is based on the premise that a disproportionately larger increase in entry of smaller eligible trophies is influencing observed trends (P3b).

Climate (H4) and habitat (H5) hypotheses.—We also evaluated predictions that followed from hypotheses related to climate and habitat alteration. First, although effects of global changes in climate are difficult to separate from density dependence (Bonenfant et al. 2009*a*), if climatic changes have affected the ability of males to grow large horn-like structures, then broad-scale climatic indices should be related to the underlying trends in size of antlers at the continent-wide scale of this analysis (P4a). Climatic patterns can affect growth of antlers and horns similarly, but effects of climate on antler size are realized annually, whereas effects of climate on horn size are cumulative because horns grow continuously throughout the life of the animal. Because most horn growth occurs during numerous years prior to harvest, the absence of age data prevented an evaluation of potential climate effects on size of horns (Loehr et al. 2010). Therefore, we assessed effects of climate on trends in size of deciduous horn-like structures (i.e., antlers and pronghorns).

Most large mammal species in North America have experienced some degree of both habitat improvement and degradation over the past century (Demarais and Krausman 2000). Quantifying these changes, however, is nearly impossible, and thus we used examples that occurred at one extreme of the continuum of habitat change to evaluate the hypothesis that loss of habitat has negatively influenced size of horn-like structures. If loss or degradation of habitat has affected growth of horn-like structures, then horn size of Dall's sheep (*Ovis dalli dalli* and *O. d. kenaiensis*), Stone's sheep (*Ovis dalli stonei*), and muskox (*Ovibos moschatus*) should be least likely to show a negative trend in horn size, because most of the range of those species is pristine and intact (Bowyer et al. 2000; P5a) and muskox have expanded into high-quality habitat in recent years (Klein 2000).

METHODS

We evaluated patterns in horn and antler size of trophy animals recorded in Records of North American Big Game by the Boone and Crockett Club. We used trophy categories defined by the Boone and Crocket Club, including typical and non-typical categories (Table 1). For cervids, non-typical categories were developed to facilitate recognition of large, asymmetrical specimens, the scores of which would otherwise be severely penalized for exhibiting excessive abnormal characteristics. In addition, because we were interested only in total size of horn-like structures, we used the sum of all measured components of size (defined as gross score by the Boone and Crockett Club). Gross score, or some derivative of that metric, has been used

Table 1. Trophy categories of native, North American big game recorded in Records of North American Big Game. We provide scientific names of all taxa included in each category, along with sample sizes of trophies within categories included in our analyses (1900–2008).

Trophy category	Scientific name	*n*
Antlered game		
Alaska-Yukon moose	*Alces alces gigas*	576
Canada moose	*Alces alces americana* and *A. a. andersoni*	774
Shiras moose	*Alces alces shirasi*	694
Non-typical Coues' white-tailed deer	*Odocoileus virginianus couesi*	95
Typical Coues' white-tailed deer	*Odocoileus virginianus couesi*	335
Non-typical white-tailed deer	*Odocoileus virginianus virginianus* and related subspecies	3,182
Typical white-tailed deer	*Odocoileus virginianus virginianus* and related subspecies	4,443
Non-typical mule deer	*Odocoileus hemionus hemionus* and related subspecies	656
Typical mule deer	*Odocoileus hemionus hemionus* and related subspecies	803
Mountain caribou	*Rangifer tarandus caribou*	374
Central Canada barren ground caribou	*Rangifer tarandus groenlandicus*	280
Woodland caribou	*Rangifer tarandus caribou*	210
Barren ground caribou	*Rangifer tarandus granti*	852
Quebec-Labrador caribou	*Rangifer tarandus*	380
Non-typical American elk	*Cervus elaphus nelsoni* and related subspecies	267
Typical American elk	*Cervus elaphus nelsoni* and related subspecies	662
Roosevelt's elk	*Cervus elaphus roosevelti*	347
Non-typical Columbia black-tailed deer	*Odocoileus hemionus columbianus*	29
Typical Columbia black-tailed deer	*Odocoileus hemionus columbianus*	943
Typical Sitka black-tailed deer	*Odocoileus hemionus sitkensis*	134
Horned game		
Bison	*Bison bison*	384
Muskox	*Ovibos moschatus*	399
Pronghorn	*Antilocapra americana*	2,338
Rocky Mountain goat	*Oreamnos americanus*	741
Bighorn sheep	*Ovis canadensis canadensis* and related subspecies	1,191
Desert sheep	*Ovis canadensis nelsoni* and related subspecies	768
Dall's sheep	*Ovis dalli dalli* and *O. d. kenaiensis*	323
Stone's sheep	*Ovis dalli stonei*	382

frequently to quantify size of horn-like structures (Jorgenson et al. 1998, Ditchkoff et al. 2001, Festa-Bianchet et al. 2004, Garel et al. 2007, Lockwood et al. 2007), and is strongly correlated with other metrics of size for horns and antlers (Stewart et al. 2000; Strickland and Demarais, 2000, 2008; Bowyer et al. 2001, 2002; Monteith et al. 2009).

Records of North American Big Game

Following the unregulated exploitation of most populations of large, hoofed mammals across North America in the late 19th and early 20th centuries, conservationists recognized the need for laws to protect wildlife. Laws and regulations promulgated at the beginning of the conservation movement in North America sharply curtailed the harvest of large mammals, which allowed for their recovery (Allen 1954, Posewitz 1994, Dunlap 1998, Rattenbury 2008). At the forefront of that conservation movement was President Theodore Roosevelt, who founded the Boone and Crocket Club in 1887. Advocating for conservation of large mammals in the late 19th century, the Boone and Crockett Club was the first to deal with issues of national prominence (Reiger 1975, Williamson 1987). Indeed, 1 of the 5 objectives of that organization was, "To work for the preservation of the large game of this country, and, so far as possible, to further legislation for that purpose, and to assist in enforcing the existing laws" (Reiger 1975:119). In accordance with that objective, the Records of North American Big Game was established in 1932 to collect biological, harvest, and location data for trophy specimens of large mammals in North America. The Boone and Crockett Club posited that such information would aid in the preservation of large mammals, and further legislation for that purpose (Reiger 1975). The Boone and Crockett Club has since compiled a database of horn, antler, and skull sizes for 38 categories of native, North American big game that spans more than a century and includes >40,000 records.

The primary goal of the Boone and Crockett Records Program at its inception was to establish a baseline against which future trends in size of trophy animals could be compared (Gray 1932). Initially, measurements were quite simple, and included only length of the skull or the longer antler or horn. In 1949, a committee was formed to develop an objective and standardized system of measurement for large mammals in North America. An approved measuring system was adopted in 1950, and has become the universally accepted standard for quantifying size of antlers and horns in North American big game. Following adoption of that standardized system of measurement, an attempt was made to re-measure all specimens recorded before 1950 using the new system. Those data were first published in the Records of North American Big Game in 1952 (The Committee on Records of the Boone and Crockett Club 1952), and included trophies collected as early as the late 19th century.

All specimens must be air-dried for a minimum of 60 days before official measurement to eliminate the effects of shrinkage over time on the total score. To be eligible for inclusion in Records of North American Big Game, hunter-harvested specimens must be taken under "fair chase" conditions, which specify ethical conduct as defined by the Boone and Crockett Club

(Buckner et al. 2009). In addition to legally harvested animals, the Boone and Crockett Club recognizes trophies possessed by state or federal agencies and those legally collected from the field following natural mortality (Buckner et al. 2009).

All measurements of antlers and horns were obtained according to strict methods and guidelines that are specific for each category of game recognized by the Boone and Crockett Club (Buckner et al. 2009). The standardized system placed emphasis on symmetry by reducing the total score based on the amount of asymmetry between the left and right antlers or horns. Eligibility of submitted specimens for the record book was determined by whether this adjusted score exceeded minimums established by the Boone and Crockett Club. Although minimum entry requirements have varied slightly for some species over the past century, we avoided this potential source of bias (i.e., an increased number of smaller specimens submitted following reduction of the minimum entry requirement) by using the highest minimum for each trophy category in our analyses.

Records of North American Big Game only incorporates data from large mammals native to North America (Table 1; Reneau and Buckner 2005, Buckner et al. 2009). The Boone and Crockett Club defines a trophy category based primarily on species, but many large mammals exhibit geographic variation in morphology; thus, some species have been divided into ≥2 categories for record-keeping purposes. For example, moose occupying the intermountain West (Shiras category; *Alces alces shirasi*) are markedly smaller than those in the remainder of North America. Moose occupying Alaska and the Yukon and Northwest Territories (Alaska-Yukon category; *Alces alces gigas*) are the largest category, and moose distributed across other areas of North America (Canada category; *Alces alces americana* and *A. a. andersoni*) are intermediate in size. As a general rule, the geographic boundaries of a category are established to reduce the probability of a specimen belonging to a category characterized by larger individuals being obtained within the boundary of a category designated for smaller geographical variants. Categories recognized by the Boone and Crockett Club do not necessarily correspond with subspecies designations (Table 1; Wilson and Reeder 2005). For instance, Hundertmark et al. (2003) delineated 4 subspecies of moose for North America based on genetic markers, but the Boone and Crockett Club recognizes only 3 categories.

Antler and horn measurements were collected with a quarter-inch (6.35 mm) steel tape; however, main-beam lengths of antlers were measured with flexible steel cables, and the width of boss and horn of muskox were measured with a caliper. Measurements for antlers and horns were rounded to the nearest eighth inch (3.18 mm). To be considered a "measurable tine" (a branch emanating from the main antler beam or from another tine), a projection must have been at least 1 inch (25.4 mm) in length, with length exceeding the width at 1 inch or more of length (Buckner et al. 2009). For caribou (*Rangifer tarandus*), however, a tine was defined as a projection that was at least 0.5 inches (12.7 mm) in length, with length exceeding the width at 0.5 inches or more of length (Buckner et al. 2009).

For most antlered species, 4 types of measurements composed the total score: 1) length of tines as they arise from the main beam or from other tines; 2) 4 circumference measurements; 3) length of the main beams; and 4) inside spread (distance between the main beams; Fig. 1). For moose and caribou, however, number of tines was added to the total score. In addition, for moose, the length and width of the palm were included, greatest outside rather than inside spread was measured, and only 1 circumference measurement was obtained at the smallest point along each main beam (Fig. 1). Additional exceptions for caribou included measurement of only 4 tines (i.e., brow palm, rear tine, and the 2 longest top tines), and measurement of width of the brow palm and top palm (Fig. 1).

For most horned species, 2 types of measurements comprised the total score: length of the outer edge of the horn and 4 circumference measurements equally spaced along each horn (Fig. 2). Two exceptions to this general approach existed: pronghorn, in which the length of the prong was added to the total score, and muskox, in which the width of the boss was substituted for the first 2 circumference measurements.

When the Boone and Crockett measuring system was adopted in the 1950s, the individuals that developed the scoring system and those that received direct training and were appointed by the Club were responsible for measuring trophies. Beginning in the 1970s, a training program for Official Measurers was developed to minimize variance in data acquisition and ensure repeatability in measuring trophies. Official Measurers appointed by the Boone and Crocket Club are certified only after completing a rigorous 5-day workshop during which they receive the training necessary to ensure that all species of North American big game are measured precisely and consistently (Buckner et al. 2009). Official measurers receive no compensation for their services and perform their duties under strict ethical and technical guidelines (Buckner et al. 2009). To date, these Official Measurers have voluntarily measured >40,000 specimens that are recorded in the Records of North American Big Game, a subset of which constituted the basis for our analyses.

Statistical Analysis

We used simple linear regression (Neter et al. 1996) to identify time trends in size of horns and antlers of trophy categories recognized by the Boone and Crockett Club. We assumed that samples between years were independent, which is reasonable given the broad geographic scale at which samples were obtained. For nearly all categories, the number of specimens recorded annually has increased through time; consequently, to meet the assumption of homogeneity of variance, we binned data temporally based on year of harvest and used the mean and associated variance from each bin in a weighted least-squares regression (Neter et al. 1996, Zar 1999). We used the method of Krebs (1999:231) to determine the minimum number of samples per bin necessary to produce 95% confidence intervals that bounded the mean by no more than ±5%. This analysis indicated that ≥20 samples per bin were sufficient for producing the desired level of precision across all categories; therefore, we used 20 as the minimum sample size per bin. To produce these temporal bins within each category, we began with the year of the earliest recorded specimen and added samples from subsequent years until the minimum sample size was achieved; we never partitioned data from a single year. Sample sizes for non-typical Columbian black-tailed deer (*Odocoileus hemionus columbianus*;

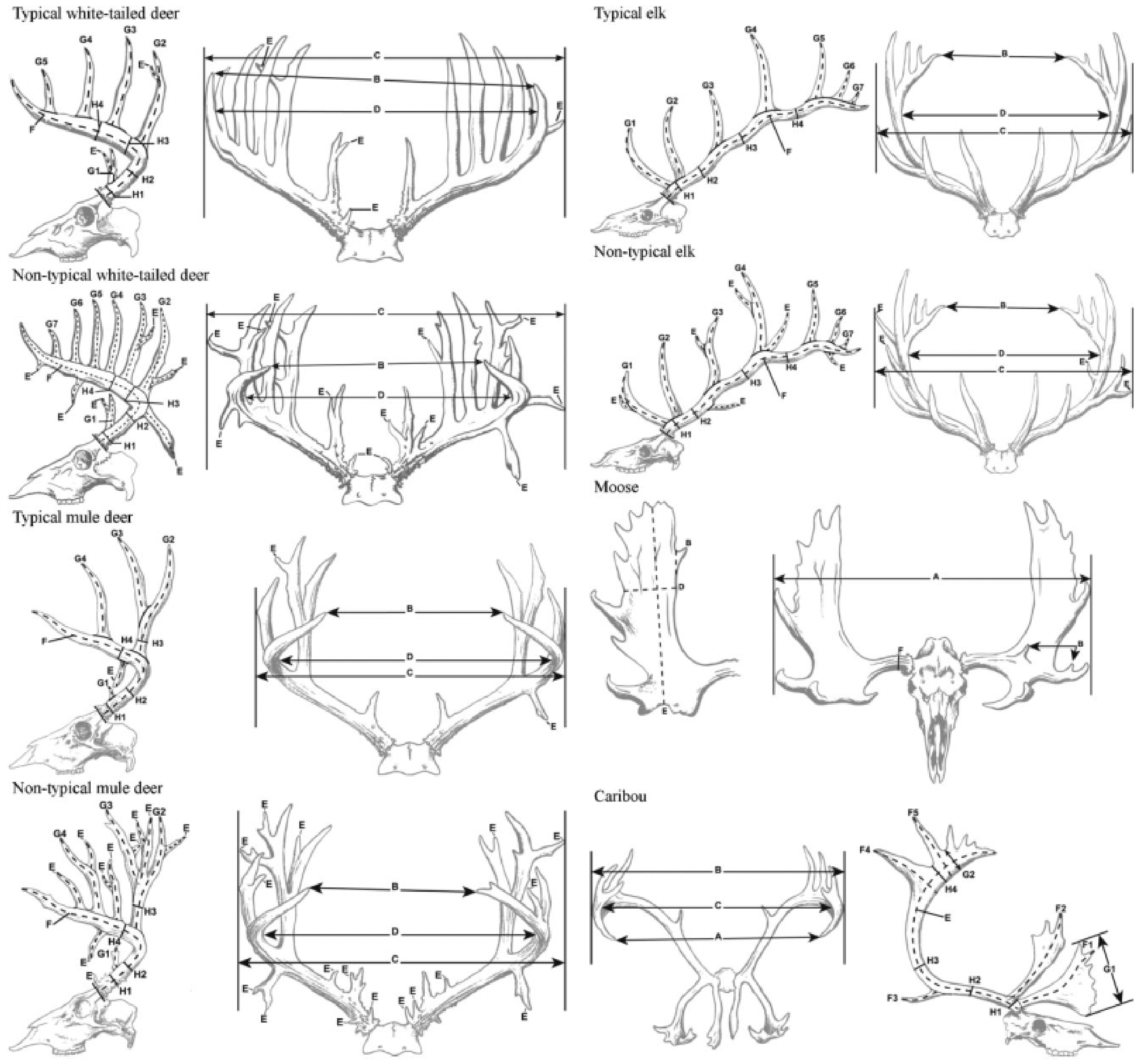


Figure 1. Illustrations of measurements of antlered game according to the Boone and Crockett scoring system. For all antlered categories except moose and caribou, total antler size comprised the sum of all D, E, F, G, and H measurements. Total antler size comprised the sum of measurements A, D, E, F, and total number of tines for moose, and the sum of measurements C, E, F, G, H, and total number of tines for caribou.

$n = 29$), non-typical Coues' white-tailed deer (*Odocoileus virginianus couesi*; $n = 95$), and typical Sitka black-tailed deer (*Odocoileus hemionus sitkensis*; $n = 134$; Fig. 3) were insufficient to produce an adequate number of bins for regression analyses.

Mean size of horns or antlers in each bin was the dependent variable in our analyses. Likewise, we used mean year of all samples in each bin as the independent variable, and weighted regressions by the inverse of the variance in size (Neter et al. 1996). We used the inverse of the variance, rather than sample size, for weighting to ensure that means from more variable bins did not receive undue weight (Neter et al. 1996). As a result, number of bins and their temporal width differed among trophy categories, but binning criteria remained consistent. Moreover, the temporal position (i.e., the value of the independent variable) of each bin was inherently weighted by the distribution of samples within that bin. Consequently, bins were representative of temporal patterns in size for each trophy category. In addition, because the official records program did not begin until the early 1950s, a potential bias existed in those data because there may have been a higher probability of only the most exceptional trophies collected prior to 1950 being "retroactively" entered. To address this potential bias, we conducted an identical series of simple linear regression analyses using only post-1950 data and compared results of this analysis with results of analyses based on the full dataset.

We used multiple linear regression weighted by the inverse of the intra-bin variance in size to determine whether time trends could be explained by broad-scale indices of climate or changes in number of entries over time within each trophy category. Broad-scale climatic patterns influence ecological processes;

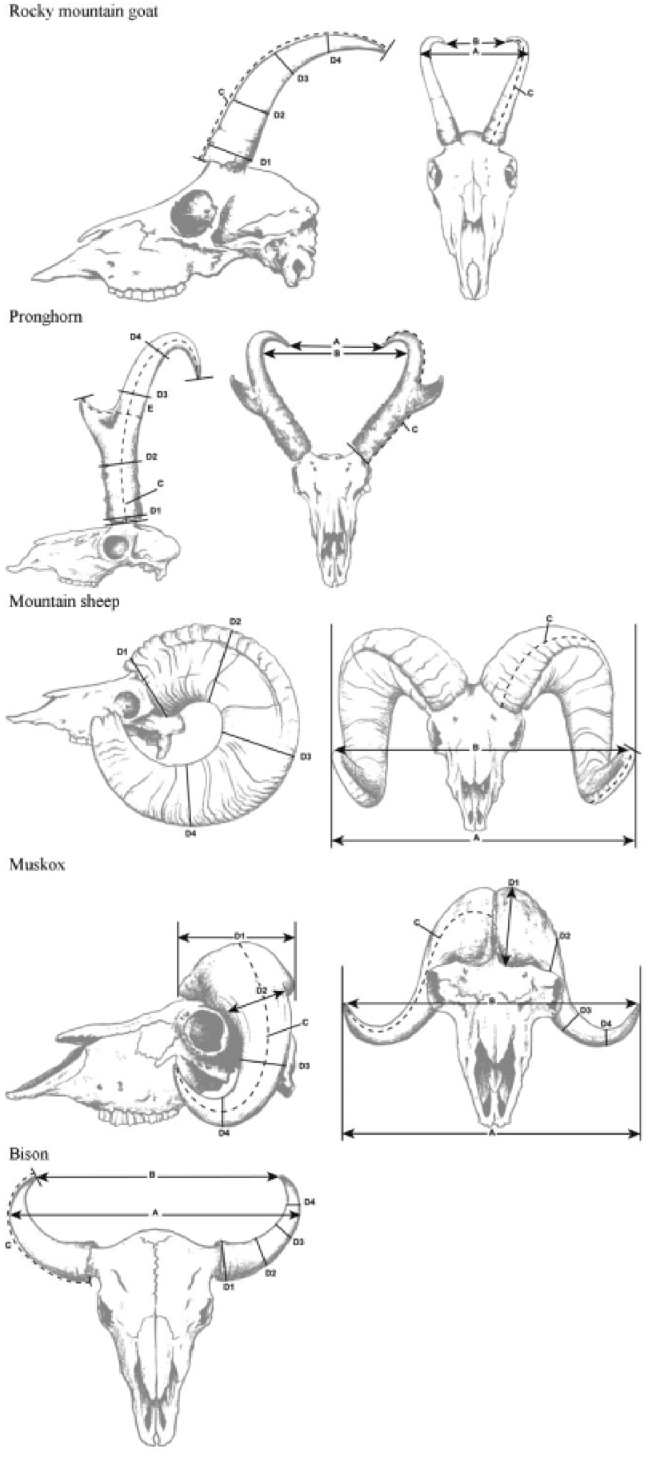


Figure 2. Illustrations of measurements of horned game according to the Boone and Crockett scoring system. Horn size comprised the sum of C and D measurements for all horned game with the exception of pronghorn, where measurement E (length of prong) was added.

such large-scale measures, rather than local weather conditions, could provide insight into ecological responses at a continental scale (Stenseth et al. 2003, Forchhammer and Post 2004, Hallett et al. 2004). Although there is no universally accepted index to describe climatic phenomena, most indices are highly correlated (Stenseth et al. 2003). Thus, we selected 2 commonly used indices of large-scale climate likely to influence large mammals in North America, the first of which was the North Atlantic Oscillation (NAO; Hurrell 1995). Effects of the NAO are manifested strongly across terrestrial ecosystems throughout much of the northern hemisphere (Hurrell et al. 2001; Ottersen et al. 2001; Stenseth et al. 2002, 2003), and are related to population dynamics of large mammals (Post and Stenseth 1999, Patterson and Power 2001, Forchhammer et al. 2002, Mysterud et al. 2003). Biological effects of the NAO are not as evident in western North America (Stenseth et al. 1999), possibly a result of the dominance of Pacific climate effects (Trenberth and Hurrell 1994). Consequently, we also included an index of the North Pacific Oscillation (NPO) in our analyses (Rogers 1981, Trenberth and Hurrell 1994, Forchhammer and Post 2004). The NPO can influence population dynamics of large mammals in North America (Forchhammer and Post 2004, Hebblewhite 2005). Values of both indices obtained during winter (Nov–Apr) are most closely related to a multitude of ecological processes (Hurrell 1995, Forchhammer and Post 2004, Hebblewhite 2005, Mysterud et al. 2005), so we used mean values of each index during that period in our analyses.

We included climatic indices as predictor variables in models only for species with deciduous horn-like structures, because those structures are re-grown every year and are more likely to reflect interannual variability in climate (Schmidt et al. 2001, Mysterud et al. 2005). We assigned values of each climatic index from the previous winter to each specimen in Records of North American Big Game based on the year it was collected. Mean values of each climatic index for all specimens included in a bin served as the climatic predictor variables in the multiple regressions.

The number of specimens meeting the minimum requirements for inclusion in Records of North American Big Game has increased markedly in recent decades for nearly all categories (Buckner et al. 2009). This increase likely is related to additional availability of trophy animals; however, we posited that it also may be influenced by a sociological effect, wherein desire to enter smaller, yet eligible, trophies has increased over time. Such an effect might bias observed trends in size of trophy horn-like structures downward. To test this hypothesis, we calculated an intra-bin measure of entry rate (mean number of entries per year for years included in each bin) for inclusion as a predictor variable in multiple regression analyses.

We used residual and sequential regression (Graham 2003) to evaluate the effects of year and submission rate, which often were correlated, on size of trophy horn-like structures. We assigned priority to the year effect, because we were most interested in investigating temporal trends in size. Consequently, we regressed submission rate against year and extracted the residuals from that analysis, which yielded a metric that was independent of the year effect and represented the unique contribution of submission rate (Graham 2003). We then included the residuals from that analysis in a multiple regression with year and climate. The goal of the multiple regression analyses was to determine whether the temporal trend represented by the effect of year was altered by the inclusion of climate or submission rate. Therefore, we used forward stepwise selection with year as the base model to assess

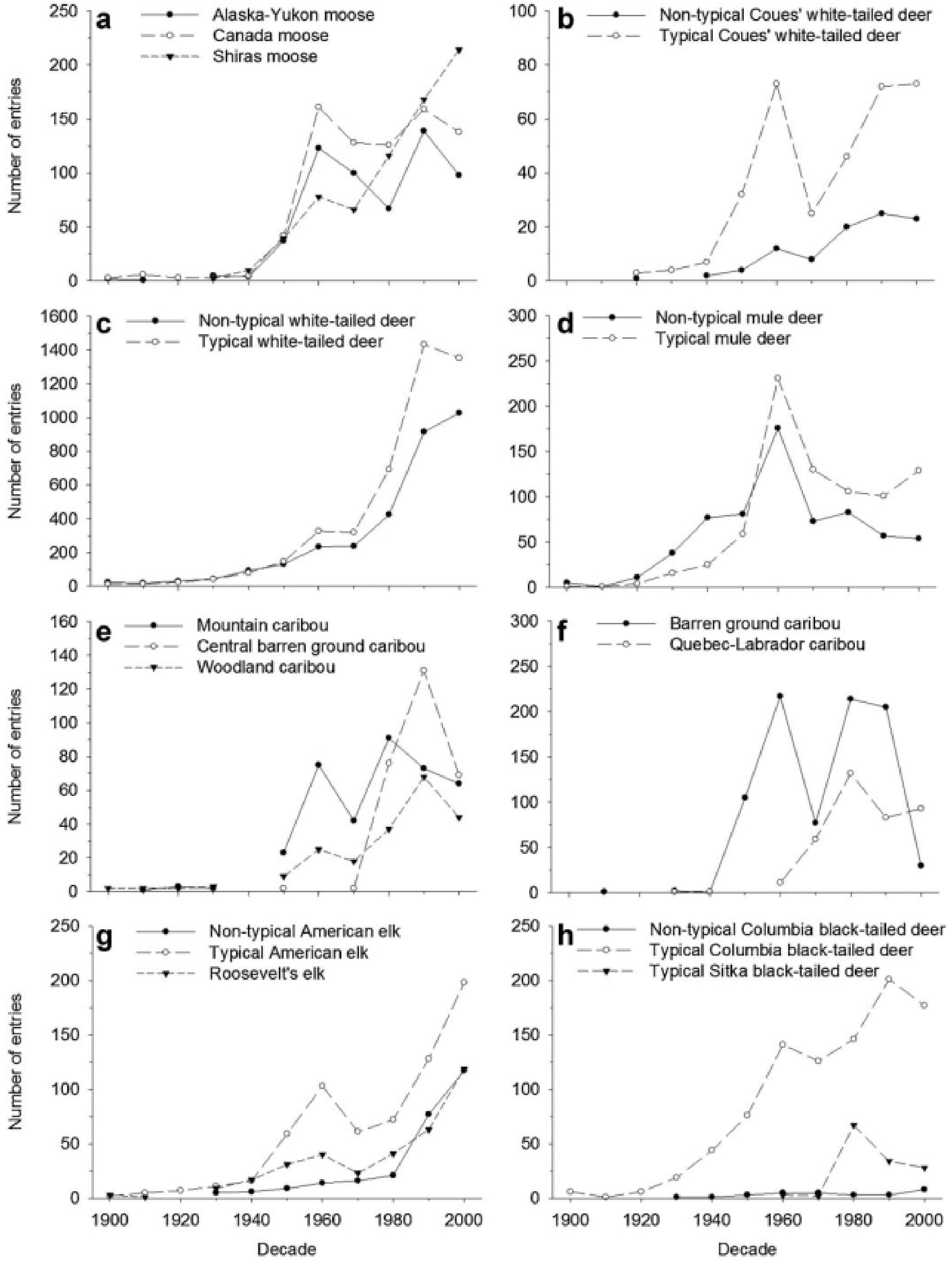


Figure 3. Decadal entries of antlered trophies recorded in Records of North American Big Game. Data points represent total number of entries for each trophy category that exceeded the highest minimum size requirement for eligibility established by the Boone and Crockett Club during the past century.

the influence of climate and submission rate on trends in size (Neter et al. 1996). We used a *P*-value of 0.10 to enter the model and 0.05 to remain.

We used an additional approach to evaluate the potential for a sociological effect on size of trophies. A prediction of the sociological hypothesis is that temporal patterns in size of horn-like structures result largely from an increase in the number of smaller, but eligible, specimens entered in the record book through time. Accordingly, temporal patterns observed in the full dataset should be less apparent when only the largest trophies are considered, because the largest specimens should be less affected by an increase in the number of smaller individuals. We tested this prediction by comparing results of weighted multiple regression analyses (Neter et al. 1996) using the full dataset with the same analyses using only the top and bottom thirds (based on size) of the dataset for each category. Partitioning the dataset resulted in intra-bin sample sizes that no longer met our criteria for sample size. Variance in size among samples in the top and bottom third of the dataset was lower, and we determined (using the method of Krebs 1999:231) that a minimum intra-bin sample size of 13 was sufficient for this analysis. We re-binned data for each trophy category to include a minimum of 40 samples per bin, and then extracted the top and bottom third of specimens from each bin for analysis.

We also tested for a specific directional trend across similar categories by combining probabilities from category-specific analyses into a single statistical test. We combined probabilities for the time trend (*P*-values for year) obtained from simple regression analyses based on the full dataset in a meta-analysis using the method of Sokal and Rolf (1995:795) for horned and antlered game separately. We also evaluated the influence of each trophy category on results of the meta-analysis by performing a series of meta-analyses in which a single category was withheld during each iteration. We recorded the minimum and maximum *P*-values, and the respective categories that were withheld to produce them, for horned and antlered game, to determine if any single category would cause results of the meta-analyses to shift from significant to non-significant (or vice-versa). For all such meta-analyses, we adopted an alpha of ≤ 0.02 to account for a potential lack of independence among tests (Bowyer et al. 2007, Monteith et al. 2009) that resulted from some species being represented by >1 category (i.e., typical and non-typical categories). For all other tests, we used an alpha of 0.05.

RESULTS

After truncating the Boone and Crockett data based on the highest recorded minimum entry score (based on net score) for each trophy category, we included 22,304 trophies obtained from 1900 to 2008 in our analyses: 15,778 for antlered game, and 6,526 for horned game. Number of trophies recorded in Records of North American Big Game per decade increased for nearly all trophy categories (Figs. 3 and 4). Decadal increases in recorded trophies were pronounced following the inception of the Boone and Crockett Records Program in the early 1950s. In contrast to this upward trend, a few categories exhibited peaks in decadal entries in the 1960s and declined thereafter, including non-typical and typical mule deer (*Odocoileus hemionus*), Dall's sheep, Stone's sheep, and Rocky Mountain goats (Figs. 3 and 4).

Temporal Trends in Size

Temporal trends in mean antler size of trophy specimens generally were negative over the last century (Fig. 5). Alaska-Yukon and Canada moose (Fig. 5a), non-typical and typical American elk (*Cervus elaphus*; Fig. 5g), and central Canada barren ground (*Rangifer tarandus groenlandicus*) and woodland caribou (*Rangifer tarandus caribou*; Fig. 5e), however, did not exhibit a significant temporal trend (Table 2). In addition, trends in antler size typically were linear, with Quebec-Labrador caribou (*Rangifer tarandus*; Fig. 5f) and Roosevelt elk (*Cervus elaphus roosevelti*; Fig. 5g) representing possible exceptions. Percent change in antler size of trophies during the past 58 years (1950–2008), predicted by simple linear regression models, was negative ($\bar{x} = -1.87\%$, SD = 1.40) for all but 1 category, and ranged from −4.93% for typical Columbia black-tailed deer to 0.18% for Canada moose (Table 2).

Temporal trends in mean horn size of trophy specimens were less consistent than patterns for antlered categories (Fig. 6). Horn size of trophy mountain sheep declined significantly over much of the past century (Table 2), with the exception of bighorn sheep, in which horn size leveled out or increased in recent decades (Fig. 6c,d). Bison and mountain goats did not exhibit a significant temporal trend in horn size of trophies (Table 2), whereas trophy

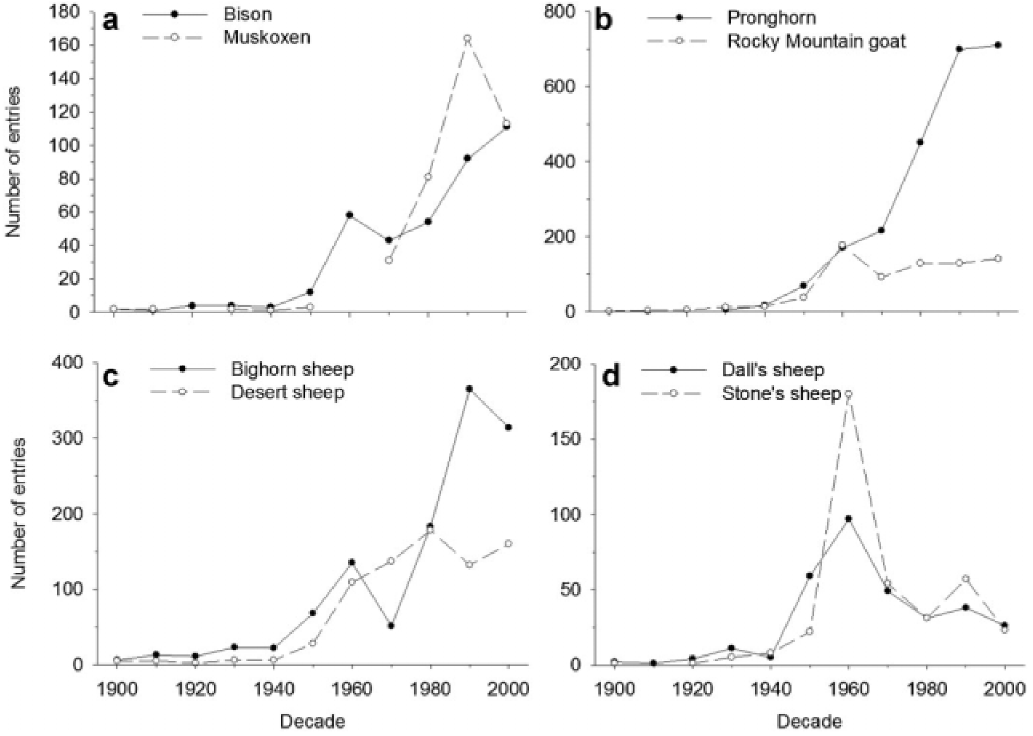


Figure 4. Decadal entries of horned trophies recorded in Records of North American Big Game. Data points represent total number of entries for each trophy category that exceeded the highest minimum size requirement for eligibility established by the Boone and Crockett Club during the past century.

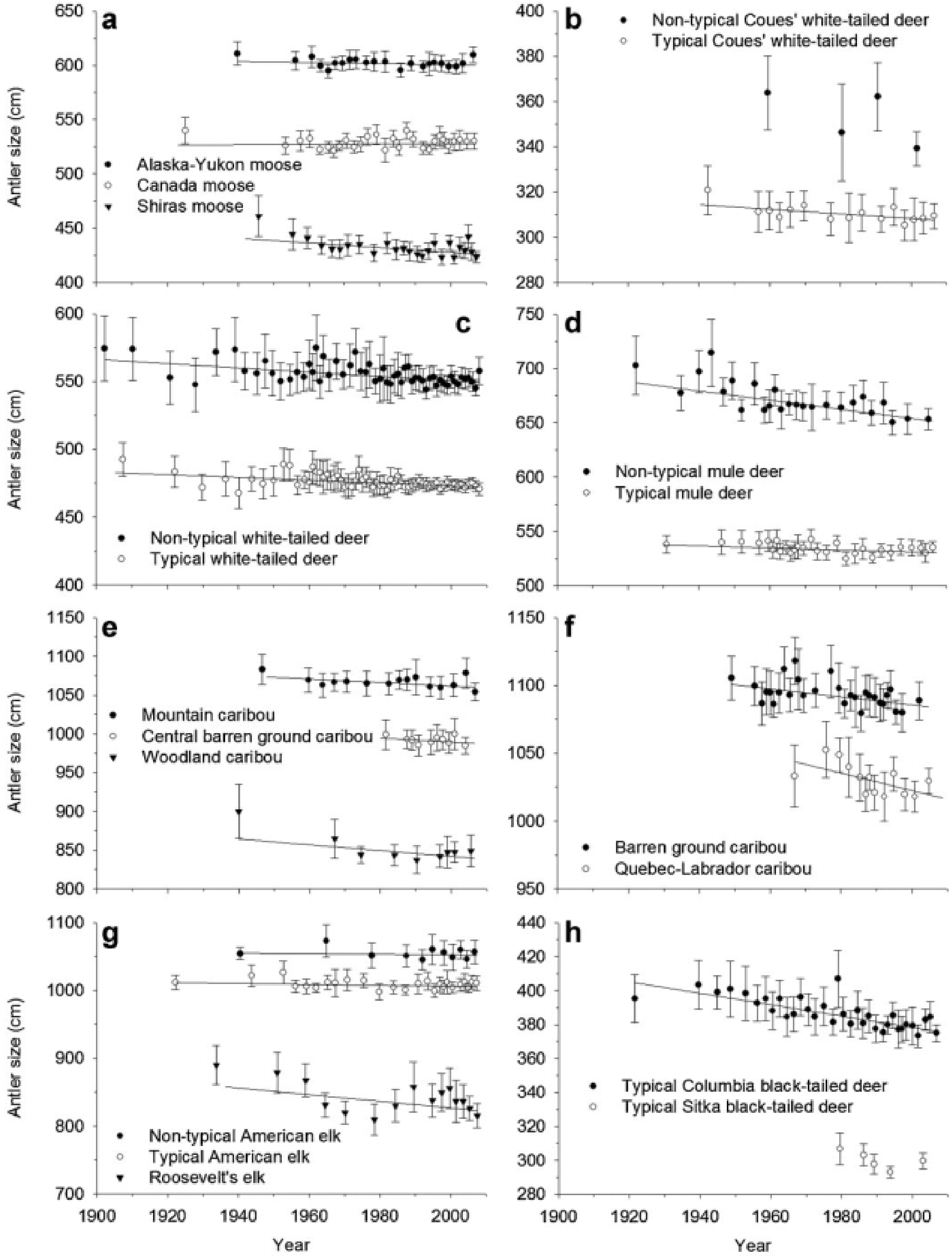


Figure 5. Temporal trends in antler size of trophies recorded in Records of North American Big Game during the past century. Data points represent mean (±95% CI) antler size (cm) of temporal bins containing a minimum of 20 samples; minimum bin size was 1 year. Lines represent fitted least-squares regressions weighted by the inverse of the variance associated with each bin.

pronghorn exhibited a slight, but significant, increase in size (Table 2). In contrast, mean horn size of muskox increased markedly since the 1970s (Fig. 6a), with a 7.12% increase predicted over the last 58 years (Table 2). For other horned game, mean predicted change in horn size of trophies was −0.68% (SD = 1.02), and ranged from −1.82% for desert sheep to 0.57% for pronghorn (Table 2).

A significant effect of climate or submission rate on size of trophy horn-like structures occurred for only 3 of 17 antlered categories, and 2 of 8 horned categories (Table 3). The addition of climate or submission rate, however, did not qualitatively alter the temporal trend for any of those 5 categories. The NPO was negatively related to antler size for Canada moose, and positively related to antler size for typical American elk (Table 3). The NAO was related negatively to antler size for central Canada barren ground caribou (Table 3). Submission rate was not related to size for any antlered category, but was related positively to horn size of bighorn sheep and Stone's sheep (Table 3).

To determine whether retroactive entry of specimens collected prior to the 1950s might bias observed trends in size of trophies during the past century, we conducted the same simple linear regression analyses for each trophy category using only post-1950

Table 2. Results of simple linear regression analyses used to evaluate trends in size of antlers and horns of trophy big game in North America during the past century. Sample size represents the number of bins for each trophy category, and % change represents the predicted change in size from 1950 to 2008 based on results of the linear regression using the full dataset for each trophy category.

Trophy category	r^2	n	P-value	Intercept	β	% change
Antlered game						
Alaska-Yukon moose	0.05	22	0.33	605.51	−0.05	−0.48
Canada moose	0.00	28	0.79	526.24	0.02	0.18
Shiras moose	0.28	25	0.01	449.27	−0.22	−2.87
Typical Coues’ white-tailed deer	0.35	15	0.02	318.45	−0.10	−1.89
Non-typical white-tailed deer	0.28	57	<0.01	566.39	−0.16	−1.65
Typical white-tailed deer	0.23	61	<0.01	483.40	−0.10	−1.24
Non-typical mule deer	0.47	25	<0.01	696.21	−0.42	−3.62
Typical mule deer	0.14	28	0.05	540.30	−0.09	−1.00
Mountain caribou	0.32	15	0.03	1,084.50	−0.23	−1.23
Central Canada barren ground caribou	0.12	10	0.32	1,014.91	−0.25	−1.47
Woodland caribou	0.27	9	0.16	879.09	−0.37	−2.51
Barren ground caribou	0.25	29	0.01	1,115.17	−0.30	−1.55
Quebec-Labrador caribou	0.31	13	0.05	1,086.64	−0.64	−3.53
Non-typical American elk	0.04	11	0.55	1,057.29	−0.05	−0.26
Typical American elk	0.08	25	0.19	1,013.19	−0.07	−0.41
Roosevelt’s elk	0.23	15	0.07	875.56	−0.49	−3.33
Typical Columbia black-tailed deer	0.67	34	<0.01	411.89	−0.34	−4.93
Horned game						
Bison	0.00	15	0.84	310.07	−0.01	−0.17
Muskox	0.56	17	<0.01	257.01	0.49	7.12
Pronghorn	0.08	46	0.05	214.19	0.02	0.57
Rocky Mountain goat	0.01	28	0.62	130.61	0.01	0.22
Bighorn sheep	0.01	38	0.63	473.74	−0.01	−0.17
Desert sheep	0.44	29	<0.01	455.45	−0.14	−1.82
Dall’s sheep	0.79	13	<0.01	452.31	−0.14	−1.80
Stone’s sheep	0.29	15	0.04	451.71	−0.12	−1.60

data. Among antlered game, the time trend changed from negative and significant to not significant for mountain caribou, typical Coues’ white-tailed deer, and typical mule deer, but did not change for any of the other 14 categories (Table 4). Among horned game, the time trend changed from not significant to positive and significant for bighorn sheep, and negative and significant to not significant for Stone’s sheep, but did not change for any of the other 6 categories (Table 4).

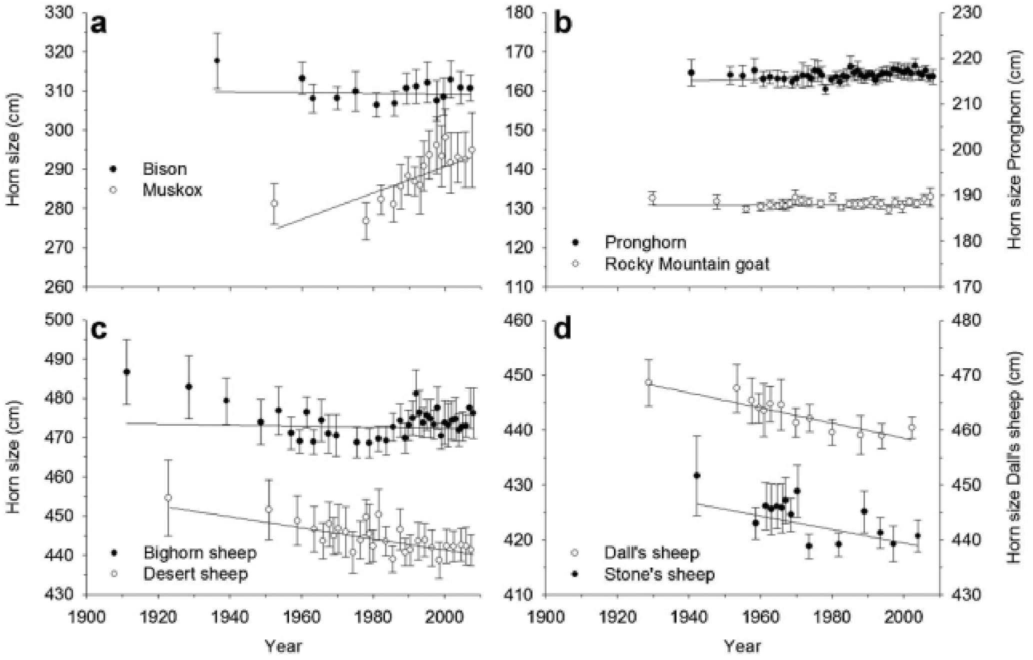


Figure 6. Temporal trends in horn size of trophies recorded in Records of North American Big Game during the past century. Data points represent mean (±95% CI) horn size (cm) of temporal bins containing a minimum of 20 samples; minimum bin size was 1 year. Lines represent fitted least-squares regressions weighted by the inverse of the variance associated with each bin.

Table 3. Results of step-wise, multiple linear regression analyses to evaluate the influence of climate and submission rate on temporal trends in size of antlers and horns of trophy big game in North America during the past century. We binned samples temporally based on a minimum sample size of 20, and weighted regressions by the inverse of the variance within each bin; sample size represents the number of bins for each trophy category. We show only trophy categories with a significant effect of climate (North Atlantic Oscillation [NAO] or North Pacific Oscillation [NPO]) or submission rate (SubRate). We did not include climate variables for horned game (na) and indicated non-significant variables with "ns."

				Parameter estimates and *P* values								
Trophy category	**Adj. R^2**	***n***	***P*-value**	**Intercept**	**Year**	***P*-value**	**NAO**	***P*-value**	**NPO**	***P*-value**	**SubRate**	***P*-value**
Antlered game												
Canada moose	0.31	28	<0.01	557.92	−0.08	0.17	ns	ns	−2.39	<0.01	ns	ns
Central Canada barren ground caribou	0.43	10	0.06	1,027.57	−0.38	0.09	−4.06	0.04	ns	ns	ns	ns
Typical American elk	0.17	25	0.05	987.88	−0.02	0.67	ns	ns	2.25	0.04	ns	ns
Horned game												
Bighorn sheep	0.13	38	0.04	474.73	−0.03	0.37	na	na	na	na	0.17	0.01
Stone's sheep	0.44	15	0.01	451.20	−0.11	0.03	na	na	na	na	0.25	0.04

Size-Specific Trends

Sample size was sufficient to partition data into upper and lower thirds for 10 categories of antlered game and 4 categories of horned game. Based on regression analyses, the temporal trend in size of trophies was similar (i.e., significance and direction) between the largest third and the full data set for all but 2 antlered categories (i.e., Shiras moose and typical mule deer), and all horned categories (Table 5). Similarly, the trend for the smallest third was the same as that observed in the full dataset for 8 of 10 antlered categories (typical mule deer and barren ground caribou were the exceptions), and all horned categories except pronghorn (Table 5).

Although we expected less variation within the smallest third of specimens, because their inclusion in the dataset was bounded by a minimum net score, patterns in size among bins for the largest individuals closely resembled patterns observed in the full dataset, whereas trends in size among the smallest individuals often were less apparent and did not reflect temporal patterns in the full dataset (Figs. 7 and 8). Parameter estimates for the smallest and largest thirds were highly correlated with those of the full dataset ($r > 0.84$), but a post hoc, paired *t*-test indicated that parameter estimates from the full dataset did not differ from those of the largest third ($t_{13} = 1.80$, $P = 0.09$), whereas parameter estimates differed between the full dataset and the smallest third ($t_{13} = 3.67$, $P = 0.003$). Thus, temporal trends in size of trophies observed in the full dataset were influenced primarily by specimens in the largest third of the entries.

Meta-Analysis

Results of the meta-analysis indicated a significant, negative trend in antler ($\chi^2_{34} = 104.84$, $P < 0.001$) and horn ($\chi^2_{14} = 37.53$, $P = 0.0017$) sizes of trophy North American

Table 4. Results of simple linear regression analyses used to evaluate trends in size of antlers and horns of trophy big game in North America during 1950–2008. Sample size represents the number of bins for each trophy category based on results of the linear regression using post-1950 data for each trophy category.

Trophy category	**r^2**	***n***	***P*-value**	**Intercept**	**β**
Antlered game					
Alaska-Yukon moose	0.00	21	0.83	601.55	−0.01
Canada moose	0.04	27	0.30	525.28	0.07
Shiras moose	0.22	24	0.02	436.70	−0.18
Typical Coues' white-tailed deer	0.21	14	0.10	311.93	−0.07
Non-typical white-tailed deer	0.16	48	<0.01	557.73	−0.14
Typical white-tailed deer	0.28	54	<0.01	479.66	−0.14
Non-typical mule deer	0.31	20	0.01	670.98	−0.29
Typical mule deer	0.08	26	0.17	535.19	−0.08
Mountain caribou	0.17	14	0.14	1,070.27	−0.16
Central Canada barren ground caribou	0.12	10	0.32	1,002.21	−0.25
Woodland caribou	0.01	8	0.81	847.02	−0.05
Barren ground caribou	0.25	29	0.01	1,100.39	−0.30
Quebec-Labrador caribou	0.31	13	0.05	1,054.56	−0.64
Non-typical American elk	0.12	10	0.33	1,063.03	−0.23
Typical American elk	0.01	23	0.68	1,007.88	−0.03
Roosevelt's elk	0.07	14	0.35	842.03	−0.27
Typical Columbia black-tailed deer	0.55	30	<0.01	394.93	−0.33
Horned game					
Bison	0.07	14	0.37	307.80	0.04
Muskox	0.56	17	<0.01	273.81	0.34
Pronghorn	0.11	45	0.02	215.07	0.03
Rocky Mountain goat	0.09	26	0.14	130.46	0.02
Bighorn sheep	0.17	34	0.01	469.64	0.07
Desert sheep	0.37	28	<0.01	448.08	−0.13
Dall's sheep	0.71	12	<0.01	445.33	−0.14
Stone's sheep	0.23	14	0.09	444.97	−0.11

Table 5. Results of linear regression analyses used to evaluate differences in temporal trends in size of antlers and horns of the largest and smallest third of trophy big game in North America during the past century, while controlling for effects of climate and submission rate if they were significant in the previous analysis. We binned samples temporally based on a minimum sample size of 13, and weighted regressions by the inverse of the variance associated with each bin; sample size represents the number of bins for each trophy category. The last 3 columns present the direction of the temporal trend in size for statistically significant time trends based on regression analyses, negative (−), positive (+), or non-significant (ns).

	Largest third of specimens					Smallest third of specimens					Summary		
				Time-trend					Time-trend				
Trophy category	Adj. R^2	n	Intercept	β	P-value	Adj. R^2	n	Intercept	β	P-value	Largest	Smallest	All
Antlered game													
Alaska-Yukon moose	0.17	12	636.96	−0.15	0.18	0.10	12	586.95	−0.04	0.32	ns	ns	ns
Canada moose	0.00	16	542.76	0.09	0.61	0.00	16	511.76	−0.02	0.65	ns	ns	ns
Shiras moose	0.26	14	478.77	−0.27	0.06	0.28	14	416.13	−0.08	0.05	ns	−	−
Non-typical white-tailed deer	0.20	43	616.13	−0.23	<0.01	0.42	43	526.96	−0.09	<0.01	−	−	−
Typical white-tailed deer	0.41	45	521.00	−0.22	<0.01	0.18	45	454.76	−0.04	<0.01	−	−	−
Non-typical mule deer	0.49	14	758.41	−0.68	0.01	0.61	14	650.47	−0.22	<0.01	−	−	−
Typical mule deer	0.15	17	568.11	−0.15	0.12	0.07	17	516.65	−0.04	0.32	ns	ns	−
Barren ground caribou	0.26	16	1,173.73	−0.46	0.04	0.00	16	1,056.55	−0.01	0.91	−	ns	−
Typical American elk	0.00	14	1,010.49	−0.01	0.97	0.19	14	967.44	0.00	0.91	ns	ns	ns
Typical Columbia black-tailed deer	0.74	19	455.54	−0.52	<0.01	0.49	19	372.52	−0.14	<0.01	−	−	−
Horned game													
Pronghorn	0.14	36	218.42	0.05	0.02	0.05	36	210.85	0.01	0.17	+	ns	+
Rocky Mountain goat	0.02	16	133.89	0.01	0.62	0.10	16	128.54	0.00	0.24	ns	ns	ns
Bighorn sheep	0.03	22	485.60	0.05	0.55	0.26	22	461.66	0.01	0.64	ns	ns	ns
Desert sheep	0.63	15	478.44	−0.23	<0.01	0.40	15	435.99	−0.05	0.01	−	−	−

big game. Iteratively withholding any single trophy category did not alter the results of the meta-analysis for antlered (maximum $P < 0.001$) or horned (maximum $P = 0.05$) game, indicating robustness of the overall negative trend in size of trophy horn-like structures among North American big game.

DISCUSSION

Although some variability existed among trophy categories, trends in horn and antler size of trophy big game harvested or collected in North America were predominantly negative over the past 50–100 years. The absence of age data precluded us from directly evaluating age-class specific changes in size. Nevertheless, our analyses revealed clear patterns of change among trophy horn-like structures, and knowledge of such patterns is important for management of large ungulates. We used a weight-of-evidence approach that was based on differences among trophy categories in life-history characteristics, geographic distribution, morphological attributes, harvest regimes, and anthropogenic disturbance to test predictions that followed directly from the aforementioned hypotheses for explaining negative trends in size and, thereby, evaluated the relative amount of support for each hypothesis (Table 6). Our results provided no support for a sociological effect (H3), effects of large-scale climate (H4), or broad-scale habitat change (H5) as the primary explanations for downward trends in size (Table 6). In contrast, our results provided moderate support for the hypothesis that intensive harvest may have resulted in a gradual shift in male age structure towards younger males (H1), and limited support for genetic effects as a result of selective male harvest (H2), as potential explanations for observed trends in size of horn-like structures.

Based on the intensive-harvest hypothesis, we expected that trophy categories with conservative harvest regimes would be less likely to exhibit a decline in horn or antler size than those experiencing heavy harvest of males, which shifts age structures toward young males that have relatively smaller horns and antlers (Noyes et al. 1996, Langvatn and Loison 1999, Solberg et al. 2000, Jenks et al. 2002, Milner et al. 2007). Although we did not have data on temporal patterns in age structure, several of our results support that prediction. First, 2 of the 3 species that arguably experience the most conservative harvest regimes in North America (bighorn sheep, desert sheep, and bison) did not exhibit a significant, long-term trend in horn size. In particular, horn size of trophy bighorn sheep declined steadily from the early to mid-20th century, but leveled out and has increased during the last few decades. Coincident with that shift in trend, harvest regimes for bighorn sheep became increasingly conservative and reintroduction efforts were well underway (Douglas and Leslie 1999, Toweill and Geist 1999, Krausman and Shackleton 2000, Festa-Bianchet and Lee 2009), which likely resulted in older males in superb nutritional condition with larger horns (Geist 1986). Secondly, if intensive harvest of males was at least partially responsible for the observed trends in horn and antler size, then pronghorn should be less prone to that effect because they develop large horns at an early age (Table 6; Mitchell and Maher 2001, 2006). The positive, significant trend in horn size of trophy pronghorn is consistent with this prediction, providing additional support for the intensive-harvest hypothesis.

In the southwestern United States, conservative harvest strategies were adopted for desert bighorn sheep with reopening of recreational harvest in the 1950s (Festa-Bianchet and Lee 2009). Nevertheless, horn size of trophy, desert bighorn sheep continued to decline during 1950–2008 (Fig. 6c). Horn size of desert sheep harvested in Arizona indicated a similar negative trend during 1980–2009; however, mean winter rainfall experienced during the lifetime of individual males was positively related to their horn size when harvested (Hedrick 2011). Therefore, persistent drought and declines in winter snowfall and snowpack during

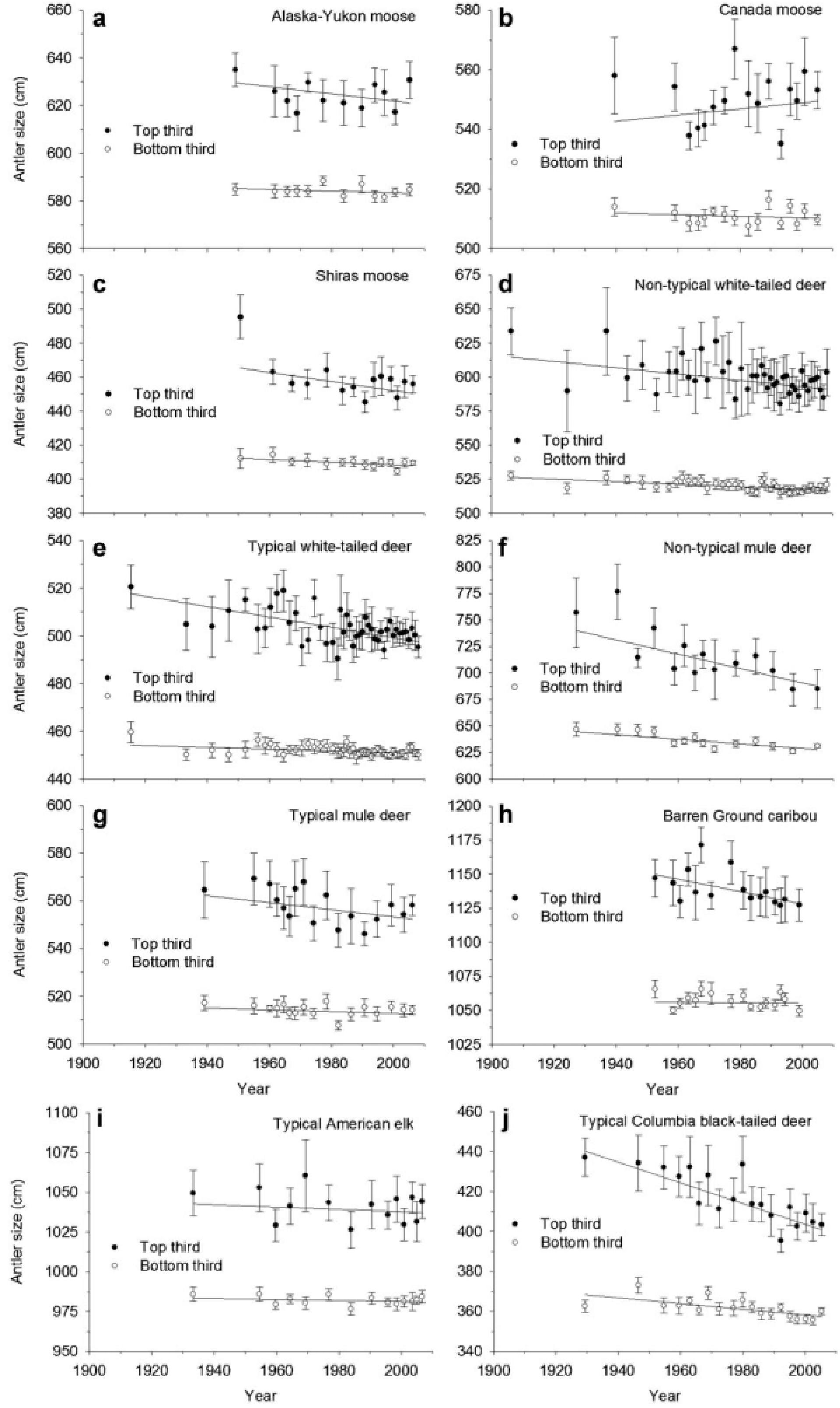


Figure 7. Temporal trends in antler size of the largest and smallest third of trophies recorded in Records of North American Big Game during the past century. Data points represent mean (±95% CI) antler size (cm) of temporal bins containing a minimum of 13 samples; minimum bin size was 1 year. Lines represent fitted least-squares regressions weighted by the inverse of the variance associated with each bin.

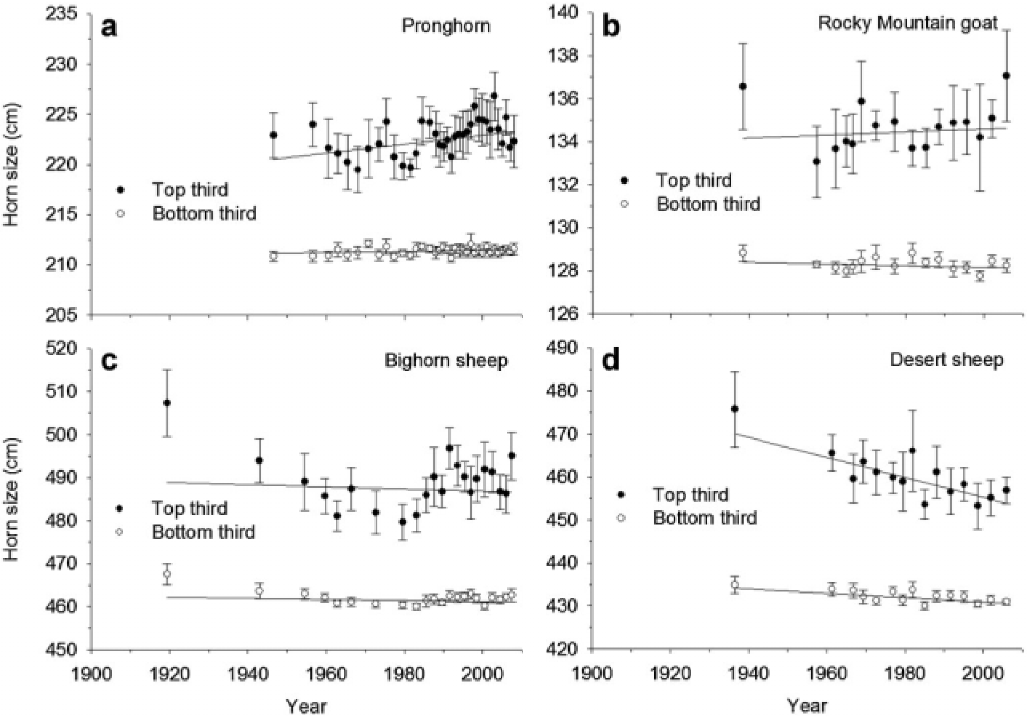


Figure 8. Temporal trends in horn size of the largest and smallest third of trophies recorded in Records of North American Big Game during the past century. Data points represent mean (±95% CI) horn size (cm) of temporal bins containing a minimum of 13 samples; minimum bin size was 1 year. Lines represent fitted least-squares regressions weighted by the inverse of the variance associated with each bin.

recent decades in the western United States (Hamlet et al. 2005, Knowles et al. 2005, Barnett et al. 2008) may be partially responsible for the negative trends in horn size observed for desert bighorn sheep, conservative harvests notwithstanding.

Under the selective-harvest hypothesis, we expected that ability to accurately assess size of males in the field would influence the amount of selective pressure imposed on the targeted trait. Accordingly, horn size of trophy Rocky Mountain goats, which are difficult to accurately judge in the field, should be less likely to exhibit long-term declines than other trophies that can be easily field judged (Table 6). Consistent with that prediction, mountain goats did not exhibit a significant trend in horn size over the past century. From the selective-harvest hypothesis, we also predicted that trophy horned game would be more susceptible to negative effects of selective harvest because once those bovids attain trophy size, they express that characteristic throughout the remainder of their lifetime. In contrast to horns, antlers are cast and regrown each year, and antler growth can be influenced by environmental

Table 6. Hypotheses for explaining long-term trends in horn and antler size of trophy big game in North America. Each hypothesis is followed by specific predictions evaluated using data from Records of North American Big Game (1900–2008) and the relative of amount support for each prediction based on results of our analyses.

Hypothesis	Mechanism	Predicted outcome	Empirical support
Intensive harvest	Intensive harvest of males has shifted age structure towards young males	1a) Trophy categories experiencing heavy harvest of males should exhibit steeper, negative slopes than those with a conservative harvest regime	Limited support
		1b) Trophy categories with early maturation in horns and antlers should be less prone to a reduction in size of those structures caused by a premature age distribution	Supported
Selective harvest	Trophy hunting has selected against genes for large horn-like structures	2a) Trophy categories for which horn or antler size is difficult to assess in the field will be less prone to selection against large horn-like structures and thus, less likely to exhibit a negative trend	Supported
		2b) Horned game should be more prone to a reduction in size of horn-like structures than antlered game, because size of horns is expressed consistently through time	No support
Sociological effect	Increased desire to submit smaller, yet eligible trophies to the Boone and Crockett record book has negatively biased observed size of hornlike structures	3a) Submission rate should be negatively related to size of horn-like structures	No support
		3b) Negative trend in hornlike structures should be less apparent in the largest third of samples than in the entire dataset	No support
Climate	Global changes in climatic regime have limited the ability of males to grow large horn-like structures	4a) Size of antlers should be negatively related to large-scale climatic indices and be largely responsible for the underlying trend	No support
Habitat	Loss and degradation of habitat has limited growth of horn-like structures	5a) Trophy categories that have experienced minimal loss or degradation of habitat should not exhibit a negative trend over time	No support

conditions and age in any particular year. Contrary to our prediction, declines in size of cranial appendages were nearly ubiquitous among antlered game, but were less consistent among horned game, which does not support the selective-harvest hypothesis.

Several factors could have confounded interpretation of temporal trends identified in our analyses, many of which related directly to the potential for a sociological effect (H3). During the past century, the appeal of animals with large antlers or horns has increased dramatically (Sudbeck 1993, Festa-Bianchet 2008, Messner 2011), resulting in a concomitant increase in the desire among individuals to harvest and receive recognition for those trophies. If changes in the desire to receive recognition are dependent upon trophy size, then observed trends in size of trophy horns and antlers could be a function of this sociological effect (H3).

We evaluated several specific predictions that followed from the sociological-effect hypothesis. The first such prediction was that entry rate should be negatively related to size of horn-like structures. With only 2 exceptions (bighorn sheep and Stone's sheep), entry rate was not a significant predictor of size for any trophy category (Table 3). In the 2 instances in which entry rate was significant, the relationship with size was positive (Table 3), contrary to the prediction of the sociological effect hypothesis. Because a sociological effect would depend upon increased rate of entry of smaller eligible trophies through time, then those trends should be less apparent in the largest samples than in the entire dataset. Once again, our results did not support that prediction because negative trends in size were most apparent among the largest specimens (Figs. 7 and 8). Our results were inconsistent with the sociological-effect hypothesis and often were contradictory to predictions of that hypothesis. We conclude that the long-term trends in size of trophy horn-like structures identified in our analyses were not a sociological artifact. Moreover, the relative declines in size of the largest animals in the dataset were consistent with predictions of the intensive-harvest hypothesis (H1).

In addition to having strong heritable and age-dependent components, patterns of growth in horns and antlers have nutritional underpinnings that are influenced by climate (Schmidt et al. 2001, Kruuk et al. 2002, Mysterud et al. 2005, Loehr et al. 2010) and habitat conditions (Strickland and Demarais 2000, 2008; Monteith et al. 2009; Mahoney et al. 2011). We evaluated the potential influence of climate and habitat on long-term patterns of horn and antler size of trophy big game in North America using 2 separate approaches. Ample evidence indicates nutritionally mediated effects of climate on interannual growth of horn-like structures (Schmidt et al. 2001, Kruuk et al. 2002, Mysterud et al. 2005, Loehr et al. 2010); however, our results did not support an effect of the climate indices that we assessed for explaining long-term patterns in size of deciduous horn-like structures of trophy ungulates. Likewise, declines in number of antler points for harvested caribou in Newfoundland, Canada during 1986–2005 were not related strongly to climate (Mahoney et al. 2011). Although we were unable to test for a climate effect directly for horned game, climate affects horn and antler growth via the same nutritional mechanisms (Goss 1983, Bubenik and Bubenik 1990, Mysterud et al. 2005, Loehr et al. 2010).

At the continent-wide scale of our analysis, we could not quantify changes in the quality, abundance, or distribution of habitat available to the various trophy categories included in our analyses. In addition, the scale of our analysis precluded incorporating information on population size, which is highly variable spatially and temporally across North America. Indeed, most ungulate populations have increased markedly in the recent century following the cessation of commercial hunting and adoption of regulated-harvest regimes (Demarais and Krausman 2000), which may have led to density-dependent effects on horn and antler size. Nevertheless, the degree of spatial and temporal heterogeneity in population size and habitat change across North America is precisely the reason why these factors are unlikely explanations for the near ubiquitous declines we observed, particularly among antlered game. If habitat change was the underlying reason for those trends, Dall's sheep, Stone's sheep, and muskox should have been the least likely to exhibit a decline, given that nearly all of their range remains both intact and pristine (Bowyer et al. 2000). In contrast to this expectation, trophy Dall's and Stone's sheep exhibited one of the steepest declines in horn size (Table 2); however, trophy muskox exhibited a substantial increase in horn size (Fig. 6a). Muskox have experienced nutritional and demographic benefits from range expansions that occurred throughout the Arctic (Klein 2000). Such range expansions led to increased hunting opportunity in recently established populations that likely contained abundant, prime-aged males, yielding greater potential for harvest of trophy males.

Potential Weaknesses of the Selective-Harvest Hypothesis

Hunting influences populations of ungulates by altering social structure, age structure, sex ratios, and population dynamics (Milner et al. 2007, Mysterud 2010). Furthermore, mortality as a result of hunting is not always functionally redundant with natural causes of mortality. For example, individuals most susceptible to natural mortality (i.e., young, senescent, nutritionally compromised, diseased) often are not the most susceptible to hunting mortality, and the temporal patterns of mortality between the 2 causes often differ (Berger 2005, Bischof et al. 2008). Under intensive harvest regimes that are regulated solely by size criteria, fast-growing males are more susceptible to harvest at a younger age than slow-growing males (Bonenfant et al. 2009*b*, Hengeveld and Festa-Bianchet 2011). The only example in North America demonstrating negative genetic effects of selective harvest on size of horn-like structures of ungulates was published by Coltman et al. (2003), who reported significant declines in horn size and body mass in bighorn sheep in a selectively and intensively hunted population. This sheep population at Ram Mountain, Alberta, Canada, was a small, isolated population where harvest was restricted to individuals having horns with a 4/5 curl, but with an unlimited number of hunters. Consequently, about 40% of males that attained legal size were harvested each year, allowing males with slow-growing horns to reach older age classes (Bonenfant et al. 2009*b*) and, thus, do a disproportionate amount of mating (Coltman et al. 2003). Such heavy harvest resulted in selection against males with fast-growing horns before their reproductive peak, and thereby reduced their genetic contribution to the population

(Coltman et al. 2003), although declining horn size may have been confounded by increasing population density (Coltman 2008).

Other factors decreasing the potential influence of trophy hunting on selection for horn and antler size among artiodactyls are skewed sex ratios, and age structures of young males that are biased downward as a result of heavy harvest (Laurian et al. 2000, Jenks et al. 2002, Webb et al. 2012). One potential effect common to a skewed sex ratio and an altered age distribution is disruption of the structure of the mating system, which is characterized by intense intraspecific competition among males (Geist 1966*a*, Andersson 1994, Mysterud 2010). Indeed, mating systems of sexually dimorphic ungulates typically are polygynous (Weckerly 1998, Loison et al. 1999), wherein mature, dominant males limit the mating opportunities of younger subordinates (Bowyer 1986, Maher and Byers 1987, Mysterud et al. 2003, Bergeron et al. 2010, Bowyer et al. 2011). The degree of participation in mating by young males, however, is related to the proportion of young relative to prime-age males in the population (Komers et al. 1994, Noyes et al. 1996, Mysterud et al. 2003, DeYoung et al. 2006, Bowyer et al. 2007), and heavy harvest may increase mating opportunities and reproductive effort among young, subordinate males (Stevenson and Bancroft 1995; Laurian et al. 2000; Mysterud et al. 2004, 2008; Garel et al. 2006). As a result, increased reproduction by young males holds consequences for the evolution of life-history strategies, in particular age at first reproduction (Festa-Bianchet 2003, Garel et al. 2006, Proaktor et al. 2007). In addition, because growth of horn-like structures increases until prime age in cervids and bovids, a harvest-induced reduction in age structure will yield a disproportionate increase in the number of young males that are harvested prior to attaining asymptotic body mass and, thus, peak horn or antler size (Monteith et al. 2009, Loehr et al. 2010).

The nutritional consequences of density dependence and habitat quality directly influence size of secondary sexual characters of large ungulates, and both have the potential to override demographic or selective effects of harvest (McCullough 1982, Geist 1986, Mysterud et al. 2005, Schmidt et al. 2007, Monteith et al. 2009). For example, based on standard genetic theory and heritability of antler size, Kruuk et al. (2002) predicted that antler size should have increased by 0.146 standard deviations per generation in a wild population of red deer (*Cervus elaphus*). Despite the positive genetic contribution to antler size, however, antlers actually declined in size during the 30-year study because of nutritional limitation in response to rising population density (Kruuk et al. 2002). Current simulations of the effects of various harvest regimes on frequency of genes for growing large antlers or horns indicate the potential for selective harvest to result in genetic change, but those responses are highly variable relative to harvest criteria and may take decades to be expressed (Thelen 1991, Hundertmark et al. 1998, Sæther et al. 2009). Such examples highlight the importance of considering effects of nutrition on patterns of horn and antler growth before assuming that selective harvest was responsible for observed trends (Kruuk et al. 2002, Schmidt et al. 2007). Indeed, maternal effects can have life-lasting consequences on growth and development, regardless of environmental conditions later in life or genetic potential for growth (Monteith et al. 2009). In contrast, compensatory growth in horn or antler size in response to slow development early in life may limit the potential for selective harvest to affect size of horn-like structures, because size of those structures in early life may not be indicative of the genetic potential of an individual for growth and maximum size (Bunnell 1978, Côté et al. 1988, Rughetti and Festa-Bianchet 2010).

Additional Considerations

We also considered incorporating an additional hypothesis. The size-distribution hypothesis is based on the distribution of horn and antler size, specifically the right-hand tail of the distribution in size. Trophy categories that have a strongly skewed distribution with a long right-hand tail should: 1) exhibit increases in trophy size as ungulate populations grow and expand because of a potential increase in the number of large males in the tail of the distribution and, consequently, 2) would be more sensitive to harvest pressure because removal of individuals in the right-hand tail would have a dramatic effect on average size compared with a trophy category with a truncated distribution (i.e., short right-hand skew). We were already dealing solely with what likely were the largest recorded specimens in each trophy category and, in essence, our data represent the tail of the tail of the distribution in size. As a result, the predictions, although elegant given a more broadly representative dataset, would not be expected to be supported by the Boone and Crockett dataset even if the size-distribution hypothesis was correct. To effectively test that hypothesis, we would need to quantify skewness of the entire distribution in horn or antler size of each trophy category—a worthwhile consideration for future research with other datasets.

We chose 2 indices of climate that are known to influence important ecological patterns and processes at a broad geographic scale (Stenseth et al. 2003). Although other indices exist (e.g., Southern Oscillation Index), they are generally more regional in nature, which was not consistent with the scale of our dataset. Ecological processes are sometimes more strongly associated with broad-scale climate metrics, because such metrics may better capture complex associations between local climate and ecological processes (Hallett et al. 2004). Our ability to detect nutritionally mediated effects of climate on size of horn-like structures was hindered by the absence of age-specific data. Nutritional effects on growth can be most influential during ontogeny, which may render individuals unable to garner considerable benefit from enhanced nutrition later in life (Kruuk et al. 2002, Monteith et al. 2009). Furthermore, we were unable to evaluate climate indices for bovids directly, because size of permanent horn structures is an accumulation over the life of an individual, and climate has much less of an effect once an individual has attained trophy size (Geist 1986, Hedrick 2011). Data on age of specimens would have allowed for a more rigorous evaluation of the nutritionally mediated effects of climate on trends in horn and antler size, even though our data likely consisted of mostly prime age, or older, animals in which the largest horn-like structures occur.

Our analyses and interpretations were based on horn and antler sizes that were biased towards exceptionally large individuals, which may bring into question how such data reflect ungulate populations in general, or even trophy ungulates. Although these data were heavily biased towards one end of the phenotypic range, we find no reason to believe that such individuals are in any way inherently devoid of meaningful biological information, or that the Boone and Crockett dataset is not representative of the size of trophy ungulates in North America. Because Records of North American Big Game contains data on horn and antler sizes for 38 categories of native, North American big game that span more than a century and includes >40,000 records, it is difficult to imagine that these data are not meaningful with respect to trophy animals. In addition, we took a number of methodological steps to identify and account for potential biases in our evaluation of predictions that stemmed from the sociological effect hypothesis—none of which were supported.

We used a weight-of-evidence approach to evaluate potential explanations for observed trends in size, mainly because of an absence of age data and the broad geographic and temporal scale of the dataset. Nonetheless, those very characteristics should make it difficult to detect temporal trends; that we detected near-ubiquitous patterns in size supports the existence of a meaningful biological signal in those data. The likelihood of this pattern occurring by chance alone is negligible. Although we were unable to unequivocally extricate the specific mechanisms that potentially underlie the trends in horn-like structures that we observed, we believe our efforts invite discussion on the long-term sustainability of harvest strategies for ungulates and will help foster and guide future research. Elucidating how well data recorded by conservation organizations, such as the Boone and Crockett Club, reflect morphological patterns within ungulate populations is warranted, especially because such data-rich sources are an under-appreciated resource for promoting conservation and management.

MANAGEMENT IMPLICATIONS

We documented significant declines in size of trophy horns and antlers among most categories recorded in Records of North American Big Game during much of the past century. Whether such declines predicate the need for a change in management strategies is uncertain. Indeed, a mean of 1.87% and 0.68% reduction in size of trophy antlers and horns, respectively, during 1950–2008 may be inconsequential relative to the benefits that accrue from recreational hunting opportunities and resultant overall benefits to conservation (Singer and Zeigenfuss 2002, Whitfield 2003, Lindsey et al. 2007, Groves and Leslie 2011, Heffelfinger 2013). The dramatic increases in entries of trophies for most categories during the last few decades (Figs. 3 and 4) also are a testament to the success of management programs for these North American species. If reductions in size of trophy horns and antlers represent concerns for social or biological reasons, managers may want to reevaluate the current harvest paradigm, wherein harvest is focused largely on males. Our weight-of-evidence approach indicated that such male-biased harvest may have gradually reduced male age structure, which in turn has resulted in smaller average horns and antlers among trophy animals. If intensive harvest of males was the underlying reason for the observed declines in size of horn-like structures among trophy males, then a reduction in harvest pressure on males could simultaneously increase male age structure, yield a more balanced sex ratio, and lessen harvest of large, fast-growing males, all of which may help reverse the negative trends we observed (Webb et al. 2007; Hengeveld and Festa-Bianchet 2011; Mysterud 2010, 2011).

In addition to reducing harvest pressure on males, the most effective means of lowering density to enhance nutritional condition and stimulate recruitment when resources are limited is through female harvest (McCullough 1979, McCullough et al. 1990, Jorgenson et al. 1993). Density of males has a limited effect on recruitment patterns of young (McCullough 1979), largely because sexually dimorphic ruminants sexually segregate and, thus, partition use of resources throughout much of the year (Bleich et al. 1997, Kie and Bowyer 1999, McCullough 1999, Bowyer 2004). Moreover, large males likely are most susceptible to resource limitation as a result of density dependence because they often enter the most nutritionally challenging time of year (i.e., winter) after nutritional reserves have been depleted during the mating season. Density dependence may have a greater influence on size of males than that of females (Verme and Ozoga 1980, Clutton-Brock et al. 1982, Ashley et al. 1998, Keyser et al. 2005) because nutritional limitation affects body mass (and size of horn-like structures) in males, as opposed to reproductive status of females (Clutton-Brock et al. 1982, Stewart et al. 2005, Monteith et al. 2009). Achieving desirable female harvest, however, can be difficult given public perception of harvesting females and the growing emphasis on trophy size (Festa-Bianchet and Lee 2009, Messner 2011).

Disentangling effects of selective harvest, demographic responses to harvest, and nutritional effects on size of horn-like structures is a daunting task, but one worthy of further investigation. We documented statistically significant changes in trophy horn and antler sizes of numerous North American ungulates during the past century that may be harvest-related, although we were unable to completely unravel causal mechanisms. Monitoring programs, such as the Records of North American Big Game, that rely on characteristics of harvested animals have been invaluable for assessing long-term trends in morphological characteristics. Nonetheless, collecting information on age, in addition to size, would help clarify mechanisms of potential change. To increase the relevance of their data to conservation and management of wildlife, the Boone and Crockett Club recently initiated efforts to obtain ages of all trophy submissions; such efforts help to dispel the notion that Records of North American Big Game is merely a records book (Spring 2012). Quantitative genetics is a powerful alternative approach, but such investigations require knowledge of phenotypes and pedigrees among known individuals (Garant and Kruuk 2005), which precludes their application in most situations for large free-ranging ungulates. Data from long-term field studies that monitor horn or antler size of individuals and their influence on probability of survival likely will provide the most effective means of differentiating between demographic and selective effects of harvest (e.g., Bonenfant et al. 2009*b*). Those data must be corroborated with data on population density in relation to carrying capacity, climate, and forage quality, although measures of nutritional condition will likely provide an integrated measure of current nutritional status of the population (Parker et al. 2009).

SUMMARY

- We evaluated long-term trends in size of trophy horn-like structures of native, North American ungulates during the past century using data recorded in Records of North American Big Game. Trophy specimens that were harvested, collected, or possessed by agencies were included in our analyses.
- We used a weight-of-evidence approach to evaluate the relative merit of several competing hypotheses for explaining long-term trends in size of horns and antlers at a continental scale. Hypotheses included intensive harvest, selective harvest, sociological effect, broad-scale climate, and habitat alteration.
- The number of entries per decade increased for most trophy categories. Trends in size of horn-like structures were negative and significant for 11 of 17 antlered categories and 3 of 8 horned categories. Muskox and pronghorn were the only trophy categories that exhibited a significant, positive trend in size of horn-like structures.
- Our results provided support for harvest-based hypotheses for explaining long-term trends in size, but no support for sociological, climatic, or habitat-based explanations.
- The intensive-harvest hypothesis is based on the premise that heavy harvest of males has gradually shifted age structure toward younger males, resulting in smaller average size of trophy horn-like structures. The absence of a significant decline in horn size for 2 of the 3 species that experience the most conservative harvest regimes in North America, and a significant increase in horn size among pronghorn (which exhibit an early peak in horn size) both support the intensive-harvest hypothesis.
- The selective-harvest hypothesis is based on the premise that trophy hunting has selected against genes for large horn-like structures. One of 2 specific predictions that followed from that hypothesis was supported by our results.
- Although we documented significant declines in size of trophy horns and antlers recorded in Records of North American Big Game, average predicted declines of 0.68% and 1.87% in size of trophy horns and antlers, respectively, may be less important relative to the benefits that have accrued from recreational opportunities and resultant overall contributions to conservation.
- Our results provided some support for a potential effect of harvest on size of trophy horn-like structures; however, we were unable to directly assess causal mechanisms because of the nature of the dataset. Disentangling those mechanisms is an important pursuit for the conservation of large ungulates; thus, additional research should focus on elucidating the relative influence of harvest and nutrition on horn and antler size.

ACKNOWLEDGMENTS

We thank the Boone and Crockett Club for allowing us access to the Records of North American Big Game, the Official Measurers that have dedicated their time to meticulous measuring and recording of trophy size during the past century, and for the contributions of J. Reneau, J. Spring, and E. Buckner. We thank K. Slayer for assistance with graphic design, and we are grateful to T. Bynum for provision of photographs for the cover. We thank A. M. Perez and the Advanced Translation class (SPAN4095) for Spanish translation of our abstract, and J. Taillon for the French translation. We thank C. Mitchell, M. Boyce, R. Putman, M. Festa-Bianchet, J. Whiting, M. Garel, C. DeYoung, V. Geist, D. Leslie, Jr. and 1 anonymous reviewer for constructive comments that greatly improved the manuscript. We thank E. C. Hellgren for enhancing the quality of the manuscript for publication. Support was provided by the Department of Biological Sciences at Idaho State University, the Wyoming Cooperative Fish and Wildlife Research Unit at the University of Wyoming, the Boone and Crockett Program in Wildlife Conservation at the University of Montana, the Arizona Game and Fish Department, Monteith Taxidermy, and the Eastern Sierra Center for Applied Population Ecology. Publication costs were covered by the Boone and Crockett Program in Wildlife Conservation at the University of Montana, and the Boone and Crockett Club. This is professional paper 088 from the Eastern Sierra Center for Applied Population Ecology.

LITERATURE CITED

Adams, K., J. Hamilton, and M. Ross. 2012. QDMA's Whitetail Report 2012. Quality Deer Management Association. <http://www.qdma.com/uploads/pdf/WR2012.pdf>. Accessed 20 Jun 2012.

Allen, D. L. 1954. Our wildlife legacy. Funk and Wagnalls, New York, New York, USA.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, New Jersey, USA.

Ashley, E. P., G. B. McCullough, and J. T. Robinson. 1998. Morphological responses of white-tailed deer to a severe population reduction. Canadian Journal of Zoology 76:1–5.

Barnett, T. P., D. W. Pierce, H. G. Hidalgo, C. Bonfils, B. D. Santer, T. Das, G. Bala, A. W. Wood, T. Nozawa, A. A. Mirin, D. R. Cayan, and M. D. Dettinger. 2008. Human-induced changes in the hydrology of the western United States. Science 319:1080–1083.

Becker, M. S., F. G. R. Watson, E. Droge, K. Leigh, R. S. Carlson, and A. A. Carlson. 2013. Estimating past and future male loss in three Zambian lion populations. Journal of Wildlife Management 77:128–142.

Berger, J. 2005. Hunting by carnivores and humans: does functional redundancy occur and does it matter? Pages 315–341 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island Press, Washington, D.C., USA.

Berger, J., and M. E. Gompper. 1999. Sex ratios in extant ungulates: products of contemporary predation or past life histories? Journal of Mammalogy 80:1084–1113.

Bergeron, P., M. Festa-Bianchet, A. Von Hardenberg, and B. Bassano. 2008. Heterogeneity in male horn growth and longevity in a highly sexually dimorphic ungulate. Oikos 117:77–82.

Bergeron, P., S. Grignolio, M. Apollonio, B. Shipley, and M. Festa-Bianchet. 2010. Secondary sexual characters signal fighting ability and determine social rank in Alpine ibex (*Capra ibex*). Behavioral Ecology and Sociobiology 64:1299–1307.

Bischof, R., A. Mysterud, and J. E. Swenson. 2008. Should hunting mortality mimic the patterns of natural mortality? Biology Letters 4:307–310.

Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:1–50.

Bonenfant, C., J.-M. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe, P. Blanchard, N. Pettorelli, N. Owen-Smith, J. du Toit, and P. Duncan. 2009*a*. Empirical evidence of density-dependence in populations of large herbivores. Advances in Ecological Research 41:313–357.

Bonenfant, C., F. Pelletier, M. Garel, and P. Bergeron. 2009*b*. Age-dependent relationship between horn growth and survival in wild sheep. Journal of Animal Ecology 78:161–171.

Bowyer, R. T. 1986. Antler characteristics as related to social status of male southern mule deer. Southwestern Naturalist 31:289–298.

Bowyer, R. T. 2004. Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. Journal of Mammalogy 85:1039–1052.

Bowyer, R. T., V. C. Bleich, X. Manteca, J. C. Whiting, and K. M. Stewart. 2007. Sociality, mate choice, and timing of mating in American bison. Ethology 113:1048–1060.

Bowyer, R. T., G. M. Blundell, M. Ben-David, S. C. Jewett, T. A. Dean, and L. K. Duffy. 2003. Effects of the *Exxon Valdez* oil spill on river otters: injury and recovery of a sentinel species. Wildlife Monographs 153:1–53.

Bowyer, R. T., D. M. Leslie, Jr., and J. L. Rachlow. 2000. Dall's and Stone's sheep. Pages 491–516 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

Bowyer, R. T., M. C. Nicholson, E. M. Molvar, and J. B. Faro. 1999. Moose on Kalgin Island: are density-dependent processes related to harvest? Alces 35: 73–89.

Bowyer, R. T., J. L. Rachlow, K. M. Stewart, and V. V. Ballenberghe. 2011. Vocalizations by Alaskan moose: female incitation of male aggression. Behavioral Ecology and Sociobiology 65:2251–2260.

Bowyer, R. T., K. M. Stewart, J. G. Kie, and W. C. Gasaway. 2001. Fluctuating asymmetry in antlers of Alaskan moose: size matters. Journal of Mammalogy 82:814–824.

Bowyer, R. T., K. M. Stewart, B. M. Pierce, K. J. Hundertmark, and W. C. Gasaway. 2002. Geographical variation in antler morphology of Alaskan moose: putative effects of habitat and genetics. Alces 38:155–165.

Brown, R. D. 1983. Antler development in Cervidae. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, USA.

Bubenik, G. A., and A. B. Bubenik. 1990. Horns, pronghorns, and antlers. Springer-Verlag, New York, New York, USA.

Buckner, E. L., C. R. Byers, and J. Reneau. 2009. Measuring and scoring North American big game trophies. Boone and Crockett Club, Missoula, Montana, USA.

Bunnell, F. L. 1978. Horn growth and population quality in Dall sheep. Journal of Wildlife Management 42:764–775.

Byers, J. A. 1997. American pronghorn. The University of Chicago Press, Chicago, Illinois, USA.

Clutton-Brock, T. H. 1982. The functions of antlers. Behaviour 79:108–125.

Clutton-Brock, T. H., F. E. Guiness, and S. D. Albon. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois, USA.

Coltman, D. W. 2008. Molecular ecological approaches to studying the evolutionary impacts of selective harvesting in wildlife. Molecular Ecology 16:221–235.

Coltman, D. W., M. Festa-Bianchet, J. T. Jorgenson, and C. Strobeck. 2002. Age-dependent sexual selection in bighorn rams. Proceedings of the Royal Society B 269:165–172.

Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. Nature 426:655–658.

Côté, S. D., M. Festa-Bianchet, and K. G. Smith. 1988. Horn growth in mountain goats (*Oreamnos americanus*). Journal of Mammalogy 79: 406–414.

Darimont, C. T., S. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen, and C. C. Wilmers. 2009. Human predators outpace other agents of trait change in the wild. Proceedings of the National Academy of Sciences 106:952–954.

Demarais, S., and P. R. Krausman, editors. 2000. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

DeYoung, R. W., S. Demarais, R. L. Honeycutt, K. L. Gee, and R. A. Gonzales. 2006. Social dominance and male breeding success in white-tailed deer: instability, unpredictability, and individual heterogeneity. Wildlife Society Bulletin 34:131–136.

Ditchkoff, S. S., R. L. Lochmiller, R. E. Masters, W. R. Starry, and D. M. Leslie, Jr. 2001. Does fluctuating asymmetry of antlers in white-tailed deer (*Odocoileus virginianus*) follow patterns predicted for sexually selected traits? Proceedings of the Royal Society B 268:891–898.

Douglas, C. L., and D. M. Leslie, Jr. 1999. Management of bighorn sheep. Pages 238–262 *in* R. Valdez and P. R. Krausman, editors. Mountain sheep of North America. University of Arizona Press, Tucson, Arizona, USA.

Dunlap, R. R. 1998. Sport hunting and conservation, 1880–1920. Environmental Review 12:51–60.

Ezenwa, V. O., and A. E. Jolles. 2008. Horns honestly advertise parasite infection in male and female African buffalo. Animal Behaviour 75:2013–2021.

Fenberg, P. B., and K. Roy. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Molecular Ecology 17: 209–220.

Festa-Bianchet, M. 2003. Exploitative wildlife management as a selective pressure for the life history evolution of large mammals. Pages 191–207 *in* M. Festa-Bianchet and M. Apollonio, editors. Animal behavior and wildlife conservation. Island Press, Washington, D.C., USA.

Festa-Bianchet, M. 2008. Ecology, evolution, economics, and ungulate management. Pages 183–202 *in* T. E. Fulbright and D. G. Hewitt, editors. Wildlife science: linking theory and management applications. CRC Press, Boca Raton, Florida, USA.

Festa-Bianchet, M., D. W. Coltman, L. Turelli, and J. T. Jorgenson. 2004. Relative allocation to horn and body growth in bighorn rams varies with resource availability. Behavioral Ecology 15:305–312.

Festa-Bianchet, M., and S. D. Côté. 2008. Mountain goats: ecology, behavior, and conservation of an alpine ungulate. Island Press, Washington, D.C., USA.

Festa-Bianchet, M., and R. Lee. 2009. Guns, sheep, and genes: when and why trophy hunting may be a selective pressure. Pages 94–107 *in* B. Dickson, J. Hutton, and W. M. Adams, editors. Recreational hunting, conservation and rural livelihoods: science and practice. Wiley-Blackwell, Oxford, United Kingdom.

Forchhammer, M. C., and E. Post. 2004. Using large-scale climate indices in climate change ecology studies. Population Ecology 46:1–12.

Forchhammer, M. C., E. Post, T. B. G. Berg, T. T. Hoye, and N. M. Schmidt. 2005. Local-scale and short-term herbivore-plant spatial dynamics reflect influences of large-scale climate. Ecology 86:2644–2651.

Forchhammer, M. C., E. Post, N. C. Stenseth, and D. M. Boertmann. 2002. Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. Population Ecology 44:113–120.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

Garant, D., and L. E. B. Kruuk. 2005. How to use molecular marker data to measure evolutionary parameters in wild populations. Molecular Ecology 14:1843–1859.

Garel, M., J.-M. Cugnasse, D. Maillard, J.-M. Gaillard, A. J. M. Hewison, and D. Dubray. 2007. Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. Ecological Applications 17:1607–1618.

Garel, M., E. J. Solberg, B.-E. Sæther, I. Herfindal, and K.-A. Høgda. 2006. The length of growing season and adult sex ratio affect sexual size dimorphism in moose. Ecology 87:745–758.

Geist, V. 1966*a*. The evolution of horn-like organs. Behaviour 27:175–214.

Geist, V. 1966*b*. The evolutionary significance of mountain sheep horns. Evolution 20:558–566.

Geist, V. 1971. Mountain sheep: a study in behavior and evolution. The University of Chicago Press, Chicago, Illinois, USA.

Geist, V. 1986. Super antlers and pre-World War II european research. Wildlife Society Bulletin 14:91–94.

Ginsberg, J. R., and E. J. Millner-Gulland. 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. Conservation Biology 8:157–166.

Gomendio, M., A. F. Malo, J. Garde, and E. R. S. Roldan. 2007. Sperm traits and male fertility in natural populations. Reproduction 134:19–29.

Goss, R. J. 1983. Deer antlers: regeneration, function, and evolution. Academic Press, New York, New York, USA.

Gould, S. J. 1974. The origin and function of 'bizarre' structure: antler size and skull size in the 'Irish Elk' *Megaloceros giganteus*. Evolution 28:191–220.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815.

Gray, P. N. 1932. Records of North American big game. Derrydale Press, Lanham, Maryland, USA.

Groves, C. P., and D. M. Leslie, Jr. 2011. Family bovidae (hollow-horned ruminants). Pages 444–457 *in* D. E. Wilson and R. A. Mittermeier, editors. Handbook of the mammals of the world. Lynx Edicions, Bacelona, Spain.

Hallett, T. B., T. Coulson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and B. T. Grenfell. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430: 71–75.

Hamlet, A. F., P. W. Mote, M. P. Clark, and D. P. Lettenmaier. 2005. Effects of temperature and precipitation variability on snowpack trends in the western United States. Journal of Climate 18:4545–4561.

Harmel, D. E. 1982. Effects of genetics on antler quality and body size in white-tailed deer. Pages 339–348 *in* R. D. Brown, editor. Antler development in Cervidae. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, USA.

Harris, R. B., and D. H. Pletscher. 2002. Incentives toward conservation of argali *Ovis ammon*: a case study of trophy hunting in western China. Oryx 36:373–381.

Hartl, G. B., F. Klein, R. Willing, M. Apollonio, and G. Lang. 1995. Allozymes and the genetics of antler development in red deer (*Cervus elaphus*). Journal of Zoology 237:83–100.

Hartl, G. B., G. Lang, F. Klein, and R. Willing. 1991. Relationships between allozymes, heterozygosity and morphological characters in red deer (*Cervus elaphus*), and the influence of selective hunting on allele frequency distributions. Heredity 66:343–350.

Hebblewhite, M. 2005. Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. Journal of Animal Ecology 74:226–233.

Hedrick, P. W. 2011. Rapid decrease in horn size of bighorn sheep: environmental decline, inbreeding depression, or evolutionary response to trophy hunting? Journal of Heredity 102:770–781.

Heffelfinger, J. R. 2013. Hunting and trapping. Pages xx–xx *in* P. R. Krausman and J. W. Cain III, editors. Wildlife management: contemporary principles and practices. John Hopkins University Press, Baltimore, Maryland, USA. In press.

Hengeveld, P. E., and M. Festa-Bianchet. 2011. Harvest regulations and artificial selection on horn size in male bighorn sheep. Journal of Wildlife Management 75:189–197.

Hundertmark, K. J., R. T. Bowyer, G. F. Shields, and C. C. Schwartz. 2003. Mitochondrial phylogeography of moose (*Alces alces*) in North America. Journal of Mammalogy 84:718–728.

Hundertmark, K. J., T. H. Thelen, and R. T. Bowyer. 1998. Effects of population density and selective harvest on antler phenotype in simulated moose populations. Alces 34:375–383.

Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation regional temperatures and precipitation. Science 269:676–679.

Hurrell, J. W., Y. Kushnir, and M. Visbeck. 2001. The North Atlantic Oscillation. Science 291:603–605.

Jenks, J. A., W. P. Smith, and C. S. DePerno. 2002. Maximum sustained yield harvest versus trophy management. Journal of Wildlife Management 66:528–535.

Jorgenson, J. T., M. Festa-Bianchet, and W. D. Wishart. 1993. Harvesting bighorn ewes: consequences for population size and trophy ram production. Journal of Wildlife Management 57:429–436.

Jorgenson, J. T., M. Festa-Bianchet, and W. D. Wishart. 1998. Effects of population density on horn development in bighorn rams. Journal of Wildlife Management 62:1011–1020.

Keyser, P. D., D. C. Guynn, Jr., and H. S. Hill, Jr. 2005. Population density: physical condition relationships in white-tailed deer. Journal of Wildlife Management 69:356–365.

Keyser, P. D., D. C. Guynn, Jr., W. M. Knox, K. E. Kammermeyer, and J. M. Crum. 2006. Responses of adult sex ratios to simulated harvest strategies in white-tailed deer. Wildlife Society Bulletin 34:1273–1279.

Kie, J. G., and R. T. Bowyer. 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. Journal of Mammalogy 80:1004–1020.

Klein, D. R. 2000. The muskox. Pages 545–558 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

Knowles, N., M. D. Dettinger, and D. R. Cayan. 2005. Trends in snowfall versus rainfall in the western United States. Journal of Climate 19:4545–4559.

Komers, P. E., F. Messier, and C. C. Gates. 1994. Plasticity of reproductive behaviour in wood bison bulls: when subadults are given a chance. Ethology, Ecology, and Evolution 6:313–330.

Krausman, P. R., and D. M. Shackleton. 2000. Bighorn sheep. Pages 517–544 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

Krebs, C. J. 1999. Ecological methodology. Second edition. Addison Wesley Longman, Menlo Park, California, USA.

Kruuk, L. E. B., J. Slate, J. M. Pemberton, S. Brotherstone, F. Guinness, and T. Clutton-Brock. 2002. Antler size in red deer: heritability and selection but no evolution. Evolution 56:1683–1695.

Langvatn, R., and A. Loison. 1999. Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. Wildlife Biology 5:213–223.

Laurian, C., J. Ouellet, R. Courtois, L. Breton, and S. St-Onge. 2000. Effects of intensive harvesting on moose reproduction. Journal of Applied Ecology 37:515–531.

Lindsey, P. A., P. A. Roulet, and S. S. Romañach. 2007. Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. Biological Conservation 134:455–469.

Lockwood, M. A., D. B. Frels, Jr., W. E. Armstrong, E. Fuchs, and D. E. Harmel. 2007. Genetic and environmental interaction in white-tailed deer. Journal of Wildlife Management 71:2732–2735.

Loehr, J., J. Carey, M. Hoefs, J. Suhonen, and H. Ylönen. 2007. Horn growth rate and longevity: implications for natural and artificial selection in thinhorn sheep (*Ovis dalli*). Journal of Evolutionary Biology 20:818–828.

Loehr, J., J. Carey, R. B. O'Hara, and D. S. Hik. 2010. The role of phenotypic plasticity in responses of hunted thinhorn sheep ram horn growth to changing climate conditions. Journal of Evolutionary Biology 23:783–790.

Loison, A., J.-M. Gaillard, C. Pélabon, and N. G. Yoccoz. 1999. What factors shape sexual size dimorphism in ungulates? Evolutionary Ecology Research 1:611–633.

Lukefahr, S. D., and H. A. Jacobson. 1998. Variance component analysis and heritability of antler traits in white-tailed deer. Journal of Wildlife Management 62:252–268.

Maher, C. R., and J. A. Byers. 1987. Age-related changes in reproductive effort of male bison. Behavioral Ecology and Sociobiology 21:91–96.

Mahoney, S. P., J. N. Weir, J. G. Luther, J. A. Schaefer, and S. F. Morrison. 2011. Morphological change in Newfoundland caribou: effects of abundance and climate. Rangifer 31:21–34.

Mainguy, J., S. D. Côté, E. Cardinal, and M. Holle. 2008. Mating tactics and mate choice in relation to age and social rank in male mountain goats. Journal of Mammalogy 89:626–635.

Malo, A. F., E. R. S. Roldan, J. Garde, A. J. Soler, and M. Gomendio. 2005. Antlers honestly advertise sperm production and quality. Proceeding of the Royal Society of London B 272:1449–1457.

Marshal, J. P., P. R. Krausman, V. C. Bleich, W. B. Ballard, and J. S. McKeever. 2002. Rainfall, El Niño, and dynamics of mule deer in the Sonoran Desert, California. Journal of Wildlife Management 66:1283–1289.

McCullough, D. R. 1979. The George Reserve deer herd: population ecology of a K-selected species. University of Michigan, Ann Arbor, Michigan, USA.

McCullough, D. R. 1982. Antler characteristics of George Reserve white-tailed deer. Journal of Wildlife Management 46:821–826.

McCullough, D. R. 1999. Density dependence and life-history strategies of ungulates. Journal of Mammalogy 80:1130–1146.

McCullough, D. R., D. S. Pine, D. L. Whitmore, T. M. Mansfield, and R. H. Decker. 1990. Linked sex harvest strategy for big game management with a test case on black-tailed deer. Wildlife Monographs 112:1–41.

Messner, T. C. 2011. White-tailed deer management strategies and domestication processes. Human Ecology 39:165–178.

Milner, J. M., E. B. Nilsen, and H. P. Andreassen. 2007. Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology 21:36–47.

Mitchell, C. D., and C. R. Maher. 2001. Are horn characteristics related to age in male pronghorns? Wildlife Society Bulletin 29:908–916.

Mitchell, C. D., and C. R. Maher. 2006. Horn growth in male pronghorns *Antilocapra americana*: selection for precocial maturation in stochastic environments. Acta Theriologica 51:4045–4409.

Monteith, K. L., L. E. Schmitz, J. A. Jenks, J. A. Delger, and R. T. Bowyer. 2009. Growth of male white-tailed deer: consequences of maternal effects. Journal of Mammalogy 90:651–660.

Mysterud, A. 2010. Still walking on the wild side? Management actions as steps towards 'semi-domestication' of hunted ungulates. Journal of Applied Ecology 47:920–925.

Mysterud, A. 2011. Selective harvesting of large mammals: how often does it result in directional selection? Journal of Animal Ecology 48:827–834.

Mysterud, A., and R. Bischof. 2010. Can compensatory culling offset undesirable evolutionary consequences of trophy hunting? Journal of Animal Ecology 79:148–160.

Mysterud, A., C. Bonenfant, L. E. Loe, R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2008. Age-specific feeding cessation in male red deer during rut. Journal of Zoology 275:107–412.

Mysterud, A., Ø. Holand, K. H. Røed, H. Gjøstein, J. M. Kumpula, and M. Niemen. 2003. Effects of age, density, and sex ratio on reproductive effort in male reindeer (*Rangifer tarandus*). Journal of Zoology 264:209–215.

Mysterud, A., R. Langvatn, and N. C. Stenseth. 2004. Patterns of reproductive effort in male ungulates. Journal of Zoology London 264:209–215.

Mysterud, A., E. Meisingset, R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2005. Climate-dependent allocation of resources to secondary sexual traits in red deer. Oikos 111:245–252.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. Fourth edition. WCB McGraw-Hill, Boston, Massachusetts, USA.

Noyes, J. H., B. K. Johnson, L. D. Bryant, S. L. Findholt, and J. W. Thomas. 1996. Effect of bull age on conception dates and pregnancy rates of cow elk. Journal of Wildlife Management 60:508–517.

Noyes, J. H., B. K. Johnson, B. L. Dick, and J. G. Kie. 2002. Effects of male age and female nutritional condition on elk reproduction. Journal of Wildlife Management 66:1301–1307.

O'Gara, B. W., and J. D. Yoakum. 2004. Pronghorn: ecology and management. Wildlife Management Institute, University Press of Colorado, Boulder, USA.

Ottersen, G., B. Planque, A. Belgrano, E. Post, P. C. Reid, and N. C. Stenseth. 2001. Ecological effects of the North Atlantic Oscillation. Oecologia 128:1–14.

Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57–69.

Patterson, B. R., and V. A. Power. 2001. Contributions of forage competition, harvest, and climate fluctuation to changes in population growth of northern white-tailed deer. Oecologia 128:244–255.

Pérez, J. M., E. Serrano, M. González-Candela, L. León-Vizcaino, G. G. Barberá, M. A. de Simón, P. Fandos, J. E. Granados, R. C. Soriguer, and M. Festa-Bianchet. 2011. Reduced horn size in two wild trophy-hunted species of Caprinae. Wildlife Biology 17:102–112.

Pierce, B. M., V. C. Bleich, K. L. Monteith, and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. Journal of Mammalogy 93:977–988.

Posewitz, J. 1994. Beyond fair chase. Falcon Press Publishing, Helena, Montana, USA.

Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322–1339.

Post, E., N. C. Stenseth, R. Langvatn, and J. M. Fromentin. 1997. Global climate change and phenotypic variation among red deer cohorts. Proceedings of the Royal Society B 262:1317–1324.

Preston, B. T., I. R. Stevenson, J. M. Pemberton, D. W. Coltman, and K. Wilson. 2003. Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. Proceedings of the Royal Society of London B 270:633–640.

Proaktor, G., T. Coulson, and E. J. Milner-Gulland. 2007. Evolutionary responses to harvesting in ungulates. Journal of Animal Ecology 76:669–678.

Rasmussen, H. B., J. B. A. Okello, G. Wittemyer, H. R. Siegismund, P. Arctander, F. Vollrath, and I. Douglas-Hamilton. 2008. Age- and tactic-related paternity success in male African elephants. Behavioral Ecology 19:9–15.

Rattenbury, R. C. 2008. Hunting the American West. Boone and Crockett Club, Missoula, Montana, USA.

Reiger, J. F. 1975. American sportsmen and the origins of conservation. The Winchester Press, New York, New York, USA.

Reneau, J., and E. L. Buckner. 2005. Records of North American big game. Boone and Crockett Club, Missoula, Montana, USA.

Rogers, J. C. 1981. The North Pacific Oscillation. International Journal of Climatology 1:39–57.

Rughetti, M., and M. Festa-Bianchet. 2010. Compensatory growth limits opportunities for artificial selection in alpine chamois. Journal of Wildlife Management 74:1024–1029.

Sæther, B.-E., S. Engen, and E. J. Solberg. 2009. Effective size of harvested ungulate populations. Animal Conservation 12:488–495.

Schmidt, J. I., J. M. Ver Hoef, and R. T. Bowyer. 2007. Antler size of Alaskan moose *Alces alces gigas*: effects of population density, hunter harvest and use of guides. Wildlife Biology 13:53–65.

Schmidt, K. T., A. Stien, S. D. Albon, and F. E. Guinness. 2001. Antler length of yearling red deer is determined by population density, weather and early life-history. Oecologia 127:191–197.

Servanty, S., J.-M. Gaillard, F. Ronchi, S. Focardi, É. Baubet, and O. Gimenez. 2011. Influence of harvesting pressure on demographic tactics: implications for wildlife management. Journal of Applied Ecology 48:835–843.

Shackleton, D. M., and D. A. Hutton. 1971. An analysis of the mechanisms of brooming of mountain sheep horns. Zeitschrift für Säugetierkunde 36:342–350.

Shaw, J. H., and M. Meagher. 2000. Bison. Pages 447–466 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

Singer, F. J., and L. C. Zeigenfuss. 2002. Influence of trophy hunting and horn size on mating behavior and survivorship of mountain sheep. Journal of Mammalogy 83:682–698.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third edition. W.H. Freeman and Company, New York, New York, USA.

Solberg, E. J., A. Loison, B.-E. Sæther, and O. Strand. 2000. Age-specific harvest mortality in a Norwegian moose *Alces alces* population. Wildlife Biology 6: 41–52.

Solberg, E. J., and B.-E. Sæther. 1993. Fluctuating asymmetry in the antlers of moose (*Alces alces*): does it signal male quality? Proceedings of the Royal Society of London B 254:251–255.

Spring, J. 2012. Age data implementation. Fair Chase 27:56–62.

Stenseth, N. C., K.-S. Chan, H. Tong, R. Boonstra, S. Boutin, C. J. Krebs, E. Post, M. O'Donoghue, N. G. Yoccoz, M. C. Forchhammer, and J. W. Hurrell. 1999. Common dynamic structure of Canada lynx populations within three climatic regions. Science 285:1071–1073.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292–1296.

Stenseth, N. C., G. Ottersen, J. W. Hurrell, A. Mysterud, M. Lima, K.-S. Chan, N. G. Yoccoz, and J. Adlandsvik. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proceedings of the Royal Society B 270:2087–2096.

Stevenson, I. R., and D. R. Bancroft. 1995. Fluctuating trade-offs favour precocial maturity in male Soay sheep. Proceedings of the Royal Society B 262:267–275.

Stewart, K. M., R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143:85–93.

Stewart, K. M., R. T. Bowyer, J. G. Kie, and W. C. Gasaway. 2000. Antler size relative to body mass in moose: tradeoffs associated with reproduction. Alces 36:77–83.

Strickland, B. K., and S. Demarais. 2000. Age and regional differences in antlers and mass in white-tailed deer. Journal of Wildlife Management 64:903–911.

Strickland, B. K., and S. Demarais. 2008. Influence of landscape composition and structure on antler size of white-tailed deer. Journal of Wildlife Management 72:1101–1108.

Sudbeck, O. 1993. Awesome antlers of North America. HTW Publications, Seneca, Kansas, USA.

The Committee on Records of the Boone and Crockett Club. 1952. Records of North American Big Game. First edition. Charles Scribner's Sons, New York, New York, USA.

Thelen, T. H. 1991. Effects of harvest on antlers of simulated populations of elk. Journal of Wildlife Management 55:243–249.

Tiilikainen, R., T. Nygrén, J. Pusenius, and V. Ruusila. 2010. Variation in growth patterns of male moose *Alces alces* after two contrasted periods of hunting. Annales Zoologici Fennici 47:159–172.

Toweill, D. E., and V. Geist. 1999. Return of royalty: wild sheep of North America. Boone and Crockett Club, Missoula, Montana and Foundation for North, American Wild Sheep, Cody, Wyoming.

Trenberth, K. E., and J. W. Hurrell. 1994. Decadal atmosphere-ocean variations in the Pacific. Climate Dynamics 9:303–319.

Vanpé, C., J.-M. Gaillard, P. Kjellander, O. Liberg, D. Delorme, and A. J. M. Hewison. 2010. Assessing the intensity of sexual selection on male body mass and antler length in roe deer *Capreolus capreolus*: is bigger better in a weakly dimorphic ungulate? Oikos 119:1484–1492.

Vanpé, C., J.-M. Gaillard, P. Kjellander, A. Mysterud, P. Magnien, D. Delorme, G. Van Laere, F. Klein, O. Liberg, and A. J. M. Hewison. 2007. Antler size provides an honest signal of male phenotypic quality in roe deer. American Naturalist 169:481–493.

Verme, L. J., and J. J. Ozoga. 1980. Effect of diet on growth and lipogenesis in deer fawns in autumn. Journal of Wildlife Management 44:315–324.

Walker, R. 2011. State status reports. Pages 46–64 *in* S. G. Liley, editor. Proceedings of the 9th Western States and Provinces Deer and Elk Workshop-2011. New Mexico Department of Game and Fish, Santa Fe, New Mexico, USA.

Webb, S. L., S. Demarais, B. K. Strickland, R. W. DeYoung, B. P. Kinghorn, and K. L. Gee. 2012. Effects of selective harvest on antler size in white-tailed deer: a modeling approach. Journal of Wildlife Management 76: 48–56.

Webb, S. L., D. G. Hewitt, and M. W. Hellickson. 2007. Survival and cause-specific mortality of mature male white-tailed deer. Journal of Wildlife Management 71:555–558.

Weckerly, F. W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. Journal of Mammalogy 79:33–52.

Whitfield, J. 2003. Sheep horns downsized by hunters' taste for trophies. Nature 426:595.

Whitten, K. R. 2001. Effects of horn-curl regulations on demography of Dall's sheep: a critical review. Alces 37:483–495.

Wild Sheep Foundation Professional Biologist Meeting Attendees. 2008. Ram harvest strategies for Western states and provinces-2007. Biennial Symposium of the Northern Wild Sheep and Goat Council 16:92–98.

Williams, J. D., W. F. Krueger, and D. H. Harmel. 1994. Heritabilities for antler characteristics and body weight in yearling white-tailed deer. Heredity 73:78–83.

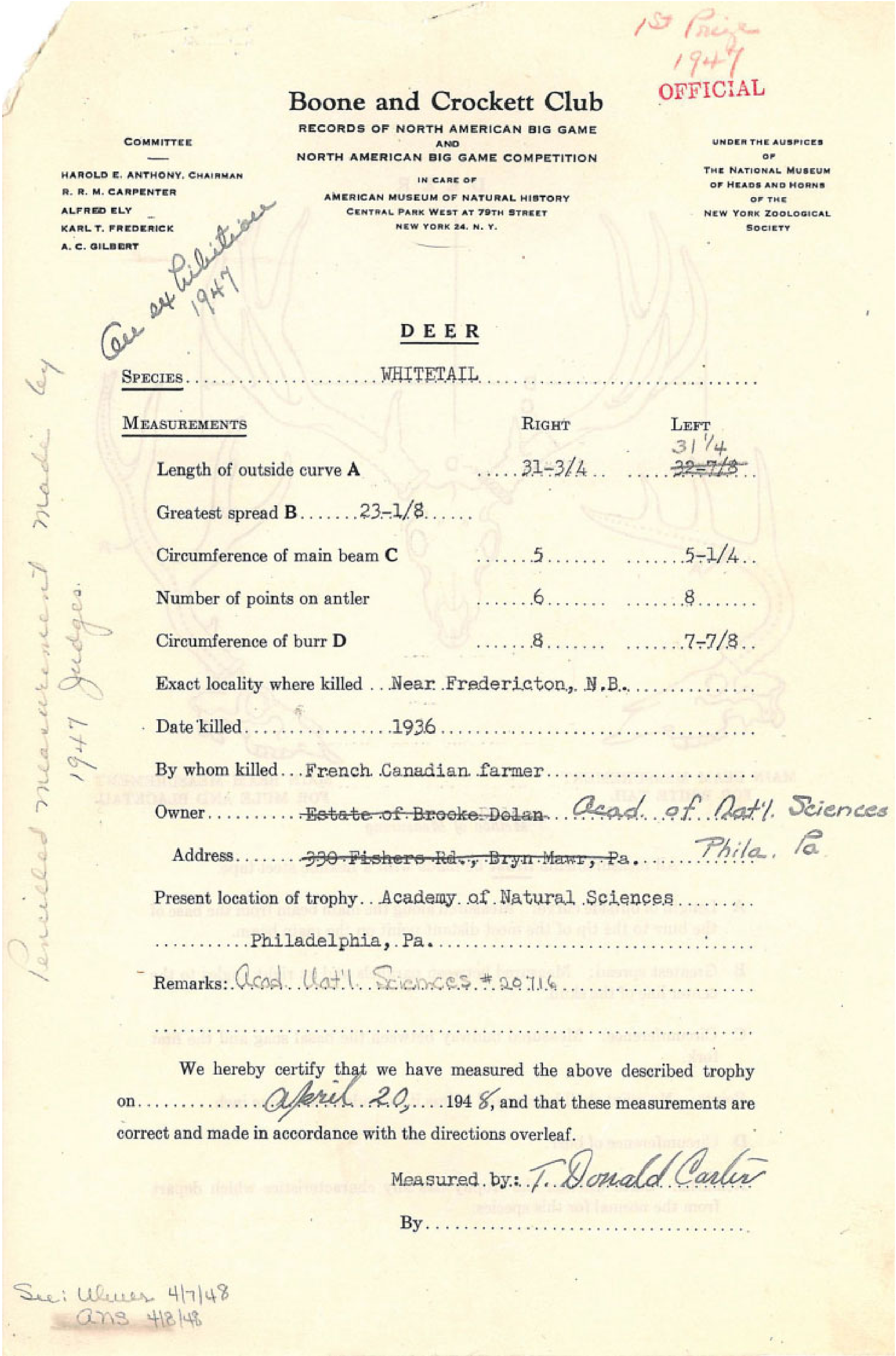
Williamson, L. F. 1987. Evolution of a landmark law. Pages 1–17 *in* H. Kallman, C. P. Agee, W. R. Goforth, and J. P. Linduska, editors. Restoring America's wildlife 1937–1987. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

Wilson, D. E., and R. A. Mittermeier. 2011. Handbook of the mammals of the world. Lynx Edicions, Barcelona, Spain.

Wilson, D. W., and D. M. Reeder. 2005. Mammal species of the world. Third edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Winkler, C. 1987. Desert bighorn sheep hunting regulations and methodology for determining harvest quotas. Desert Bighorn Council Transactions 31:37–38.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.



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THE NATIONAL MUSEUM
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OF THE
NEW YORK ZOOLOGICAL
SOCIETY

Case at Exhibition 1947

DEER

SPECIES WHITETAIL

MEASUREMENTS	RIGHT	LEFT
Length of outside curve **A**	31-3/4	~~32-7/8~~ 31 1/4
Greatest spread **B** 23-1/8		
Circumference of main beam **C**	5	5-1/4
Number of points on antler	6	8
Circumference of burr **D**	8	7-7/8

Exact locality where killed Near Fredericton, N.B.

Date killed 1936

By whom killed French Canadian farmer

Owner ~~Estate of Brooke Dolan~~ Acad. of Nat'l. Sciences

Address ~~330 Fishers Rd., Bryn Mawr, Pa.~~ Phila. Pa

Present location of trophy Academy of Natural Sciences Philadelphia, Pa.

Remarks: Acad. Nat'l. Sciences #20716

We hereby certify that we have measured the above described trophy on April 20, 1948, and that these measurements are correct and made in accordance with the directions overleaf.

Measured by: T. Donald Carter

By

Pencilled measurement made by 1947 judges.

See: Ulmer 4/7/48
ans 4/8/48

Score chart for white-tailed deer in 1947 before the adoption of the standardized measuring system in 1950. Photo courtesy Boone and Crockett Club.

POLICY PERSPECTIVE

License to kill: reforming federal wildlife control to restore biodiversity and ecosystem function

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Keywords
Apex predators; ecosystem resilience; endangered species; keystone species; lethal control; livestock depredation; trophic cascades; Wildlife Services.

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Received
26 April 2013
Accepted
30 May 2013

Editor
Phillip Levin

doi: 10.1111/conl.12045

Abstract

For more than 100 years, the US government has conducted lethal control of native wildlife, to benefit livestock producers and to enhance game populations, especially in the western states. Since 2000, Wildlife Services (WS), an agency of the US Department of Agriculture, has killed 2 million native mammals, predominantly 20 species of carnivores, beavers, and several species of ground-dwelling squirrels, but also many nontarget species. Many are important species in their native ecosystems (e.g., ecosystem engineers such as prairie dogs and beavers, and apex predators such as gray wolves). Reducing their populations, locally or globally, risks cascading negative consequences including impoverishment of biodiversity, loss of resilience to biotic invasions, destabilization of populations at lower trophic levels, and loss of many ecosystem services that benefit human society directly and indirectly. Lethal predator control is not effective at reducing depredation in the long term. Instead, we recommend that WS and its government partners involved in wildlife conflict management emphasize training livestock producers in methods of nonlethal control, with sparing use of lethal control by methods that are species-specific, and cease all lethal control in federal wilderness areas and for the purpose of enhancing populations of common game species.

Introduction

Utilitarian valuation of wildlife—including large carnivores—in Western societies increasingly is being replaced with noncommodity valuation (Schwartz *et al.* 2003; Treves & Karanth 2003; Loomis 2012). In the United States, this has led to growing public support for preservation of our diverse native fauna and naturally functioning native ecosystems, particularly in the larger landscapes of western public lands (Bengtson *et al.* 1999). More than 70 million Americans spend $55 billion and generate over $100 billion in total economic activity on nonconsumptive uses of wildlife in native habitats, especially on federal public lands (Leonard 2008; USFWS 2012a).

At the same time, leading ecologists have concluded that many of the world's pandemics, irruptions of undesirable species and collapses of desirable ones, and destabilization of ecosystems, resulting in lost ecosystem services, have been caused by the loss of apex predators (Estes *et al.* 2011) and of important small native herbivores (Delibes-Mateos *et al.* 2011). Still, the US government spends tens of millions of dollars annually killing predators and other mammals and birds that private agribusiness regards as pests (WS 2012a).

Table 1 Federally threatened (T), endangered (E), and ESA petitioned (P)[a] mammals killed by Wildlife Services (1990–2011)

Species	States Where Killed	Year (# Killed)	TOTAL
NRM gray wolf (*Canis lupus*) (E)[b]	ID, MT, WY	1996 (6), 1997 (10), 1998 (15), 1999 (16), 2000 (25), 2001 (13), 2002 (42), 2003 (49), 2004 (75), 2005 (77), 2006 (129), 2007 (178), 2008 (210), 2009 (255), 2010 (262), 2011 (154)	**1,516**
Western Great Lakes gray wolf (*Canis lupus*) (T)[c]	MI, MN, WI, ND	1990 (94), 1991 (70), 1992 (114), 1993 (141), 1994 (165), 1995 (85), 1996 (134), 1997 (212), 1998 (168), 1999 (157), 2000 (149), 2001 (105), 2002 (152), 2003 (138), 2004 (115), 2005 (175), 2006 (149), 2007 (162), 2008 (186), 2009 (223), 2010 (190), 2011 (211)	**3,295**
Mexican gray wolf (*C. lupus baileyi*) (E)	AZ, NM	2004 (1), 2005 (1), 2006(3), 2007 (4)	**9**
Island gray fox (*Urocyon littoralis*) (E)[d,e]	CA	1990 (2), 1998 (2), 1999 (13)	**17**
San Joaquin kit fox (*Vulpes macrotis mutica*) (E)[f]	CA	1990 (1)	**1**
Louisiana black bear (*Ursus americanus luteolus*) (T)	LA	1990 (2), 1995 (1), 1999 (2), 2002 (1)	**6**
Grizzly bear (*Ursus arctos horribilis*) (T)	MT, WY	1990 (9), 1997 (1), 1999 (2), 2000 (1), 2001 (1), 2002 (2), 2003 (3), 2005 (2), 2010 (2)	**23**
Canada lynx (*Lynx canadensis*) (T)	UT	1990 (1)	**1**
Wolverine (*Gulo gulo*) (P)	ID	2010 (1)	**1**
Black-tailed prairie dog (P) (*Cynomys ludovicianus*)	CO, KS, ND, NE, NM, MT, OK, TX, WY	1990 (54), 1991 (354), 1992 (408), 1993 (220), 1994 (256), 1995 (391), 1996 (1,302), 1997 (696), 1998 (833), 1999 (321), 2000 (43), 2001 (19), 2002 (337), 2003 (52), 2004 (53), 2005 (88), 2006 (961), 2007 (1,132), 2008 (3,537), 2009 (10,533), 2010 (20,515), 2011 (16,277)	**58,382**
Black-tailed prairie dog- Burrow/Den[g] (P) (*Cynomys ludovicianus*)	CO, NE, OK, WY	2007 (18), 2008 (12), 2009 (13,252), 2010 (24,204), 2011(15,821)	**53,307**
Gunnison's prairie dog (P) (*Cynomys gunnisoni*)	AZ[h], CO, NM	1996 (57), 1997 (16), 1998 (108), 1999 (101), 2000 (755), 2001 (58), 2005 (30), 2006 (259), 2007 (11), 2008 (72), 2009 (387), 2010 (394), 2011 (808)	**3,056**
Gunnison's prairie dog- Burrow/Den[g] (P) (*Cynomys gunnisoni*)	CO	2009 (625), 2010 (5,918), 2011 (4,775)	**11,318**
White-tailed prairie dog (P) (*Cynomys leucurus*)	CO, NM, UT, WY	1996 (4), 1997 (120), 1999 (72), 2001 (1), 2004 (2022), 2005 (3), 2006 (317), 2007 (94) 2008 (116), 2009 (1,694), 2010 (1), 2011 (4)	**4,448**
White-tailed prairie dog- Burrow/Den[g] (P) (*Cynomys leucurus*)	CO	2009 (1,950), 2010 (59), 2011 (4)	**2,013**

[a] Four species were candidates for ESA listing as either T or E at some time during the period, following citizen petitions to the US Fish and Wildlife Service (USFWS); of these, wolverine in its entire range and Gunnison's prairie dog in parts of CO and NM were found by USFWS to be warranted for listing but precluded by higher priority species; subsequently and as of this writing USFWS, under court order, is reevaluating the entire Gunnison's prairie dog species for listing; black-tailed prairie dog and white-tailed prairie dog were found not warranted for listing in 2009 and 2010, respectively; [b] NRM gray wolf was reintroduced in 1995 and 1996 and then designated under the ESA as a nonessential experimental population; listed as T in ID and MT, and E in WY; the ID and MT wolves were delisted in 2011; [c] Western Great Lakes gray wolf was listed as T in MN and E in MI and WI; delisted in Mar 2007, reversed in Sept 2008, delisted again in Jan 2012; [d] four of six subspecies listed as Endangered under the ESA; IUCN lists entire species as critically endangered; increased take in 1999 partly due to depredation on endangered shrike *Lanius ludovicianus anthonyi;* [e] lumped into "gray foxes" by WS since 2000; [f] lumped into "kit foxes" by WS since 2000; [g] listed as "Removed/Destroyed" by WS; [h] listed as "Prairie-Dog, z-(Other)" by Wildlife Services, included in Gunnison's category here based on geographic range of *Cynomys* in Arizona.

With 10 name changes and several department transfers during its 126-year legacy of animal control, the stated purpose of Wildlife Services (WS, an agency of the US Department of Agriculture's [USDA] Animal and Plant Health Inspection Services [APHIS]) is "to provide Federal leadership and expertise to resolve wildlife conflicts to allow people and wildlife to coexist" and more specifically to "apply the integrated wildlife damage management (WDM) approach to provide technical assistance and direct management operations" (WS 2012a). Yet, since 2000, WS has killed—intentionally and unintentionally—2 million native mammals (WS 2012a), including 12 taxa of federally endangered, threatened or "candidate" mammals (Table 1), numerous state-protected mammals (Table 2), and 15 million native birds including—unintentionally—protected golden eagles (*Aquila chrysaetos*) and bald eagles (*Haliaeetus leucocephalus*) (Knudson 2012a; WS 2012a; WS unpubl. data); WS unintentionally killed an endangered California condor (*Gymnogyps californianus*) in 1983 (US Congress

Table 2 State-listed threatened (T), endangered (E), and special concern (SC) mammals killed by Wildlife Services (1996–2011)[a]

Species	State	Status	Year (# taken)	TOTAL
Swift fox (*Vulpes velox*)	CO	SC	1998 (6)[b], 2001 (1), 2003 (4), 2005 (2), 2006 (6), 2010 (3)	**22**
	NE	E	2008 (2)	**2**
	WY	SC	1999(1), 2001 (1), 2002 (2), 2004 (6), 2005 (2)[c], 2006 (3), 2007 (6), 2008 (12), 2009 (5), 2010 (8), 2011 (8)	**54**
Kit fox (*Vulpes macrotis*)	UT	SC	1996 (5)[b], 1997 (4)[b], 1998 (3)[b], 1999 (4), 2000 (4), 2001 (1), 2003 (14), 2004 (3), 2005 (29), 2007 (2)	**69**
River otter (*Lontra canadensis*)	CO	T	2003 (1)	**1**
	IL	T[d]	2002 (1), 2005 (3), 2006 (4), 2007 (6)	**14**
	NE	T	2009 (1)	**1**
Black-tailed prairie dog[c] (*Cynomys ludovicianus*)	CO	SC	2000 (1), 2005 (4), 2006 (918), 2007 (1,108), 2008 (3,520), 2009 (6,042), 2010 (14,029), 2011 (8,906)	**34,258**
	MT	SC	2002 (200), 2003 (5), 2004 (3), 2009 (20), 2010 (29)	**257**
White-tailed prairie dog[c] (*Cynomys leucurus*)	UT	SC	1996 (4)[b], 1997 (120)[b], 1999 (72), 2005 (1), 2006 (317), 2007 (94), 2008 (100), 2009 (1,625)	**2,333**

[a] Reported take by WS was unintentional (nontarget) unless otherwise indicated; [b] intention of take unknown; [c] take was intentional; [d] delisted in September 2004.

1992). Vertebrates of 150 species have been killed unintentionally by WS since 2000 (Knudson 2012a; WS 2012a) by nonselective control methods including snares, leghold traps, poison-laced bait, baited explosive cyanide cartridges (M44s), and gassing of burrows and dens (Knudson 2012a; WS 2012a).

WS's National Wildlife Research Center (NWRC) conducts important research in nonlethal control, but those methods NWRC concludes are effective rarely are adopted by WS field operations, particularly on livestock grazing allotments in the West, which are heavily biased toward lethal control (GAO 1995; Niemeyer 2010); WS claims it *cannot* determine what proportion of its WDM expenditures go toward nonlethal methods (WS 2012b).

WS conducts little or no population monitoring of lethally controlled mammals nor of their alternate natural prey, no studies of whether WS control is additive with other causes of mortality, and no studies of how control affects populations of nontarget species that are unintentionally killed. Moreover, WS operations have never been the subject of an independent cost-benefit analysis, and their internal economic analyses do not adhere to guidelines used by most federal agencies, nor do they consider lost ecological or economic values of the predators themselves (Loomis 2012). In this policy perspective, we argue that the federal government's ongoing and century-old program of widespread lethal control of western predators, and of other keystone species such as prairie dogs (*Cynomys* spp.), requires cost-benefit analysis-driven reform in order to represent broader societal interests, restore biodiversity and ecosystem function, and align with current scientific knowledge on wildlife control.

The western United States possesses numerous large national parks, roughly 300 million acres of national forests and grasslands and federal public range lands, and 50 million acres of designated wilderness (Vincent 2004). Presettlement biodiversity and trophic relationships still can be represented on these significant land areas (Bailey *et al.* 1928; USDI BLM 1997). Unfortunately, many of these lands are overgrazed by livestock and by native ungulates whose predators have been depleted (Beschta *et al.* 2013). Simultaneously restoring apex predators and retiring livestock grazing on these lands hold promise for restoring western ecosystems and mitigating the likely effects of climate change (Beschta *et al.* 2013), but such restoration is inhibited in part by a legacy of predator and rodent control on these lands (GAO 1995; Estes *et al.* 2011; Davidson *et al.* 2012).

Evolution and environmental legacy of a federal wildlife control agency

Coincident with 3 million European families settling the western United States from 1865 to 1890 (Turner 1935), tens of millions of bison (*Bison bison*), mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and pronghorn (*Antilocapra americana*) that had populated the region were dramatically depleted by unregulated hunting, with bison nearly driven to extinction and largely replaced by domestic livestock (Isenberg 2000). Yet, mammalian carnivore populations retained much of their presettlement abundance (Kay 2007). Wolf and coyote (*C. latrans*) populations briefly thrived on bison carcasses littering the Plains; then, following the decline in their prey, these predators increasingly targeted domestic livestock, which elicited a campaign of large-scale predator extermination (Isenberg 2000; Robinson 2005).

After state and private bounties on predators became unreliable around 1900, livestock interests lobbied successfully for direct federal involvement in predator eradication, which began as a collaboration between USDA's Forest Service and Bureau of the Biological Survey (BBS) in the early 1900s and received direct congressional funding in 1915 (Hawthorne *et al.* 1999). Federal control of nuisance rodents soon followed, and, by 1939, government and western livestock interests cooperatively funded the Division of Predatory Animal and Rodent Control (PARC) under BBS at >$1 million (Cain *et al*. 1972; McIntyre 1982 *in* Feldman 2007).

Mass extermination of wolves and coyotes across the western United States began in the early 1900s; by the 1920s, overpopulation of rabbits induced their mass culling (600,000 rabbits were killed in 1 year in Idaho by government hunters; Hawthorne *et al.* 1999). Such lethal control mentality failed to recognize herbivore irruptions as consequences of predator release (Henke & Bryant 1999), or "trophic downgrading" (Estes *et al.* 2011). Extermination of prairie dogs—perceived as competitors with domestic livestock—also began in the early 1900s. New deal relief agencies greatly bolstered BBS/PARC's control programs; by 1936, the Civilian Conservation Corps alone had poisoned 21.5 million acres of prairie dog colonies across the western United States (Robinson 2005).

Controversial from the start: historical critiques of federal wildlife control

Early 20th century conservationists criticized federal government predator-eradication programs, after the successful extirpation of grizzly bears (*Ursus arctos horribilis*) from most of their range in the western United States, and the ongoing campaign against wolves (Robinson 2005). As early critics warned, extirpation of gray wolves from the western United States by 1930 caused interruption of natural trophic cascades, which became evident following their reintroduction to Northern Rocky Mountain (NRM) ecosystems in 1995 (Bergstrom *et al.* 2009).

Poisoning of prairie dog colonies by PARC and its successor agency Animal Damage Control (ADC, under the US Department of the Interior (USDI)) was implicated in the near extinction of the black-footed ferret (*Mustela nigripes*; Cain *et al.* 1972). The American Society of Mammalogists, repeatedly from 1924 to 2012 criticized federal wildlife control programs as overly reliant on lethal measures, driven by special interests rather than science, and causing excessive mortality of nontarget species. Over many decades, prominent conservationists, three study committees appointed by USDI, and several Government Accounting Office (GAO) reports echoed these concerns (see Supporting Information). The 1931 ADC Act (7 U.S.C. § 426) remains WS's primary enabling legislation (Robinson 2005); its provision for private cooperator funding of federal wildlife control programs creates a conflict of interest in setting WS management policy (Ketcham 2008).

Lethal control and its unintended consequences continue

Despite severe population reductions and extirpation of prairie dogs across 92–98% of their original range (Miller *et al.* 2007), there has been a resurgence of lethal control by WS, with 50,613 prairie dogs killed in 2009–2011, compared to 9960 in 2000–2008 (not counting Burrow/Den; Table 1; WS 2012a). Yet, it is questionable whether livestock directly benefit from extermination of prairie dogs, whose colonies have been shown to increase nutritional content and digestibility of forage plants, and increase live-plant to dead-plant ratio, for both bison and cattle (*Bos taurus;* Davidson *et al.* 2012). The loss of most large colony complexes of prairie dogs, partly due to continued government-funded extermination programs, has had cascading effects throughout North America's central grasslands, including declines of many other animal species that depend on prairie dogs as prey and for the unique habitats they create (Davidson *et al.* 2012; Figure 1), and the invasion of shrubs into those grasslands (Weltzin *et al.* 1997; Jones 2000). The US Fish and Wildlife Service (USFWS) program to recover endangered black-footed ferrets, almost solely dependent on prairie dogs as prey, currently is hindered by lack of reintroduction sites (Davidson *et al.* 2012).

Numbers of WS's primary mammalian targets of lethal control and certain other carnivores killed annually since 2000 has remained remarkably constant (Figure 2); data in Berger (2006) indicate a similar pattern from 1939 to 1998. Without monitoring of these populations, we do not know whether this represents a constant proportional annual mortality, but it at least implies that predator control has not effected any long-term solution to the perceived problem, and it shows there is no downward trend in lethal control, despite GAO (1995) admonishments. WS officials recently admitted that relatively few ranching operations, on an estimated 5–10% of native coyote range in the West, account for a large percentage of their annual coyote kills (Clay 2012;

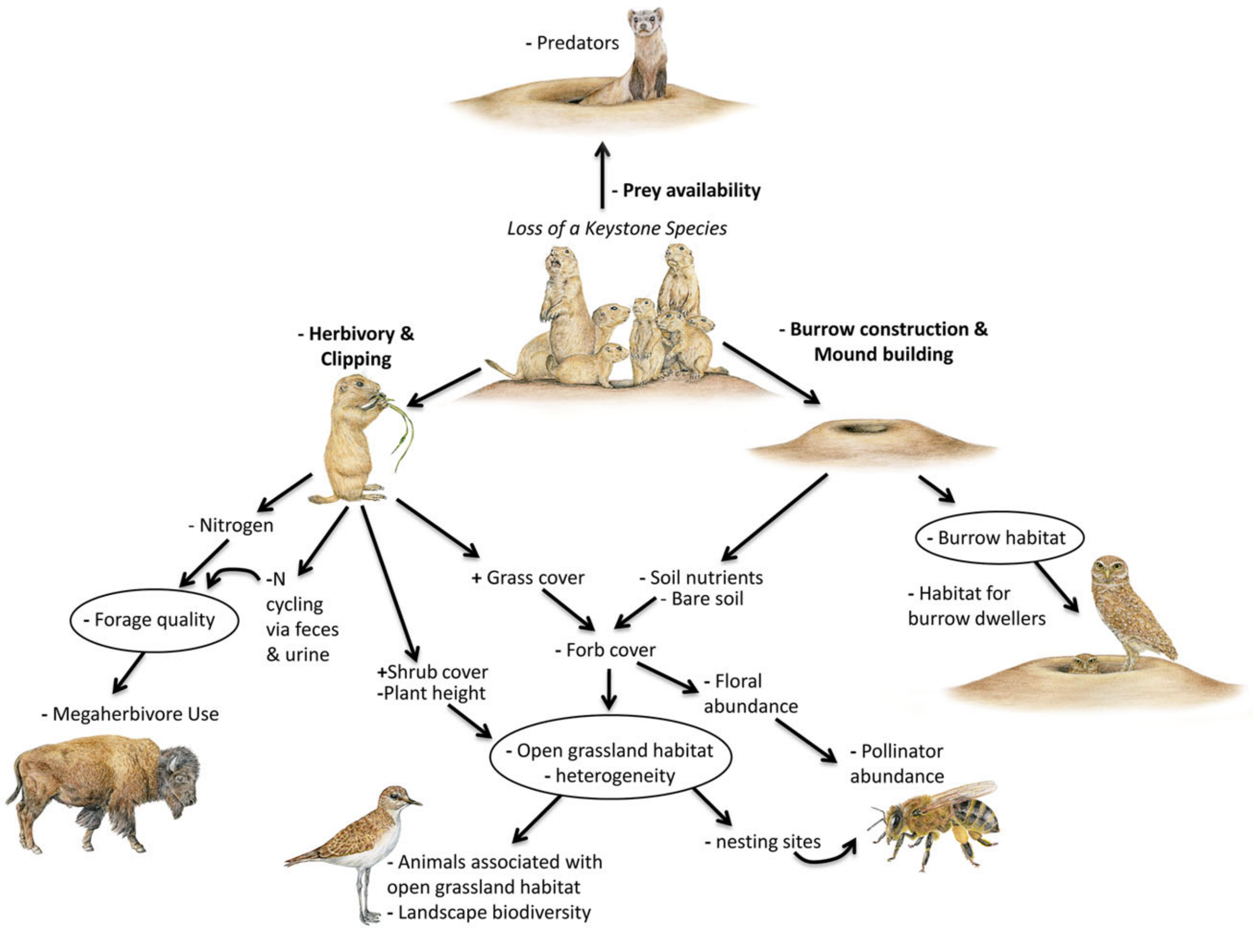

Figure 1 Conceptual diagram illustrating how the loss of a keystone species cascades throughout an ecosystem, using the black-tailed prairie dog (*Cynomys ludovicianus*) in North America's central grasslands as an example. Declines in prairie dogs result in the loss of their trophic (herbivory, prey) and ecosystem engineering (clipping, burrow construction, and mound building) effects on the grassland, with consequent declines in predators [e.g., black-footed ferrets (*Mustela nigripes*), raptors, swift and kit foxes (*Vulpes velox, V. macrotis*), coyotes (*Canis latrans*), badgers (*Taxidea taxus*)], megaherbivore activity [e.g., Bison (*Bison bison*)], invertebrate pollinators, and species that associate with the open habitats and burrows that they create [e.g., burrowing owls, (*Athene cunicularia*), mountain plovers (*Charadrius montanus*), pronghorn (*Antilocapra americana*), swift and kit foxes, cottontail rabbits (*Sylvilagus* spp.), rodents, and many species of herpetofauna and invertebrates]. Black arrows depict the effects of prairie dogs. Plus signs indicate an increase in an ecosystem property as a result of the loss of prairie dogs; minus signs indicate a decrease. Drawings are by Sharyn N. Davidson.

Knudson 2012c). State and federal managers removed 23.2% of the estimated coyote population of Wyoming in 1994–1995 (Taylor 2009). WS will not reveal exactly where coyote control occurs (WS 2012b), suggesting that localized population effects are a potential conservation concern. We acknowledge that range-wide effects likely are negligible, because coyotes have greatly expanded their range east and west during the period of WS control (Kays *et al*. 2010). Coyote removal at a local scale, however, can destabilize small-mammal communities, causing irruptions and reduced diversity (Wagner & Stoddart 1972; Henke & Bryant 1999).

Despite abundant evidence of top-down restoration of NRM ecosystems by reintroduced gray wolves (reviewed in Bergstrom *et al.* 2009), the number of wolves killed by WS has increased substantially since 2000, peaking at 480 in FY2009 (WS 2012a). Additionally, NRM wolves are now hunted in three states. Idaho and Montana killed 525 wolves—or 32% of their total population—by licensed hunting and WS control actions in 1 year, from 2009 to 2010 (Bergstrom 2011; USFWS 2012b). WS has not assessed whether their continued management kills of wolves is additive with hunting mortality and thus jeopardizes wolf recovery as a cumulative effect. Simulation modeling of NRM wolf populations indicates that this level of mortality is unsustainable, and with a likely increase in human offtake, NRM wolf populations will decline substantially (Creel & Rotella 2010).

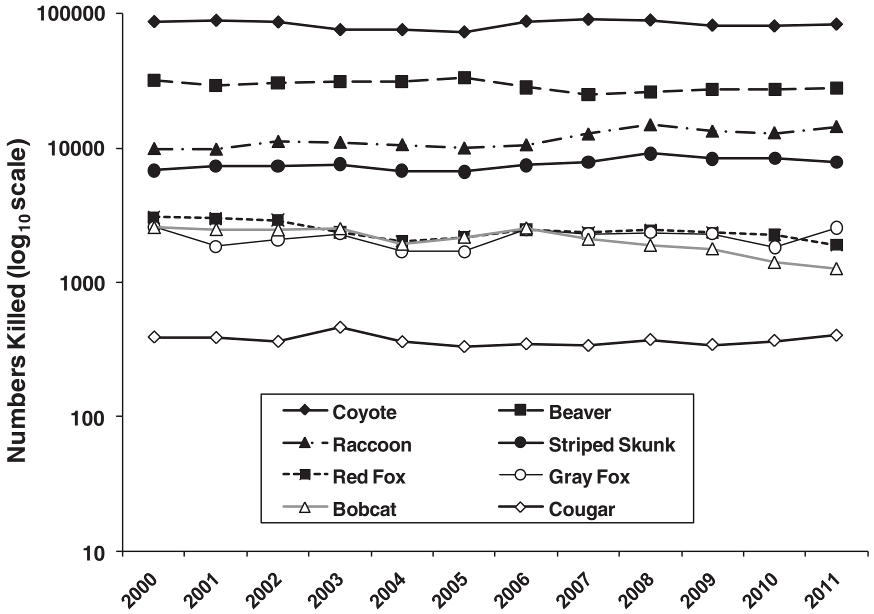

Figure 2 Numbers of the top seven species of native carnivores, plus beavers (*Castor canadensis*), killed annually by USDA-APHIS Wildlife Services from 2000 through 2011 (WS 2012a). Note: coyote (*Canis latrans*), beaver, raccoon (*Procyon lotor*), and striped skunk (*Mephitis mephitis*), in descending order, were the top four mammal species reported killed during the period by WS; fifth and sixth ranks, respectively, were "ground squirrels" and "prairie dogs," but several species are combined in each of those two categories.

Conversely, unmanaged populations of gray wolves in the Yellowstone ecosystem preferentially prey on old and diseased elk (Wright *et al.* 2006), so allowing wolves to establish and maintain natural pack structure could theoretically aid disease prevention in ungulate populations (Roy & Holt 2008). Reducing wolf populations increases coyote populations through "mesopredator release" and can have other unintended consequences on native ungulate populations (Berger *et al.* 2008; Prugh *et al.* 2009). For example, pronghorn fawn survival in areas with wolves was four times higher than in areas without wolves, because wolves suppressed coyotes and consequently fawn depredation (Berger *et al.* 2008). Predator control may, at least locally, decrease ecosystem resilience and lead to state shifts where invasive species become dominant (Wallach *et al.* 2010), which only increases the need for invasive control while decreasing its likelihood of success.

The legacy and legislative history of federal wildlife control reveal agriculture as its primary beneficiary, and lethal control of top carnivores and burrowing mammals such as prairie dogs particularly benefits western ranchers (see WS 2011). A relatively few influential western ranchers and major agribusiness lobbying groups, such as the American Farm Bureau, have prevented Congress from reforming WS in the past (Robinson 2005; Ketcham 2008). Nearly half of WS's annual $57 million federal allocation directly benefits already heavily taxpayer-subsidized agriculture (FY2010; WS 2012a; Ketcham 2012). This subsidy supports merely 7 million head of livestock, primarily cattle, which graze 268 million acres (>1 million km^2) of leased federal land, or 70% of the land area of 11 western states, including active allotments within 35% of the nation's wilderness areas (Fleischner 1994; 7 million head represented only 6.3% of the nation's total cattle, sheep and goats in 1994 [USDA 1999a, 1999b]). This subsidy contravenes other federal expenditures; e.g., USDI has spent over $43 million since 1974 reintroducing and conserving the gray wolf (USFWS 2011).

Cattle losses to all predators account for 5.5% of total mortality in the United States (USDA 2011) and even in the NRM wolf recovery zone, wolf predation accounts for a fraction of total predator losses (USFWS 2012b). Yet, WS increased control kills of wolves in recent years in the Wyoming recovery area, even though confirmed wolf depredations of cattle and number of packs depredating have declined steadily since 2006, while the wolf population has increased by 31% (USFWS 2012b).

In addition to increasing human-wildlife conflict, overstocking public rangelands with livestock reduces forage and habitat for small mammals (Bock *et al.* 1984; Heske & Campbell 1991) and other vertebrates (reviewed in Beschta *et al.* 2013) that are important prey of carnivores.

Ohmart & Anderson (1986) concluded livestock grazing likely was the major factor negatively affecting wildlife populations in 11 western states. Sacks & Neal (2007) found a significant negative association between wild prey biomass and sheep predation by coyotes, suggesting that healthy and productive native small-mammal habitats act as buffers against livestock depredation by coyotes. With a declining natural prey base, predators may switch to more abundant domestic stock, prompting greater demand for lethal predator control (Knowlton *et al.* 1999). Heavy cattle grazing has significantly depressed black-tailed jackrabbit (*Lepus californicus*) density (Flinders & Hansen 1975), and when black-tailed jackrabbit populations became severely depressed, ewe and lamb depredation by coyotes increased dramatically (Stoddart *et al.* 2001).

As long as private livestock producers can externalize the costs of predator losses via government-subsidized predator control, they will have little incentive for responsible animal husbandry techniques, i.e., reduce stocking levels, clear carcasses and after-births quickly, confine herds at night or during calving/lambing, install fencing and fladry, or adopt numerous other nonlethal preventive methods to avoid depredation (Shivik *et al.* 2003). The easiest and most obvious places to reduce human-wildlife conflict are wilderness areas. As long as the practice of lethally controlling "problem animals" persists wherever livestock graze (see Linnell *et al.* 1999), livestock-free wilderness areas and national parks may provide the only refuges and source populations for most rare and endangered North American large carnivores.

Lethal wildlife control for livestock: ineffective and wasteful

In 1887, Albert Fisher, C. Hart Merriam's assistant at BBS, examined stomach contents of hawks and owls shot for $90,000 in bounties in Pennsylvania, estimating the lost value of rodent and insect control by removing these predators at $3.9 million; the direct savings in chickens was $1,875 (Robinson 2005; the federal government long ago ceased targeting avian predators for lethal control but has not altered its approach to mammalian predators). Cole (1970) estimated a 5:1 cost-benefit ratio of WS killing Arizona coyotes for livestock depredation, adding lost forage due to compensatory increases in jackrabbits to taxpayer costs for lethal control (see Wagner & Stoddart 1972; Henke & Bryant 1999).

Eradication of predators ended livestock depredation, but lethal control measures, short of eradication, appear no more effective in the long term than no lethal control at all. Three gray wolf removal studies in different decades in different areas of North America indicate that effects are short-lived, because remaining individuals and recolonizing packs just as often depredate as those removed (Treves & Naughton-Treves 2005). Coyote control usually has involved population reduction rather than selective killing (Mitchell *et al.* 2004); this can create temporary local extirpations, soon attracting immigrants that experience dramatically higher reproductive output, resulting in no long-term effect on depredation (Connolly 1978; Knowlton *et al.* 1999). Removing more than the territorial breeding pair of coyotes (which commit most depredations of sheep) from a wider zone around a depredation site may even *increase* the overall problem by allowing more breeding pairs to immigrate (Sacks *et al.* 1999). Despite considerable effort by WS at lethal coyote control in the western United States, evaluation of a 60-year data set indicated that the decline of the sheep industry in both eastern and western United States could be attributed to market trends and production costs, and that predator control (lacking in the East) did not have a significant impact on the decline (Berger 2006).

Lethal control often proceeds without certain knowledge that targeted individuals are responsible or that a depredation has occurred (as in "preventive" culling of coyotes; GAO 1990; Knudson 2012c). But the compensatory aspect of depredation control described above suggests that even highly specific lethal control methods such as poison collars (Connolly *et al.* 1978) would not be a long-term solution. Preventive, nonlethal methods, such as fencing, guard dogs, and taste aversion conditioning hold more promise for long-term reduction of depredation (Green *et al.* 1984; Gustavson & Nicholas 1987; Treves & Karanth 2003; Knudson 2012b). That the unmanaged wolf population of Yellowstone National Park has declined 40% since its peak density in 2006 and appears to have stabilized at $\leq$100 animals (Figure 3) suggests that simply ending lethal control elsewhere in the NRM could lead to, at worst, a stable rate of depredation (<5%; Bergstrom *et al.* 2009; USDA 2011), which could be decreased by aggressive application of nonlethal methods. The latest annual report for the NRM projects a declining growth rate for the wolf population as it stabilizes at a lower equilibrium in line with natural carrying capacity (USFWS 2012b). Affirming what generally is hypothesized for a territorial mammal, WS/NWRC's own research indicates that gray wolf populations are not prey-limited but rather are intrinsically density-dependent, i.e., self-regulating (Cariappa *et al.* 2011).

Even assuming scientifically supportable benefits of targeted killing of mammals by WS, 2000–2011 kill data reveal several striking examples of waste of nontarget species. Badgers are targeted in most states where they

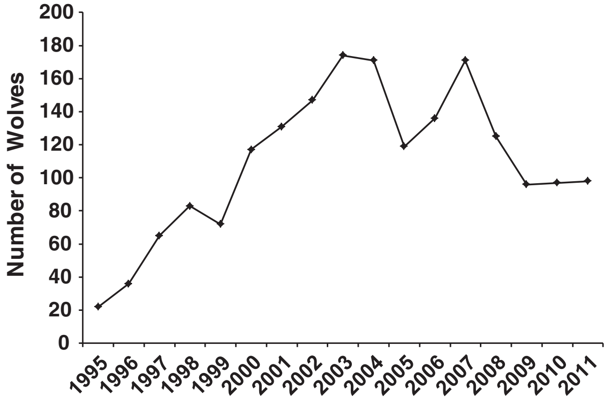

Figure 3 Annual numbers of wolves in Yellowstone National Park from initial reintroduction in 1995 and 1996 through 2011 (winter counts; data from NPS 2011; USFWS 2012b).

occur, but fully a third (>180 per year) of those killed were killed unintentionally (WS 2012a). (Hall 1930 also reported excessive nontarget killing of badgers by PARC agents). Virtually all kit foxes (*Vulpes macrotis*) and swift foxes (*V. velox*) killed (95% of 339 and 99.5% of 225, respectively) were killed unintentionally by neck snares, leghold traps, or M44s set for coyotes (WS 2012a). Ironically, swift foxes were extirpated in many areas by the 1930s as a result of nontarget mortality from federal coyote and wolf control programs (Stephens & Anderson 2005). Swift foxes were identified as the one predator ADC may have killed in FY1989 over a significant portion of its range and therefore put at risk of extinction (GAO 1990). Eighty-six percent of 82 ringtails (*Bassariscus astutus*) killed from 2000 to 2011 were killed unintentionally, as were 97.3% of 2,413 collared peccaries (*Pecari tajacu*; WS 2012a). An average of >400 river otters (*Lontra canadensis*) annually were killed unintentionally by WS, after considerable efforts by at least 21 states to reintroduce the species (Raesly 2001). Unfortunately, eyewitness accounts suggest that not all protected species unintentionally killed are being reported by WS field agents (Niemeyer 2010).

The other reason for lethal predator control

Increasing participation of WS in what was identified in its 2001 Research Needs Assessment as "the growing and expanding negative impact of predators (for example, coyotes, foxes, wolves, and raccoons) on wildlife resources (for example, deer and antelope)" highlights renewed emphasis on WS's role as promoter of particular wildlife species over others (Bruggers *et al.* 2002). This emphasis contradicts the evidence that, where apex predators have been reduced or extirpated, native ungulate populations exceed carrying capacity and are causing increasing habitat deterioration (Beschta *et al.* 2013). In its collaboration with states, WS controls wolves and other predators by aerial gunning in remote areas to reduce predation on elk (Robbins 2011; WS 2012b), especially in Idaho, despite the fact that in 2009, 26 of 29 management units in that state had elk populations at or above state management objectives (Bergstrom *et al.* 2009). Despite wolf recovery and while its aggressive wolf-reduction plan was awaiting federal approval, Wyoming had a record elk harvest in 2010 (WGFD 2013). The political power of western ranching has long been a primary determinant of WS's mammalian predator control (Robinson 2005), but conducting it for the ostensible benefit of common native game species specifically favors certain segments of the US population over others. The Wildlife Society (TWS), in its recent technical review of carnivore management, states "Although the Public Trust Doctrine for Wildlife Management clearly articulates that federal and state agencies manage wildlife for the benefit of all citizens, often the opinions of nonconsumptive users are ignored. Unbalanced information that supports the perceptions of some stakeholders over others can increase conflicts (Peek *et al.* 2012)." This seems to us to be the case when state or federal agencies conduct predator control on wilderness areas (see WS 2012b) and/or implement predator control to promote certain game species over other native wildlife. The latter arguably benefits 11.6 million people in the United States who hunt big game to the detriment of 22.5 million active wildlife watchers, whose direct expenditures are three times that of big-game hunters (USFWS 2012a). TWS goes on to say "In places where human presence and impact is minimized, wildlife populations of all species should be allowed to fluctuate with as little anthropogenic interference as possible (Peek *et al.* 2012)."

Even if enhancing wild ungulate populations were a justifiable goal, predator control is an unproven instrument for achieving it. A meta-analysis of predator-removal experiments in 113 systems found prey populations subsequently *declined* in 54 of them (Sih *et al.* 1985). In Idaho, wolf predation on elk is <10% of total elk mortality and mostly replaceable (IDFG 2007; see Wright *et al.* 2006). In a long-term, large-scale manipulative study of coyote and cougar (*Puma concolor*) removal in Idaho, the effects on mule deer abundance were marginal and short term; winter severity in the current and previous winters was the best predictor of deer population trends (Hurley *et al.* 2011). Three years of elk-calf mortality data from northern Yellowstone indicated wolves did not meet an important criterion of ability to control elk populations, as they were not the dominant predator on all stages of the life cycle of the prey (NRC 1997), accounting for only 14–17% of calf mortality (Barber-Meyer *et al.* 2008).

Conclusion

The continuing heavy reliance of the federal government on lethal control of native mammals is a vestige of the outmoded mentality of western expansionism, in which the goal was to "tame" the wilderness, replacing the ecosystem's primary-consumer trophic level entirely with domesticated herbivores and a few favored game species and all higher trophic levels with humans (Robinson 2005). Its survival into the 21st century defies the consensus among ecologists that significant reductions in local populations of native primary consumers and apex predators has had far-reaching consequences on primary production, nutrient flows, disease incidence, and biodiversity at all levels and at all spatial scales (Delibes-Mateos *et al.* 2011; Estes *et al.* 2011; Davidson *et al.* 2012).

Both to restore ecosystems and to serve broader societal interests in conservation, we recommend that all federal management agencies that deal with human-wildlife conflict collaborate with all stakeholders in adopting a more holistic and ecosystem-based management approach resulting in reduced reliance by WS on lethal control methods, especially on western public lands. An independent cost-benefit analysis of WS operations that includes full economic valuation of native wildlife subject to lethal control (possibly including a contingent valuation method study of public willingness to pay for predators; Loomis 2012) must be undertaken. This could include participatory intervention planning (PIP; Treves *et al.* 2009), which analyzes management options in light of cost effectiveness, sociopolitical acceptability, and species-specific efficacy. It will also necessitate that WS field operations move beyond promotion to actual implementation of "integrated WDM," in which lethal control is a last, not a first, resort. Specific measures to reduce the negative impacts of, and need for, lethal wildlife control in the western United States include: 1) retiring grazing leases on remote federal lands, especially those that are overgrazed or in wilderness areas; 2) requiring federal grazing permittees, under penalty of revocation, to employ best animal-husbandry practices fully; 3) prioritizing use of, and research and outreach on, nonlethal, preventive methods of depredation control; 4) ceasing lethal control methods that are not highly selective of the individual (and species) being targeted; 5) ending misguided efforts to enhance populations of common game species by predator control; 6) preparing an updated, peer-reviewed environmental impact statement on all WS lethal control programs, which analyzes potential direct, indirect, and cumulative effects of lethal control on populations and ecosystems in light of current science; and 7) making details of WS funding sources and budget expenditures transparent and readily available to the public.

Acknowledgments

We thank the American Society of Mammalogists for the opportunity to serve on the Conservation Committee, which prompted our research into this issue. We thank Sharyn Davidson for preparing artwork and Bob Myers of USDA for providing WS records not published online. We thank Andrew Smith and two anonymous reviewers for helpful comments to improve the manuscript.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Brief History of Expert Criticism of Federal Wildlife Control Programs

References

Bailey, V., Dixon, J., Goldman, E.A., Heller, E. & Adams, C.C. (1928) Report of the committee on wild life sanctuaries, including provision for predatory mammals. *J. Mammal.*, **9**, 354-358.

Barber-Meyer, S.M., Mech, L.D. & White, P.J. (2008) Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildl. Monogr.*, **169**, 1-30.

Bengston, D.N., Fan, D.P. & Celarier, D.N. (1999) A new approach to monitoring the social environment for natural resource management and policy: the case of US National Forest benefits and values. *J. Environ. Manage.*, **56**, 181-193.

Berger, K.M. (2006) Carnivore-livestock conflicts: effects of subsidized predator control and economic correlates on the sheep industry. *Conserv. Biol.*, **20**, 751-761.

Berger, K.M., Gese, E.M. & Berger, J. (2008) Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. *Ecology*, **89**, 818-828.

Bergstrom, B.J. (2011) Endangered wolves fall prey to politics. *Science*, **333**, 1092.

Bergstrom, B.J., Vignieri, S., Sheffield, S.R., Sechrest, W. & Carlson, A.A. (2009) The Northern Rocky Mountain gray wolf is not yet recovered. *BioScience*, **59**, 991-999.

Beschta, R.L., Donahue, D.L., DellaSalla, D.A. *et al.* (2013) Adapting to climate change on Western public lands: addressing the ecological effects of domestic, wild, and feral ungulates. *Environ. Manage.*, **51**, 474-491.

Bock, C.E., Bock, J.H., Kenny, W.R. & Hawthorne, V.M. (1984) Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. *J. Range Manage.*, **37**, 239-242.

Bruggers, R.L., Owens, R. & Hoffman, T. (2002) Wildlife damage management research needs: perceptions of scientists, wildlife managers, and stakeholders of the USDA/Wildlife Services program. *Int. Biodeterior. Biodegrad.*, **49**, 213-223.

Cain, S.A., Kadlec, J.A., Allen, D.L., Cooley, R.A., Hornocker, M.H. & Wagner, F.H. (1972) *Predator control–1971: report to the President's Council on Environmental Quality and the US Department of the Interior by the Advisory Committee of Predator Control*. University of Michigan Press, Ann Arbor, MI.

Cariappa, C.A., Oakleaf, J.K., Ballard, W.B. & Breck, S.B. (2011) A reappraisal of the evidence for regulation of wolf populations. *J. Wildl. Manage.*, **75**, 726-730.

Clay, W.H. (2012) Letter to American Society of Mammalogists. USDA-APHIS, Wildlife Services, Washington, DC. Available at http://mammalsociety.org/uploads/committee_files/Response_from_APHIS_2012.pdf. Accessed 11 October 2012.

Cole, G.A. (1970) An ecological gap. *Bull. Ecol. Soc. Am.*, **51**, 14-15.

Connolly, G.E. (1978) Predator control and coyote populations: a review of simulation models. Pages 327-345 in M. Bekoff, editor. *Coyote biology, behavior, and management*. Academic Press, New York.

Connolly, G.E., Griffiths, R.E. Jr. & Savarie, P.J. (1978) Toxic collar for control of sheep-killing coyotes: a progress report. *Vert. Pest. Conf. Proc.*, **8**, 197-205.

Creel, S. & Rotella, J.J. (2010) Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (*Canis lupus*). *PLoS ONE*, **5**, e12918.

Davidson, A.D., Detling, J.K. & Brown, J.H. (2012) Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Front. Ecol. Environ.*, **10**, 477-486.

Delibes-Mateos, M., Smith, A.T., Slobodchikoff, C.N. & Swenson, J.E. (2011) The paradox of keystone species persecuted as pests: a call for the conservation of abundant small mammals in their native range. *Biol. Conserv.*, **144**, 1335-1346.

Estes, J.A., Terborgh, J., Brashares, J.S. *et al.* (2011) Trophic downgrading of Planet Earth. *Science*, **333**, 301-306.

Feldman, J.W. (2007) Public opinion, the Leopold Report, and the reform of federal predator control policy. *Human-Wildl Conflicts*, **1**, 112-124.

Fleischner, T.L. (1994) Ecological costs of livestock grazing in western North America. *Conserv. Biol.*, **8**, 629-644.

Flinders, T. & Hansen, R.M. (1975) Spring population responses of cottontails and jackrabbits to cattle grazing shortgrass prairie. *J. Range Manage.*, **28**, 290-293.

GAO. (1990) Wildlife management: effects of animal damage control program on predators. US General Accounting Office. GAO/RCED-90-149.

GAO. (1995) Animal damage control program: efforts to protect livestock from predators. US General Accounting Office. GAO/RCED-96-3.

Green, J.S., Woodruff, R.A. & Tueller, T.A. (1984) Livestock-guarding dogs for predator control: costs, benefits, and practicality. *Wildl. Soc. Bull.*, **12**, 44-50.

Gustavson, C.R. & Nicholas, L.K. (1987) Taste aversion conditioning in wolves, coyotes and other canids: retrospect and prospect. Pages 3-182 in H. Frank, editor. *Man and wolf*. Dr. W. Junk Publishers, Dordrecht, NL.

Hall, E.R. (1930) Predatory mammal destruction. *J. Mammal.*, **11**, 362-372.

Hawthorne, D.W., Nunley, G.L. & Prothro, V. (1999) A history of the Wildlife Services program. *Probe Newslett. Natl. Anim. Damage Control Assoc.*, **197**, 1-7. http://digitalcommons.unl.edu/icwdmprobe/43. Accessed 2 November 2012.

Henke, S.E. & Bryant, F.C. (1999) Effects of coyote removal on the faunal community in western Texas. *J. Wildl. Manage.*, **63**, 1066-1081.

Heske, E.J. & Campbell, M. (1991) Effects of an 11-year livestock exclosure on rodent and ant numbers in the Chihuahuan Desert, southeastern Arizona. *Southwest. Nat.*, **36**, 89-93.

Hurley, M.A., Unsworth, J.W., Zager, P. *et al*. (2011) Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. *Wildl. Monogr.*, **178**, 1-33.

Idaho Department of Fish and Game (IDFG). (2007) Big game harvest survey. *Project W-170-R-31., Progress Report*, Idaho Department of Fish and Game, Boise, ID.

Isenberg, A.C. (2000) *The destruction of the bison: an environmental history, 1750–1920*. Cambridge University Press, New York, NY.

Jones, A. (2000) Effects of cattle grazing on North American arid ecosystems: a quantitative review. *West. N.A. Nat.*, **60**, 155-164.

Kay, C.E. (2007) Were native people keystone predators? A continuous-time analysis of wildlife observations made by Lewis and Clark in 1804–1806. *Can. Field-Nat.*, **121**, 1-16.

Kays, R., Curtis, A. & Kirchman, J. (2010) Reply to Wheeldon *et al.* 'Colonization history and ancestry of northeastern coyotes'. *Biol. Lett.*, **6**, 248-249.

Ketcham, C. (2008) America's secret war on wildlife. *Men's J.*, **16**, 49-51.

Ketcham, C. (2012) Wolves to the slaughter. *The American Prospect*, 13 March 2012.

Knowlton, F.F., Gese, E. & Jaeger, M.M. (1999) Coyote depredation control: an interface between biology and management. *J. Range Manage.*, **52**, 398-412.

Knudson, T. (2012a) The killing agency: Wildlife Services' brutal methods leave a trail of animal death—wildlife investigation. *The Sacramento Bee*, 29 April 2012

Knudson, T. (2012b) Suggestions in changing Wildlife Services range from new practices to outright bans. *The Sacramento Bee*, 6 May 2012.

Knudson, T. (2012c) Wildlife Services meets with its critics. *The Sacramento Bee*, 30 June 2012.

Leonard, J. (2008) *Wildlife watching in the United States: the economic impacts on national and state economies in 2006*. Wildlife and Sport Fish Restoration Programs, US Fish and Wildlife Service, Arlington, VA.

Linnell, J.D.C., Odden, J., Smith, M.E., Aanes, R. & Swenson, J.E. (1999) Large carnivores that kill livestock: do "problem individuals" really exist? *Wildl. Soc. Bull.* **27**, 698-705.

Loomis, J. (2012) Fuzzy math: Wildlife Services should improve its economic analysis of predator control. Natural Resources Defense Council Issue Paper 12-05-A. 26 pp. Available from http://www.nrdc.org/wildlife/animals/files/fuzzy-math-IP.pdf. Acessed 28 February 2013.

Miller, B.J., Reading, R.P., Biggins, D.E. *et al.* (2007) Prairie dogs: an ecological review and current biopolitics. *J. Wildl. Manage.*, **71**, 2801-2810.

Mitchell, B.R., Jaeger, M.M. & Barrett, R.H. (2004) Coyote depredation management: current methods and research needs. *Wildl. Soc. Bull.*, **32**, 1209-1218.

National Park Service (NPS). (2011) Wolves of Yellowstone. National Park Service, US Department of the Interior. Available from http://www.nps.gov/yell/naturescience/wolves.htm. Accessed 18 May 2012.

National Research Council (NRC). (1997) Wolves, bears, and their prey in Alaska: In: *Biological and social challenges in wildlife management*. The National Academies Press, Washington, DC.

Niemeyer, C. (2010) *Wolfer: a memoir*. BottleFly Press, Boise, ID.

Ohmart, R.D. & Anderson, B.W. (1986) Riparian habitat. Pages 169–199 in A.Y. Cooperrider, J. Boyd, H.R. Stuart, editors. *Inventory and monitoring of wildlife habitat*. US Bureau of Land Management Service Center, Denver, Colorado.

Peek, J., Dale, B., Hristienko, H. *et al.* (2012) *Management of large mammalian carnivores in North America*. The Wildlife Society Technical Review 12-1. The Wildlife Society, Bethesda, MD.

Prugh, L.R., Stoner, C.J., Epps, C.W. *et al.* (2009) The rise of the mesopredator. *BioScience*, **59**, 779-791.

Raesly, E.J. (2001) Progress and status of river otter reintroduction programs in the United States. *Wildl. Soc. Bull.*, **29**, 856-862.

Robbins, J. (2011) Hunting wolves out West: more, less? New York Times, Green Blog, 16 December 2011.

Robinson, M.J. (2005) *Predatory bureaucracy: the extermination of wolves and the transformation of the West*. University of Colorado Press, Boulder, CO.

Roy, M. & Holt, R.D. (2008) Effects of predation on host–pathogen dynamics in SIR models. *Theor. Pop. Biol.*, **73**, 319-331.

Sacks, B.N, Jaeger, M.M., Neale, J.C.C. & McCullough, D.R. (1999) Territoriality and breeding status of coyotes relative to sheep predation. *J. Wildl. Manage.*, **63**, 593-605.

Sacks, B.N & Neale, J.C.C. (2007) Coyote abundance, sheep predation, and wild prey correlates illuminate Mediterranean trophic dynamics. *J. Wildl. Manage.*, **71**, 2404-2411.

Schwartz, C.C., Swenson, J.E. & Miller, S.D. (2003) Large carnivores, moose and humans: a changing paradigm of predator management in the 21st century. *Alces*, **39**, 41-63.

Shivik, J.A., Treves, A. & Callahan, P. (2003) Nonlethal techniques for managing predation: primary and secondary repellents. *Conserv. Biol.*, **17**, 1531-1537.

Sih, A., Crowley, P., McPeek, M., Petranka, J. & Strohmeier, K. (1985) Predation, competition, and prey communities: a review of field experiments. *Ann. Rev. Ecol. Syst.*, **16**, 269-311.

Stephens, R.M. & Anderson, S.H. (2005) Swift fox (*Vulpes velox*): a technical conservation assessment. USDA Forest Service, Rocky Mountain Region. Available from http://www.fs.fed.us/r2/projects/scp/assessments/swiftfox.pdf. Accessed 5 June 2012.

Stoddart, L.C., Griffiths, R.E. & Knowlton, F.E. (2001) Coyote responses to changing jackrabbit abundance affect sheep predation. *J. Range Manage.*, **54**, 15-20.

Taylor, D.T., Rashford, B.S., Coupal, R.H. & Foulke, T. (2009) An economic analysis of predator management in Wyoming. Final report to Wyoming Animal Damage Management Board, Wyoming Department of Agriculture. 69 pp. Available from http://wyocre.uwagec.org/Publications/ADMB_FinalRpt19Jun09.pdf. Accessed 20 May 2013.

Treves, A. & Karanth, K.U. (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. *Conserv. Biol.*, **17**, 1491-1499.

Treves, A. & Naughton-Treves, L. (2005) Evaluating lethal control in the management of human–wildlife conflict. Pages 86-106 in R. Woodroffe, S. Thirgood, A. Rabinowitz, editors. *People and wildlife: conflict and coexistence*. Cambridge University Press, Cambridge, UK.

Treves, A., Wallace, R.B. & White, S. (2009) Participatory planning of interventions to mitigate human–wildlife conflicts. *Conserv. Biol.*, **23**, 1577-1587.

Turner, F.J. (1935) *The frontier in American history*. Henry Holt and Company, New York, NY.

United States Congress. (1992) 102nd Congress, 2nd Session, 30 January 1992. *Congressional Record*, **138**, 9.

United States Department of Agriculture (USDA). (1999a) *Cattle final estimates 1994–98*. USDA National Agricultural Statistics Service, Statistical Bulletin No. 953. Available from http://usda01.library.cornell.edu/usda/nass/SB990/sb954.pdf. Accessed 21 February 2013.

United States Department of Agriculture (USDA). (1999b) *Sheep and goats final estimates 1994-98*. USDA National Agricultural Statistics Service, Statistical Bulletin No. 954. Available from http://usda01.library.cornell.edu/usda/nass/SB990/sb954.pdf. Accessed 21 February 2013.

United States Department of Agriculture (USDA). (2011) *Cattle death loss*. USDA National Agricultural Statistics Service, Agricultural Statistics Board, released 12 May 2011. Available from http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1625. Accessed 1 June 2012.

United States Department of the Interior, Bureau of Land Management (USDI BLM). (1997) *Working together for the health of America's public lands*. US Department of the Interior, Bureau of Land Management, 1997 Annual Report, Washington, DC.

United States Fish and Wildlife Service (USFWS). (2011) *Northern Rocky Mountains Wolf Recovery Program Update 2011*. M.D. Jimenez, S.A. Becker, editors. USFWS Ecological Services, Helena, MT.

United States Fish and Wildlife Service (USFWS). (2012a) *2011 national survey of fishing, hunting, and wildlife-associated recreation: national overview*. US Department of the Interior, Arlington, VA.

United States Fish and Wildlife Service (USFWS). (2012b) Gray wolves in the Northern Rocky Mountains. Available from http://www.fws.gov/mountain-prairie/species/mammals/wolf/. Accessed 26 April 2013.

Vincent, C.H. (2004) Federal land management agencies: background on land and resources management. Congressional Research Service, The Library of Congress. Available from http://www.nationalaglawcenter.org/assets/crs/RL32393.pdf. Accessed 1 June 2012.

Wagner, F.H. & Stoddart, L.C. (1972) Influence of coyote predation on black-tailed jackrabbit populations in Utah. *J. Wildl. Manage.*, **36**, 329-342.

Wallach, A.D., Johnson, C.N., Ritchie, E.G. & O'Neil, A.J. (2010) Predator control promotes invasive dominated ecological states. *Ecol. Lett.* **13**, 1008-1018.

Weltzin, J.F., Archer, S. & Heitschnidt, R. K. (1997) Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology*, **78**, 751-763.

Wildlife Services (WS). (2011) Research needs assessment. United States Department of Agriculture, Animal Plant Health Inspection Services. Available from http://www.aphis.usda.gov/wildlife_damage/nwrc/publications/rna2011/index.shtml Accessed 16 October 2012.

Wildlife Services (WS). (2012a) Wildlife damage management. United States Department of Agriculture, Animal and Plant Health Inspection Services. Available from http://www.aphis.usda.gov/wildlife_damage/index.shtml. Accessed 26 April 2012.

Wildlife Services (WS). (2012b) Answers to questions posed by the American Society of Mammalogists concerning wildlife damage management practices in the Western US. United States Department of Agriculture, Animal and Plant Health Inspection Services. Available from http://www.mammalsociety.org/uploads/committee_files/WS_Response_ASMCC_Questions_June2012.pdf. Accessed 2 November 2012.

Wright, G.J., Peterson, R.O., Smith, D.W. & Lemke, T.O. (2006) Selection of northern Yellowstone elk by gray wolves and hunters. *J. Wildl. Manage.*, **70**, 1070-1078.

Wyoming Game and Fish Department (WGFD). (2013) Wyoming has record elk harvest in 2012. Available from http://wgfd.wyo.gov/web2011/news-1001370.aspx. Accessed 5 April 2013.

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Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone

Arthur D. Middleton, Thomas A. Morrison, Jennifer K. Fortin, Charles T. Robbins, Kelly M. Proffitt, P. J. White, Douglas E. McWhirter, Todd M. Koel, Douglas G. Brimeyer, W. Sue Fairbanks and Matthew J. Kauffman

Proc. R. Soc. B 2013 **280**, 20130870, published 15 May 2013

PROCEEDINGS OF THE ROYAL SOCIETY B

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Research

Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone

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The loss of aquatic subsidies such as spawning salmonids is known to threaten a number of terrestrial predators, but the effects on alternative prey species are poorly understood. At the heart of the Greater Yellowstone ecosystem, an invasion of lake trout has driven a dramatic decline of native cutthroat trout that migrate up the shallow tributaries of Yellowstone Lake to spawn each spring. We explore whether this decline has amplified the effect of a generalist consumer, the grizzly bear, on populations of migratory elk that summer inside Yellowstone National Park (YNP). Recent studies of bear diets and elk populations indicate that the decline in cutthroat trout has contributed to increased predation by grizzly bears on the calves of migratory elk. Additionally, a demographic model that incorporates the increase in predation suggests that the magnitude of this diet shift has been sufficient to reduce elk calf recruitment (4–16%) and population growth (2–11%). The disruption of this aquatic–terrestrial linkage could permanently alter native species interactions in YNP. Although many recent ecological changes in YNP have been attributed to the recovery of large carnivores—particularly wolves—our work highlights a growing role of human impacts on the foraging behaviour of grizzly bears.

1. Introduction

In many ecosystems, spawning salmonids provide subsidies to riparian and terrestrial food webs when predators consume them or move their carcasses to land [1,2]. The abundance of salmonids and other aquatic prey has been linked to the survival, fecundity and density of terrestrial consumers including spiders and lizards [3], passerine birds [4], coyotes (*Canis latrans*; [5]), wolves (*Canis lupus*; [6]) and brown or grizzly bears (*Ursus arctos*; [7]). However, much less is known about the indirect effects of these subsidies on alternative resources in the recipient, terrestrial community [4,8]. Such ecological interactions can have important conservation implications if the loss of a primary prey species results in disproportionate, but cryptic, impacts on alternative prey species that occur at lower abundance [9]. A recent, dramatic decline of cutthroat trout (*Oncorhynchus clarkii* bouvieri) in Yellowstone Lake, at the heart of Yellowstone National Park (YNP), has been associated with increased predation on elk (*Cervus elaphus*) calves by the omnivorous grizzly bear [10]. Here, we explore the potential influence of this diet shift on migratory elk that winter 40–100 km from Yellowstone Lake, far beyond the boundaries of YNP.

Cite this article: Middleton AD, Morrison TA, Fortin JK, Robbins CT, Proffitt KM, White PJ, McWhirter DE, Koel TM, Brimeyer DG, Fairbanks WS, Kauffman MJ. 2013 Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone. Proc R Soc B 280: 20130870.
http://dx.doi.org/10.1098/rspb.2013.0870

Received: 10 April 2013
Accepted: 23 April 2013

Subject Areas:
ecology, behaviour, environmental science

Keywords:
aquatic subsidies, cutthroat trout, elk, grizzly bears, invasive species, lake trout

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2013.0870 or via http://rspb.royalsocietypublishing.org.

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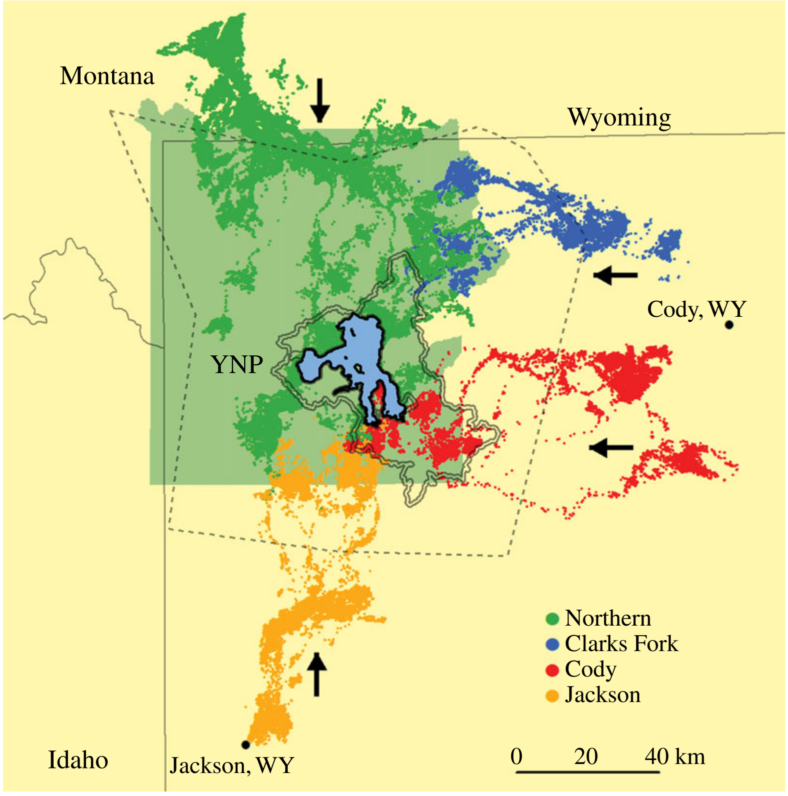

Figure 1. Individuals in four elk populations migrate each spring from outlying areas of the GYE to high-elevation summer ranges in and around the watershed of Yellowstone Lake. Here, the year-round movements of 5–10 individuals in each population are pooled to illustrate migratory movements, with a global positioning system fix rate of 1–12 locations per day. The double line delineates the Yellowstone Lake watershed; the dotted line, a polygon built from the aggregated year-round VHF locations of grizzly bears known to feed on cutthroat trout during the 1980s (adapted from Mattson & Reinhart [14]). Black arrows indicate the direction of migration from winter to summer ranges.

The Greater Yellowstone ecosystem (GYE) harbours one of the most diverse assemblages of large mammals in North America. The return of native large carnivores to YNP, including the reintroduction of wolves and recovery of grizzly bears, is widely thought to have restored ecosystem functioning [11,12]. Simultaneously, the introduction of a non-native aquatic predator, the lake trout (*Salvelinus namaycush*), has emerged as a major conservation problem for YNP [13]. Historically, Yellowstone Lake (figure 1) harboured an abundant population of cutthroat trout, but lake trout prey heavily on cutthroat trout [15] and have driven a decline of more than 90 per cent in their numbers [13]. Although cutthroat trout migrate up shallow tributary streams to spawn, and are exploited by many terrestrial predators, lake trout spawn on the lake bottom and are inaccessible to those predators [13,15]. The lake trout invasion is thought to have influenced the foraging of many birds and mammals [13,16,17], but its cascading ecological consequences are largely unknown.

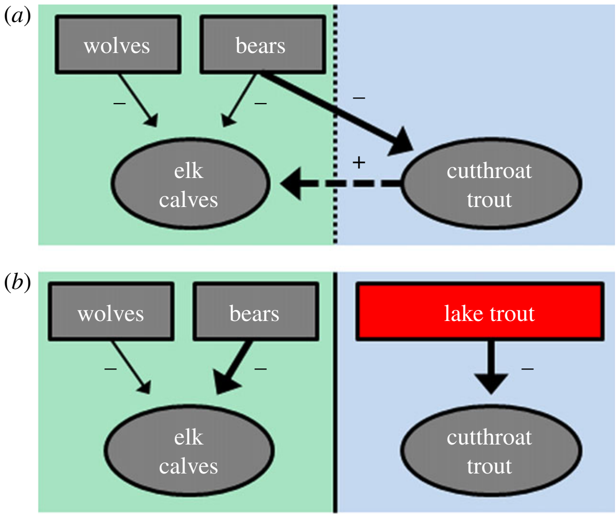

Figure 2. Focal food web interactions (*a*) before and (*b*) after the lake trout invasion in Yellowstone Lake. Predation by lake trout has driven a precipitous decline in the number of native cutthroat trout. Unlike cutthroat trout, which migrate up shallow streams to spawn, lake trout spawn on the lake bottom. Thus, the lake trout invasion has disrupted a major aquatic subsidy to terrestrial consumers, such as the grizzly bear.

Spawning cutthroat trout were an important prey species for a portion of the GYE's population of grizzly bears [14,18,19], which incorporate many vertebrates, invertebrates and plants into their diets [18,20]. We explore one consequence of this omnivory, an ecological linkage between the aquatic and terrestrial food webs of the GYE that arises from the spatial and temporal coincidence each spring of cutthroat trout spawning with elk migration. We hypothesize that an increase in the rate of grizzly predation on elk calves, caused by the lake trout invasion and cutthroat trout decline [10], has contributed to the declining productivity of migratory elk in the GYE (figure 2). Many elk that spend spring and summer in high-elevation habitats near Yellowstone Lake migrate 40–140 km to winter ranges outside of YNP—a behaviour that may transmit the consequences of the lake trout invasion far beyond park boundaries (figure 1).

We evaluate this hypothesis by first synthesizing historical and contemporary studies, including new data, that address three interrelated ecological patterns in and around the watershed of Yellowstone Lake: (i) elk migration and calving; (ii) decreased fishing activity by grizzly bears; and (iii) increasing rates of predation on elk calves by grizzly bears. Then, to evaluate the potential strength of the linkage from lake trout invasion to elk migration, we incorporate observed shifts in grizzly bear diets into a model of elk demography to evaluate changes in elk calf recruitment and population growth. We also discuss several alternative hypotheses for our observations. Ultimately, while the growing abundance of large carnivores and a recent drought have also influenced calf recruitment of migratory elk [21], the role of a changing grizzly bear diet is of singular management concern because of its anthropogenic origin at the heart of the vast YNP wilderness.

2. Elk migration and calving in and around the watershed of Yellowstone Lake

Several thousand elk migrate each spring from outlying GYE winter ranges on mixed-use lands in Montana and Wyoming, up to wilderness summer ranges inside YNP. This includes individuals from four major populations, among them the well-studied northern Yellowstone herd [21–23]. Our synthesis of recent global positioning system (GPS) collar data and population surveys reveals that many of these elk migrate to access summer ranges in or near the watershed of Yellowstone Lake (figure 1). Thus, while this watershed comprises only approximately 30 per cent of YNP and approximately 3 per cent of the GYE, perturbations in and around Yellowstone Lake might disproportionately impact the ecosystem's migratory elk.

Yellowstone's spring elk migrations typically begin in mid-May [23], and are followed by the peak of elk calving around 1 June [24,25]. Most predation by bears on elk occurs in the three weeks after calving, when elk neonates are most vulnerable [24,25]. Variation in winter severity, spring snowmelt and vegetation green-up can cause the onset of elk migrations to vary by more than a month [23], which influences the spatial distribution of elk calving sites along a gradient in bear density that reaches its peak within YNP. Nevertheless, in a typical year, large numbers of elk calve in and around the watershed, whereas others arrive later with young neonates that vary in their vulnerability to predation.

We compiled a series of winter elk surveys conducted over the past two decades in the GYE (see the electronic supplementary material). They indicate that on winter ranges dominated by migratory elk, calf recruitment has been declining since the late 1990s (figure 3*e*), with calf–cow ratios reaching 0.1 to 0.2 for most of the past decade [21]. By contrast, the median winter calf–cow ratio between 1978 and 2006 across Wyoming's elk herds outside of the GYE was 0.41 [28]. Although these surveys suggest steady declines among migrants, they have limited value in determining the role of neonate mortality because they are conducted six months or more after calving, in areas where migrants often mix with residents. Thus, we conducted new aerial surveys on elk summer ranges in and around the Lake watershed (see the electronic supplementary material). These data suggest that the calf–cow ratios have declined to low levels by late summer (figure 3*e*). Most strikingly, segments of the northern Yellowstone herd that summer near Yellowstone Lake have been observed with calf–cow ratios below 0.1 in July and August [29]. Such low calf numbers, relatively soon after calving, suggest a combination of low pregnancy [21], low birth weights [27] and/or high rates of predation [24]. However, pregnancy rates in the northern Yellowstone herd have been more than 80 per cent in recent years [29,30], and

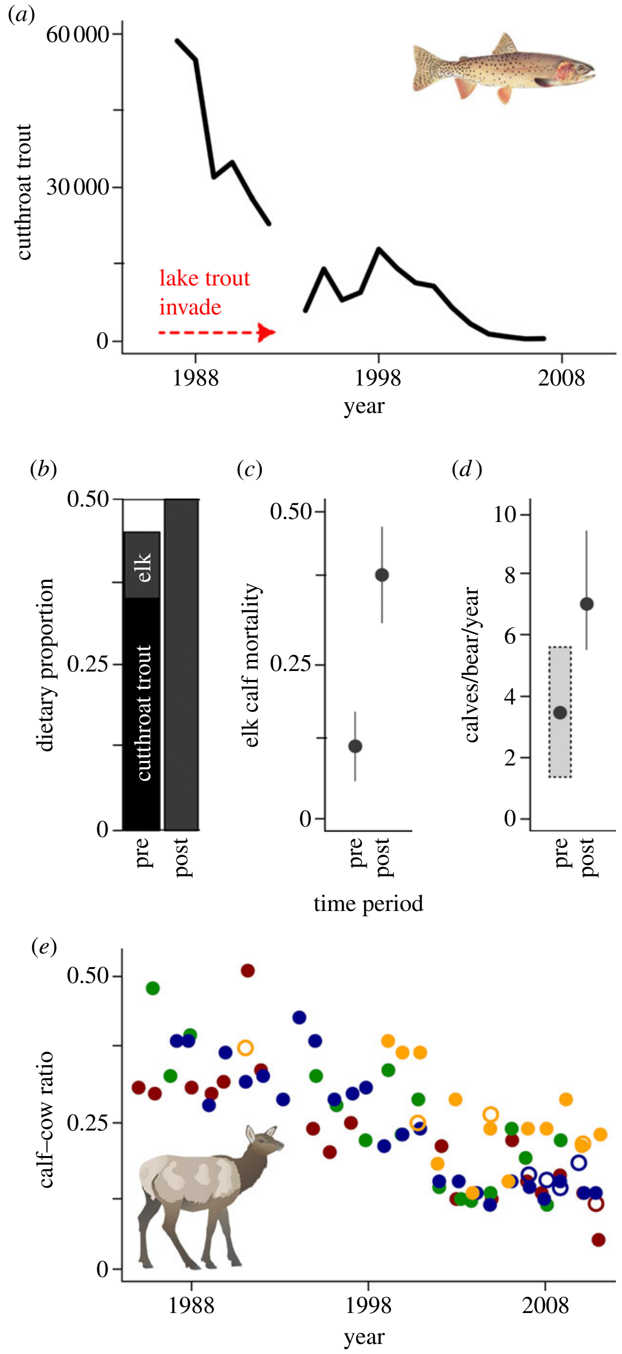

Figure 3. (*a*) Since the late 1980s, the number of spawning cutthroat trout counted each spring at Clear Creek (YNP's primary long-term monitoring site) has declined. We broadly define the 'pre-decline period' as before 1998, and the 'post-decline period' as after 1998. (*b*) In studies conducted during the post-decline period, the proportion of trout in the grizzly bear diet (black) at peak calving/spawning time has decreased, whereas the proportion of ungulate tissue (grey) has increased (estimates from Fortin *et al.* [10], Mattson & Reinhart [14] and Mattson [26]). (*c*) The proportion of elk calf mortality (±95% confidence interval (CI)) attributed to bear predation (primarily grizzly bears; [24,27]) and (*d*) the *per capita* rate of predation by grizzly bears on elk calves has increased over the same time period [10,26]. In (*d*), the shaded box indicates an estimated range for the number of ungulates killed per bear per year, and the black dot indicates its median value, which we conservatively assumed to represent elk calves only and used in our demographic models. (*e*) The winter calf–cow ratios of migratory elk from four GYE populations (closed circles) have declined steadily over the same period, and comparable summer (August–September) surveys (open circles) suggest that calf losses occur largely before summer's end. The colours in panel (*e*) correspond with those shown in figure 1. Instances where a population's summer ratio exceeds its winter ratio are probably attributable to subpopulation mixing on winter range.

recent study of calf mortality did not find any correlation between birth weight and the risk of mortality [24]. These patterns suggest that summer predation has contributed to low calf–cow ratios in migratory populations [21,24].

3. Declining grizzly fishing activity on cutthroat spawning streams

Bears are known to feed on spawning salmonids in many ecosystems [7]. Cutthroat trout have long been considered an important food for a portion of YNP's grizzly bear population [14,31], providing concentrated fat and protein at a critical time of the year when bears are recovering from hibernation [18,19]. Approximately half of Yellowstone Lake's 124 tributary streams were historically used by cutthroat trout, which spawn between mid-May and early August [14,19]. Early studies found that grizzly bears fished on most active spawning streams in most years [14]. One recent (1997–2000) estimate indicated that 68 individual grizzly bears, or 14–21% of the GYE population, visited and may have fished the tributaries of Yellowstone Lake from May to July [19]. Earlier studies indicated that cutthroat trout comprised the majority of these grizzly bears' diet during the spawning period [14].

Since the late 1980s, the number of cutthroat trout in Yellowstone Lake has declined substantially. On some key tributaries, the number of spawning trout has declined by more than 90 per cent since 1990 (figure 3*a*) [13]. Over this same period, the number of bear scats and tracks, partially consumed trout remains and grizzly bear visits per week have decreased along active spawning streams [13,19]. By 1997–2000, the estimated proportion of cutthroat trout in grizzly bear diets had dropped by as much as 90 per cent [32]. By 2007–2009, trout consumption had declined another 72 per cent, such that trout appeared only rarely in the diet (figure 3*b*; [10]). The loss of cutthroat trout has led many biologists to speculate that grizzly bears would seek alternative foods, and potentially suffer demographic consequences [13,19,33].

4. Increasing grizzly predation on elk neonates

Several lines of evidence suggest that newborn elk are an alternative prey for grizzly bears faced with declining availability of spawning cutthroat trout. Bears are adept predators of neonatal ungulates in many areas of North America [34], including the GYE [24,26,27]. Trout spawning and elk migration overlap both spatially and temporally [19,24], and the tissues of spawning trout and elk calves are similar in their nutritional value [35]. Further, in comparison with other North American landscapes occupied by grizzly bears, the GYE has less abundant nutritious plant matter [7] including relatively poor berry production [18]— leaving bears with comparatively few high-quality alternatives to animal tissue.

In the early and middle twentieth century, naturalists anecdotally described grizzly bears consuming trout commonly, but elk calves only occasionally [31,36]. More recently, in the years spanning the cutthroat decline, a growing proportion of elk calf mortality in YNP has been attributed to bear predation. In the late 1980s, grizzly and black bears (*Ursus americanus*) killed an estimated 12 per cent of the elk calves in northern Yellowstone annually [27]. By the mid-2000s, bears were estimated to kill 41 per cent of calves (figure 3*c*) [24]. In both cases, most of this predation was attributed to grizzly bears. To date, researchers have assumed that these increases in bear predation reflected an increase in bear numbers [21,24], rather than dietary shifts. However, a comparison of historical and contemporary grizzly diet studies suggests that the *per capita* rate of elk calf predation by grizzly bears increased over the same period. In the late 1980s, the first large-scale study of the use of ungulates by grizzly bears estimated that an individual grizzly killed 1.4–5.8 ungulates per year, 13 per cent of which were elk calves [26]. By contrast, more recent studies have estimated that an individual grizzly on Yellowstone's northern range kills 19 calves per year [24]—and within the Yellowstone Lake watershed, seven calves during the month of June (figure 3*d*; [10]). In parallel with these increases, in the late 1980s ungulate tissue was estimated to comprise 5 per cent of the grizzly diet at peak calving time (figure 4; [14,18,26])—but more recently, above 50 per cent [10]. Although the earlier study was based on VHF telemetry [26] and might have detected fewer calf predation events, a correction factor was applied based on observations of the amount of time grizzly bears spent at carcases of varying size (see the electronic supplementary material for additional discussion).

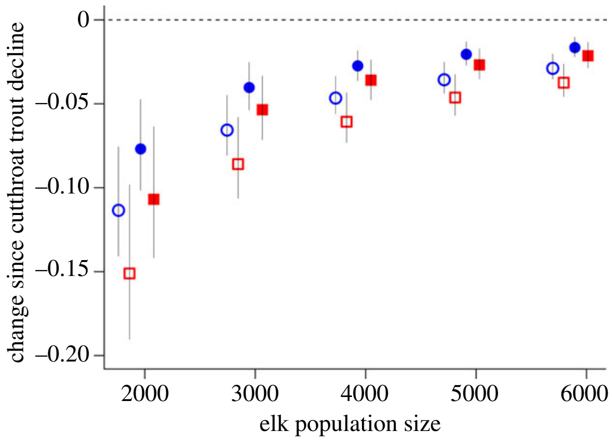

Figure 4. Predicted changes in elk calf–cow ratios (open symbols) and population growth rate (λ, closed symbols) owing to the cutthroat trout decline, using estimates based on estimated kill rates (red squares) and biomass replacement of trout with elk calves (blue circles). Elk were modelled over a range of population sizes owing to uncertainty in the number of elk that summer in and around the Yellowstone Lake watershed. For reference, a composite sum taken from summer surveys conducted in August 2008, 2010 and 2011 (conducted by the Wyoming Game and Fish Department and Montana Fish, Wildlife and Parks) suggests a minimum population of 2383 adult females. All values are presented as means ±95% CI.

This apparent historical-to-contemporary shift in bear foraging behaviour has been strongly corroborated by a comprehensive study of bear diets and behaviour conducted in the Yellowstone Lake watershed from 2007 to 2009 [10], which coupled stable isotope and mercury analyses of shed hair with GPS-based feeding site visits and faecal screening. This recent study found that while male grizzly bears (formerly the primary beneficiary of cutthroat trout) now consume one-third less meat as they did 30 years earlier, female grizzly bears consume the same amount of meat [10,32]. In concert with observations of frequent elk calf predation and large amounts of ungulate tissue in many faecal samples, these findings indicate that female grizzly bears have replaced the lost cutthroat trout biomass with that of elk neonates. This work has also found that the number of grizzly bears visiting historical spawning streams declined by 31 per cent [10] following the decline of cutthroat trout, suggesting that the effect of the cutthroat trout decline on grizzly bear behaviour could extend over a larger geographical area. Indeed, grizzly bears range widely; in the GYE, their distribution varies with the availability of human refuse, whitebark pine (*Pinus albicaulis*) seeds and ungulate 'gutpiles' left by hunters [37,38], and grizzly bears from a large area were historically thought to concentrate along tributaries of Yellowstone Lake during the spawning season (figure 1; [14]). Because very few (if any) female elk reside year-round in or near the watershed of Yellowstone Lake (P. J. White, D. E. McWhirter and D. G. Brimeyer 2012, personal communication), the influence of this diet shift can only be apportioned among migratory elk, and could impact their demography [10].

5. Evaluating the potential demographic effect of the cutthroat trout decline on migratory elk

To evaluate the hypothesis that grizzly bear diet-switching has influenced migratory elk demography, we first calculated the number of elk calves that grizzly bears might newly consume as a consequence of diet shifts, then used an age-structured elk population model to explore how this additional calf predation could influence elk calf recruitment and population growth. We assumed that the 68 bears estimated to fish along the tributaries of Yellowstone Lake in the late 1990s [19] replaced the trout biomass in their diet with equivalent elk calf biomass [10], and that the number of grizzly bears inside YNP did not change during the cutthroat decline (see fig. 5 in Schwartz *et al.* [39]). One of our most important assumptions was that calf mortality from bear predation is additive (supported by Griffin *et al.* [25]; see also [24,34]). Bear predation is thought to be additive because bears specialize on killing neonates before individual heterogeneity (e.g. body condition) begins to strongly mediate vulnerability [24,25].

We first calculated the number of elk calves that would be required to replace the trout biomass lost from the diet of grizzly bears. Prior to the cutthroat trout decline, 44 grizzly bears were estimated to eat 20 578 spawning trout, weighing 468 g each, or a total of 9630 kg per year [40]. This study probably overestimated cutthroat trout consumption [10,32] because of its assumption that scats sampled along streams [14] represented the diets of grizzly bears foraging further afield in the Yellowstone Lake watershed during the spawning period. We addressed this issue by using the product of the historical estimate of the proportion of trout in the diet (0.9; [14,40]) and the proportion of VHF locations of probable trout-eating grizzly bears that fell near (within 2 km) tributary streams during the spawning period (0.38; [14]). This resulted in a greatly revised estimate of 7820 trout (3659 kg) consumed per year. Using the more recent estimate of 68 individuals fishing in the Yellowstone Lake watershed between 1997 and 2000 when trout were still relatively abundant [19], the local population would be estimated to have consumed 5656 kg of trout per year. By contrast, after the bulk of the cutthroat trout decline (2007–2009), grizzly bears were estimated to eat only 302 spawning trout (314 kg) per year [10]. Assuming a 1 : 1 nutritional equivalency of trout and elk biomass (probably a conservative assumption owing to the high digestibility of trout [14] and potentially higher metabolic costs of hunting more sparsely distributed elk calves) and a calf weight of 18 kg each when killed by grizzly bears [26], the resulting 5342 kg loss of trout biomass would be replaced with approximately 297 elk calves.

We calculated a second, independent estimate of change in grizzly bear predation rates on elk calves using predation rates that were estimated before and after the cutthroat trout decline. Recognizing the inherent limitations of historical studies that used VHF telemetry to locate kills, we used the median (3.6) of the estimated pre-decline kill rate of 1.4–5.8 ungulates per grizzly bear per year [26] and assumed this kill rate was for *elk calves only* (a conservative assumption that reduces the predicted changes in elk calf–cow ratios and population growth). Thus, 68 individuals in the Yellowstone Lake watershed would have killed 245 elk calves annually. In the past decade in the Yellowstone Lake watershed, the same number of grizzly bears are estimated to kill 476 calves annually (seven calves per year, 10), for an estimated increase of 231 calves. Notably, this estimate broadly agrees with our above estimate, based on trout biomass replacement (297 calves).

To explore the potential impact of these changes on elk populations, we incorporated both sets of the above calculations into an age-structured elk population model (see the electronic supplementary material). Because the number of elk that mix in and around the Yellowstone Lake watershed has not been estimated and the population size may vary with annual migration timing, we predicted change in the rates of recruitment and population growth (λ) across a range of population sizes exposed to grizzly bear predation. Ultimately, our predictions were primarily determined by two inputs: (i) the estimated change in the number of calves being killed by grizzly bears and (ii) the overall size of the elk population. For reference, we note that a composite sum taken from surveys within three distinct areas of the Yellowstone Lake watershed in August 2008, 2010 and 2011 (conducted by the Wyoming Game and Fish Department and Montana Fish, Wildlife and Parks) suggests a minimum population of 2383 adult females by late summer.

Our simulations predicted an influence of grizzly bear diet-switching on elk calf recruitment and population growth rates across a wide range of potential population sizes (figure 4). Although the magnitude of the predicted changes depends both on the increase in calf mortality and the total population size, all combinations of estimates resulted in declines of both calf recruitment (0.04–0.16) and population growth (0.02–0.11). An explicit accounting of estimated changes in bear predation rates in our models indicated that shifts in bear foraging behaviour—an indirect consequence of lake trout invasion—are capable of creating meaningful changes in the population dynamics of migratory elk.

6. Alternative explanations

Our inferences draw on a large body of research conducted by biologists working independently, across multiple taxa, over several decades. The patterns we describe—the coincidence of cutthroat trout decline, grizzly diet shifts from trout to elk calves and the declining recruitment of migratory elk—are consistent with an emergent link between lake trout invasion and elk migration in the GYE. However, as is so often the case with 'natural experiments', it is challenging to determine cause and effect when evaluating food web changes spanning several decades in landscapes so vast as the GYE. Thus, we discuss several alternative explanations for our observations, and explain why we suspect they do not oppose our findings.

Although predation by non-native lake trout is widely considered the leading cause of the cutthroat trout decline [13,41], at least two other factors play a role. An unusually severe, long-term drought reduced the flow levels of some tributary streams for much of the past decade, probably reducing cutthroat trout recruitment to the lake [13]. Additionally, the parasite *Myxobolus cerebrali*s, which causes neurological damage (i.e. whirling disease), reduces the survival of juvenile cutthroat trout in some areas of Yellowstone Lake [13]. Whirling disease was introduced by humans [13], and a number of studies have linked recent drying and warming trends in the region to anthropogenic climate change [42–44]. Thus, regardless of the relative importance of lake trout predation versus secondary factors, the decline of native cutthroat trout is considered by many observers to be largely a consequence of human actions.

Although there is substantial evidence of changes in grizzly bear diets [10], recent increases in bear predation on elk calves are also probably a function of increasing grizzly bear numbers. In recent decades, the numbers and distribution of grizzly bears have grown in the GYE. However, this growth appears to have occurred primarily outside the core areas of YNP. From 1983 to 2002, the number of females with cubs, a key indicator of grizzly population productivity, did not increase inside YNP (see fig. 5 in Schwartz *et al*. [39]). This pattern suggests that grizzly bear habitat was saturated inside YNP [39]. If the proportion of elk calf mortality attributed to grizzly bears inside YNP increased more than threefold (cf. [24,27]) during a period when grizzly bear numbers did not increase, then it is logical that the *per capita* rate of predation increased (cf. [10,26]). However, it is important to note that in years of harsh winters, deep snow and late migration, more elk tend to calve in outlying areas of the GYE [23] where grizzly bears have been expanding and growing in numbers [39]. For these reasons, we suggest that the combination of more grizzly bears *outside* YNP (owing to their recovery) and changing grizzly bear diets *inside* YNP (owing to the decline of cutthroat trout) acts synergistically to reduce the calf recruitment of migratory elk.

In addition to predation by grizzly bears, predation by wolves and other predators [24] and low elk pregnancy rates in some areas [21] probably influence the calf recruitment of migratory elk. However, grizzly bears far outpace wolves and other predators as a cause of summer elk calf mortality [24,25], and reductions in pregnancy do not appear large enough to explain the decreases in summer calf–cow ratios that have recently been observed [21,24]. Wolf predation did not appear powerful enough to cause the pronounced decline of northern Yellowstone elk following wolf reintroduction [45]—and although human hunting probably played an important role, hunters tend to select adult elk, not calves. It is possible that other recent ecological and behavioural changes that are unrelated to the cutthroat decline have contributed to increasing rates of grizzly predation on elk calves. Several other key grizzly foods have declined in recent years, namely winter-killed ungulate carcases owing to predation and scavenging by reintroduced wolves, and whitebark pine seeds, owing to beetle (*Dendroctonus ponderosae*) and invasive fungal (*Cronartium ribicola*) infestations. Although we cannot rule out effects of these latter changes, we expect that their consequences have not been as dramatic as the loss of a diet item (i.e. cutthroat trout) that coincides both spatially and seasonally with the calving of many migratory elk.

7. Discussion

Recent changes in the productivity and abundance of migratory elk in the GYE are widely viewed as a consequence of recovering numbers of large carnivores, but new evidence suggests that the decline of native cutthroat trout has caused omnivorous grizzly bears to kill more elk calves in some areas of YNP. Predation by non-native lake trout has dramatically reduced the population of cutthroat trout that once provided critical nutrition to grizzly bears foraging at the core of the GYE, leaving bears to find alternative sources of fat and protein each spring. Historical and contemporary studies of grizzly bear diets and behaviour indicate that individuals in and around the watershed of Yellowstone Lake—an area which comprises 30 per cent of YNP—have made up for the loss of cutthroat trout by consuming elk calves at a higher rate (figure 3). This diet switch is consistent with summer elk surveys that reveal low calf numbers among the migratory populations that summer in and around the Yellowstone Lake watershed (figure 3*e*).

Our synthesis provides considerable support for an emergent link between lake trout invasion and the demography of migratory elk, but less clear is the magnitude of this effect. Demographic simulations suggest the effect has been large enough to contribute to meaningful reductions in the calf recruitment (4–16%) and growth rates (2–11%) of migratory elk populations (figure 4). These findings are consistent with the prediction from theory of subsidy influences in ecosystems that a consumer which aggregates to an ephemeral subsidy (i.e. spawning cutthroat trout), yet reproduces slowly (i.e. grizzly bears), will have relatively small effects on alternative resources (i.e. elk calves) in the recipient community. In the case we describe, however, this ‘protective’ effect of cutthroat trout on elk calves has been removed. While the growing abundance of large carnivores and a severe drought have probably played important roles in declining elk calf recruitment [21], we suggest that the contribution of changing grizzly bear diets to these declines is uniquely important to research and management because it represents a novel, human influence operating cryptically within core protected areas of YNP.

Our findings have important implications for ecosystem management and the conservation of aquatic–terrestrial linkages. Aquatic and terrestrial food webs have long been conceptualized as distinct ecosystem components [46]. This approach has been challenged by a growing recognition of strong cross-system subsidies and aquatic–terrestrial linkages [3,8], as in the case of spawning salmonids that subsidize upland riparian and terrestrial food webs in coastal North America [2]. Far inland, in the central watershed of YNP, a similar link appears to have been broken when the invasion of lake trout interrupted a crucial energy transfer from aquatic habitats, in the form of cutthroat trout biomass, to the terrestrial food web, via the foraging of grizzly bears (figure 2). Our work suggests that the probable consequences of lake trout invasion reach beyond the demography of cutthroat trout consumers [17], including grizzly bears [10], to that of such alternative prey as migratory elk that winter as far as 140 km away [23] in outlying areas of the GYE. Given that the grizzly bear is one of 28 mammals and birds that were thought to depend on spawning cutthroat trout [16,17], the broader ecological consequences of lake trout invasion are potentially tremendous. It remains unclear whether historic levels of cutthroat trout spawning in Yellowstone Lake tributaries can be restored, and the ecosystem consequences of breaking this aquatic–terrestrial link reversed. Fisheries biologists and managers in YNP have worked intensively for more than a decade to suppress lake trout numbers via netting and removal from Yellowstone Lake [13,41]. In recent years, the success of this programme has increased through technological improvements and increases in the spatial and temporal targeting of high densities and sensitive age classes of lake trout [41]. Our findings underscore the broad ecological importance of these efforts, the urgency of identifying new methods to suppress lake trout and the value of preventing such invasions elsewhere.

The indirect interaction of lake trout and migratory elk that we describe has implications for the interpretation, conservation and management of large mammal interactions in the GYE. Wolves have been the focus of widely popularized accounts of YNP's trophic interactions [47], perhaps partly because they were controversially reintroduced, remain active year-round and conspicuously hunt elk. Relatedly, it is often assumed that the ecological effects of recovering large carnivores herald a return to a historical condition of the GYE, providing evidence of conservation success [11,12]. However, our work suggests that important effects of human disturbance and grizzly bear predation on migratory elk are being overlooked. Globally, declines of migratory ungulates are a subject of conservation concern [48,49].

Our findings are also relevant to the wolf management plans of Idaho, Montana and Wyoming, which generally allow the flexibility to increase wolf harvests in areas of declining elk productivity and abundance. Some of the steepest elk recruitment declines in these states have occurred in the GYE, coincident with wolf reintroduction. However, complex patterns of 40–140 km elk migrations that are unique to the GYE, compounded by high rates of bear predation inside YNP's boundaries, suggest that elk calf recruitment may not be as sensitive to wolf removal on some outlying winter ranges as to the number of grizzly bears and the availability of alternative grizzly bear foods on elk summer ranges in and around YNP. As wildlife managers seek to determine whether specific interventions are likely to ameliorate declines in elk calf recruitment, they may benefit from cooperative study and monitoring of migratory herds including the timing of elk calf losses (e.g. conducting more routine summer surveys), as well as elk pregnancy and cause-specific elk calf mortality.

Wildlife biologists and managers have long recognized the importance of monitoring and securing key grizzly bear foods in the GYE [18,39]. While our findings highlight the resiliency of omnivorous grizzly bears to a changing environment [10], they also highlight the grizzly bear's growing dependency on a reduced number of high-quality foods. Our synthesis and modelling did not incorporate the declining availability of whitebark pine seeds, but the foraging options of grizzly bears may become increasingly limited as stands of whitebark pine decline throughout the GYE [20]. Future research on the nature and extent of grizzly bear diet-switching in response to changing food availability will be critical to our understanding of Yellowstone's large mammal interactions—particularly those involving the primary prey and closest competitors of grizzly bears.

A.D.M. and M.J.K. received support from the Wyoming Game and Fish Department, the Rocky Mountain Elk Foundation, the Wyoming Animal Damage Management Board and the Wyoming Governor's Big Game License Coalition. A.D.M. received additional support from the University of Wyoming's Program in Ecology, Biodiversity Institute, and NSF-EPSCoR programme (EPS-436 0447681). We thank P. Bigelow, M. Bruscino, D. Doak, J. Goheen, K. Gunther, M. Haroldson, B. Koch, C. Martinez del Rio, D. Mattson, K. Monteith, S. Newsome, J. Pauli, F. van Manen and two anonymous reviewers for discussion and comments that improved this manuscript. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the US Government. A.D.M., T.A.M and M.J.K. designed the research; A.D.M., T.A.M., J.K.F., C.T.R., K.M.P., P.J.W., D.E.M., T.M.K., D.G.B., W.S.F. and M.J.K. performed the research; A.D.M. and T.A.M. analysed the data; A.D.M. wrote the paper, incorporating revisions from the co-authors.

References

1. Hilderbrand GV, Hanley TA, Robbins CT, Schwartz CC. 1999 Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* **121**, 546–550. (doi:10.1007/s004420050961)
2. Schindler DE, Scheuerell MD, Moore J, Gende SM, Francis TB, Palen WJ. 2003 Pacific salmon and the ecology of coastal ecosystems. *Front. Ecol. Environ.* **1**, 31–37. (doi:10.1890/1540-9295(2003)001[0031:PSATEO]2.0.CO;2)
3. Polis GA, Hurd SD. 1996 Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Am. Nat.* **147**, 396–423. (doi:10.1086/285858)
4. Epanchin PN, Knapp RA, Lawler SP. 2010 Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. *Ecology* **91**, 2406–2415. (doi:10.1890/09-1974.1)
5. Rose MD, Polis GA. 1998 The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. *Ecology* **79**, 998–1007. (doi:10.1890/0012-9658(1998)079[0998:TDAAOC]2.0.CO;2)
6. Adams LG, Farley SD, Stricker CA, Demma DJ, Roffler GH, Miller DC, Rye RO. 2010 Are inland wolf-ungulate systems influenced by marine subsidies of Pacific salmon? *Ecol. Appl.* **20**, 251–262. (doi:10.1890/08-1437.1)
7. Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C. 1999 The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Can. J. Zool.* **77**, 132–138. (doi:10.1139/z98-195)
8. Takimoto G, Iwata T, Murakami M. 2009 Timescale hierarchy determines the indirect effects of fluctuating subsidy inputs on *in situ* resources. *Am. Nat.* **173**, 200–211. (doi:10.1086/595759)
9. Brashares JS, Arcese P, Sam MK, Coppolillo PB, Sinclair ARE, Balmford A. 2004 Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science* **306**, 1180–1183. (doi:10.1126/science.1102425)
10. Fortin JK, Schwartz CC, Gunther KA, Teisberg JE, Haroldson MA, Evans MA, Robbins CT. 2013 Dietary adaptability of grizzly bears and American black bears in Yellowstone National Park. *J. Wildlife Manag.* **77**, 270–281. (doi:10.1002/jwmg.483)
11. Berger J, Stacey PB, Bellis L, Johnson MP. 2001 A mammalian predator–prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecol. Appl.* **11**, 947–960. (doi:10.2307/3061004)
12. Ripple WJ, Beschta RL. 2007 Restoring Yellowstone's aspen with wolves. *Biol. Conserv.* **138**, 514–519. (doi:10.1016/j.biocon.2007.05.006)

13. Koel TM, Bigelow PE, Doepke PD, Ertel BD, Mahony DL. 2005 Non-native lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. *Fisheries* **30**, 10–19. (doi:10.1577/1548-8446(2005)30[10:NLTRIY]2.0.CO;2)
14. Mattson DJ, Reinhart DP. 1995 Influences of cutthroat trout (*Oncorhynchus clarki*) on behaviour and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975–1989. *Can. J. Zool.* **73**, 2072–2079. (doi:10.1139/z95-244)
15. Stapp P, Hayward GD. 2002 Effects of an introduced piscivore on native trout: insights from a demographic model. *Biol. Invasions* **4**, 299–316. (doi:10.1023/A:1020985331815)
16. Schullery P, Varley JD. 1996 Cutthroat trout and the Yellowstone ecosystem. In *The Yellowstone Lake crisis: confronting a lake trout invasion* (eds JD Varley, P Schullery), pp. 12–21. Yellowstone National Park, WY: National Park Service.
17. Crait JR, Blundell GM, Ott KE, Herreman JK, Ben-David M. 2006 Late seasonal breeding of river otters in Yellowstone National Park. *Am. Midl. Nat.* **156**, 189–192. (doi:10.1674/0003-0031(2006)156[189:LSBORO]2.0.CO;2)
18. Mattson DJ, Blanchard BM, Knight RR. 1991 Food-habits of Yellowstone grizzly bears, 1977–1987. *Can. J. Zool.* **69**, 1619–1629. (doi:10.1139/z91-226)
19. Haroldson MA, Gunther KA, Reinhart DP, Podruzny SR, Cegelski C, Waits L, Wyman T, Smith J. 2005 Changing numbers of spawning cutthroat trout in tributary streams of Yellowstone Lake and estimates of grizzly bears visiting streams from DNA. *Ursus* **16**, 167–180. (doi:10.2192/1537-6176(2005)016[0167:CNOSCT]2.0.CO;2)
20. Schwartz CC, Haroldson MA, White GC. 2010 Hazards affecting grizzly bear survival in the Greater Yellowstone ecosystem. *J. Wildlife Manag.* **74**, 654–667. (doi:10.2193/2009-206)
21. Middleton AD *et al*. In press. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology*. (doi:10.1890/11-2298.1)
22. Craighead JJ, Atwell G, O'Gara BW. 1972 Elk migrations in and near Yellowstone National Park. *Wildlife Monogr.* **29**, 6–48.
23. White PJ, Proffitt KM, Mech LD, Evans SB, Cunningham JA, Hamlin KL. 2010 Migration of northern Yellowstone elk: implications of spatial structuring. *J. Mammal.* **91**, 827–837. (doi:10.1644/08-MAMM-A-252.1)
24. Barber-Meyer SM, Mech LD, White PJ. 2008 Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monogr.* **169**, 1–30. (doi:10.2193/2008-004)
25. Griffin KA *et al*. 2011 Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *J. Anim. Ecol.* **80**, 1246–1257. (doi:10.1111/j.1365-2656.2011.01856.x)
26. Mattson DJ. 1997 Use of ungulates by Yellowstone grizzly bears (*Ursus arctos*). *Biol. Conserv.* **81**, 161–177. (doi:10.1016/S0006-3207(96)00142-5)
27. Singer FJ, Harting A, Symonds KK, Coughenour MB. 1997 Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *J. Wildlife Manag.* **61**, 12–25. (doi:10.2307/3802410)
28. Anonymous. 2006 Big game aerial monitoring surveys. Job completion report database. Cheyenne, WY: Wyoming Game and Fish Department.
29. Cunningham JA, Hamlin KL, Lemke TO. 2008 Northern Yellowstone elk (HD313). Annual report. Bozeman, MT: Montana Fish, Wildlife and Parks.
30. Raithel JD, Kauffman MJ, Pletscher DH. 2007 Impact of spatial and temporal variation in calf survival on the growth of elk populations. *J. Wildlife Manag.* **71**, 795–803. (doi:10.2193/2005-608)
31. Skinner MP. 1925 *Bears in the Yellowstone*. Chicago, IL: McClurg and Co.
32. Felicetti LA, Schwartz CC, Rye RO, Gunther KA, Crock JG, Haroldson MA, Waits L, Robbins CT. 2004 Use of naturally occurring mercury to determine the importance of cutthroat trout to Yellowstone grizzly bears. *Can. J. Zool.* **82**, 493–501. (doi:10.1139/z04-013)
33. Reinhart DP, Haroldson MA, Mattson DJ, Gunther KA. 2001 Effects of exotic species on Yellowstone's grizzly bears. *West N. Am. Nat.* **61**, 277–288.
34. Zager P, Beecham J. 2006 The role of American black bears and brown bears as predators on ungulates in North America. *Ursus* **17**, 95–108. (doi:10.2192/1537-6176(2006)17[95:TROABB]2.0.CO;2)
35. Mattson DJ, Barber K, Maw R, Renkin RA. 2004 Coefficients of productivity for Yellowstone's grizzly bear habitat. US Geological Survey, Biological Resources Discipline Biological Science Report USGS/BRD/BSR-2002-0007. See http://sbsc.wr.usgs.gov/cprs/research/projects/grizzly/grizzly_yellowstone.asp.
36. Murie OJ. 1951 *The elk of North America*. Harrisburg, PA: Stackpole Books.
37. Blanchard BM, Knight RR. 1991 Movements of Yellowstone grizzly bears. *Biol. Conserv.* **58**, 41–67. (doi:10.1016/0006-3207(91)90044-A)
38. Haroldson MA, Schwartz CC, Cherry S, Moody DS. 2004 Possible effects of elk harvest on fall distribution of grizzly bears in the Greater Yellowstone Ecosystem. *J. Wildlife Manag.* **68**, 129–137. (doi:10.2193/0022-541X(2004)068[0129:PEOEHO]2.0.CO;2)
39. Schwartz CC, Haroldson MA, White GC, Harris RB, Cherry S, Keating KA, Moody D, Servheen C. 2006 Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone ecosystem. *Wildlife Monogr.* **161**, 1–68. (doi:10.2193/0084-0173(2006)161[1:TSAEIO]2.0.CO;2)
40. Stapp P, Hayward GD. 2002 Estimates of predator consumption of Yellowstone cutthroat trout (*Oncorhynchus clarki* bouvieri) in Yellowstone Lake. *J. Freshw. Ecol.* **17**, 319–329. (doi:10.1080/02705060.2002.9663900)
41. Syslo JM, Guy CS, Bigelow PE, Doepke PD, Ertel BD, Koel TM. 2011 Response of non-native lake trout (*Salvelinus namaycush*) to 15 years of harvest in Yellowstone Lake, Yellowstone National Park. *Can. J. Fish. Aquat. Sci.* **68**, 2132–2145. (doi:10.1139/f2011-122)
42. Barnett TP *et al*. 2008 Human-induced changes in the hydrology of the western United States. *Science* **319**, 1080–1083. (doi:10.1126/science.1152538)
43. Pederson GT, Gray ST, Woodhouse CA, Betancourt JL, Fagre DB, Littell JS, Watson E, Luckman BH, Graumlich LJ. 2011 The unusual nature of recent snowpack declines in the North American cordillera. *Science* **333**, 332–335. (doi:10.1126/science.1201570)
44. Shuman B. 2012 Recent Wyoming temperature trends, their drivers, and impacts in a 14,000-year context. *Clim. Change* **112**, 429–447. (doi:10.1007/s10584-011-0223-5)
45. Vucetich JA, Smith DW, Stahler DR. 2004 Influence of harvest, climate, and wolf predation on Yellowstone elk, 1961–2004. *Oikos* **111**, 259–270. (doi:10.1111/j.0030-1299.2005.14180.x)
46. Likens GE, Bormann FH. 1974 Linkages between terrestrial and aquatic ecosystems. *Bioscience* **24**, 447–456. (doi:10.2307/1296852)
47. Mech LD. 2012 Is science in danger of sanctifying the wolf? *Biol. Conserv.* **150**, 143–149. (doi:10.1016/j.biocon.2012.03.003)
48. Berger J. 2004 The last mile: how to sustain long-distance migration in mammals. *Conserv. Biol.* **18**, 320–331. (doi:10.1111/j.1523-1739.2004.00548.x)
49. Bolger DT, Newmark WD, Morrison TA, Doak DF. 2008 The need for integrative approaches to understand and conserve migratory ungulates. *Ecol. Lett.* **11**, 63–77.

US protected lands mismatch biodiversity priorities

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Edited* by Edward O. Wilson, Harvard University, Cambridge, MA, and approved March 17, 2015 (received for review September 23, 2014)

Because habitat loss is the main cause of extinction, where and how much society chooses to protect is vital for saving species. The United States is well positioned economically and politically to pursue habitat conservation should it be a societal goal. We assessed the US protected area portfolio with respect to biodiversity in the country. New synthesis maps for terrestrial vertebrates, freshwater fish, and trees permit comparison with protected areas to identify priorities for future conservation investment. Although the total area protected is substantial, its geographic configuration is nearly the opposite of patterns of endemism within the country. Most protected lands are in the West, whereas the vulnerable species are largely in the Southeast. Private land protections are significant, but they are not concentrated where the priorities are. To adequately protect the nation's unique biodiversity, we recommend specific areas deserving additional protection, some of them including public lands, but many others requiring private investment.

conservation priorities | protected areas | endemism | range size | extinction

Protected areas are the most widespread and effective means to conserve natural ecosystems. Given that habitat loss is the primary threat to species survival, which places society chooses to protect will largely determine how many and which species survive. The original intent of many protected areas in the United States was to protect landscapes, not biodiversity. Nevertheless, protected areas are still the backbone of conservation in the country—as they are globally.

We describe geographic patterns of biodiversity and the distribution of protected areas and land ownership in the United States. We then combine them to map priorities for future protection. Our focus is the continental United States minus Alaska, recognizing that Alaska is biodiversity poor and a substantial fraction of it is already within protected areas. We also exclude Hawaii and US territories because, although rich in endemic species, they are comparatively data poor.

We can assess coverage of protected areas by how well they include different elements of biodiversity, be they ecosystems (1), biophysical landforms (2–4), or individual species (5–8). We focus on species, because their extinction is irreversible (9, 10). Previous studies of the US protected area system focused mainly on federally listed endangered species (11–15); we consider all species within taxa for which data are sufficient.

Knowing precisely where individual species occur limits inferences. We compiled species' range maps for taxa where all species in the taxon are relatively well-documented within the United States, recognizing the limits of such data (10, 16–18). These are, however, the most comprehensive and readily applicable data for guiding decisions. We mapped diversity by overlaying maps for various subsets of species in each taxon (*Methods*).

Geographic patterns of total species richness differ substantially among taxa (Fig. 1). Mammal richness is highest in the west, birds along the coasts, and reptiles broadly across the warmer south. Amphibians, freshwater fish, and trees are most diverse in the humid east and, especially, the warm and humid Southeast. These patterns are interesting, worthy of further study, but do not direct conservation. Widely distributed species dominate overall patterns of species richness (19), but they are generally not the species in need of conservation efforts.

In identifying conservation priorities, one must consider both existing protected areas and the intrinsic vulnerability of species. Vulnerable species tend to be in two groups (10): those with small geographic ranges, which is often correlated with local rarity, and large-bodied species that are sparsely distributed across large ranges. The latter species, which are relatively few but include predators like panthers and wolves, were largely extirpated from the east and still face persecution across large extents of the west.

Most imperiled species are of the first group: small range size is the best predictor of extinction risk and, thus, the first metric for conservation priority (20–22). We focus on small-ranged species defined in several ways. First, we consider endemics—those with their entire range in the United States (*Methods*). Amphibians (70%) and freshwater fish (68%) show the highest levels of endemism, followed by reptiles (30%), trees (29%), mammals (28%), and birds (<3%). Patterns of endemism for all taxa are consistently centered in the Southeast, although the west also has significant mammal endemism (Fig. 1).

Next, we consider "small-ranged species," those having ranges smaller than the median size, and do so from two perspectives. There are species whose ranges are small by global standards and those that are small relative to species within the United States. For globally small-ranged species, most birds and mammals are in the west (Fig. 2). This pattern is in contrast with their endemism patterns, for many globally small-ranged birds and mammals have ranges extending into Mexico or Canada. Amphibian ranges are so small (Table S1) and isolated that no location has more than two species with overlapping ranges, although 61 small-ranged species occur in the country. A general characteristic of regions with small-ranged amphibians is complex topography. For instance, 18

Significance

The United States has one of the oldest and most sophisticated systems of protected areas in the world. Given the large amount of information on the country's biodiversity, and the potential resources available, one might expect it to do well in protecting biodiversity. We find that it does not. The United States protected areas do not adequately cover the country's unique species. To improve the coverage, we map priorities for multiple taxa and recommend specific areas for immediate conservation attention. These areas contain a mix of public and private land, meaning that major progress in conservation will require actions in both the public and private sectors, and will succeed only if done in the correct areas.

Author contributions: C.N.J., K.S.V.H., S.L.P., and J.O.S. designed research; C.N.J. performed research; C.N.J. analyzed data; and C.N.J., K.S.V.H., S.L.P., and J.O.S. wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1418034112/-/DCSupplemental.

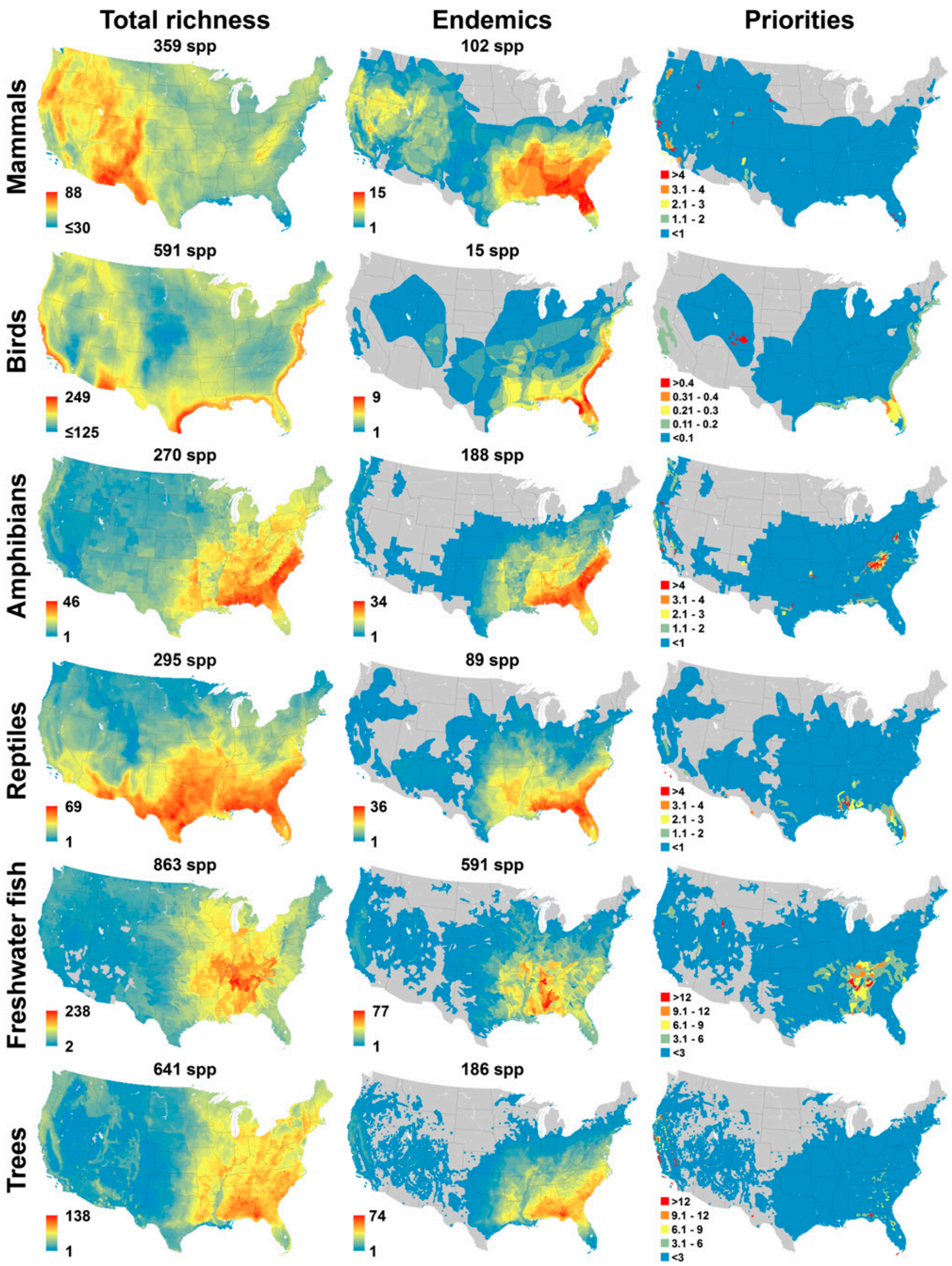

Fig. 1. Biodiversity of the lower continental United States and priority areas for individual taxa. Total richness is the number of all species within the taxonomic group. Endemics are species whose entire range is within the lower 48 states. Priorities map the sum of individual species' priority scores across the taxon.

small-ranged amphibians, all of them Plethodontid salamanders, live within the Appalachian Mountains, although their individual ranges rarely overlap. This result matches findings of earlier global-scale studies (23, 24).

Similar patterns emerge for species having ranges small relative to species in the United States (Fig. 2). Small-ranged mammals concentrate mostly in the west. Small-ranged birds concentrate in the west and the coasts, although their generally large ranges mean all areas have at least one "small-ranged" bird. The Southeast, particularly the southern Appalachians, has many small-ranged amphibians, mostly salamanders. Similar analyses were not possible for reptiles, freshwater fish, or trees because no globally comprehensive databases are available. Threatened species show no consistent geographic patterns across taxa, with few places having more than two IUCN threatened species of any particular taxon (Fig. 2).

Are available biodiversity data sufficient to make informed choices about priorities? We will always need to prioritize based on some subset of species or other proxy for overall biodiversity, but some next steps to expand our knowledge are clear. We recommend wider ranging assessments of reptiles and freshwater fish, which would enable a more precise evaluation of their endemism. A global assessment for reptiles is underway through the International Union for Conservation of Nature (IUCN), but a similarly comprehensive effort for freshwater fish seems more distant. Maps for trees need revision to reflect recent knowledge on species' distributions and taxonomy.

Assessments of other taxonomic groups would enable more comprehensive planning for the nation's biodiversity. Just as the taxa we analyze do not always coincide in their biodiversity patterns, taxa for which we lack range data may have their own

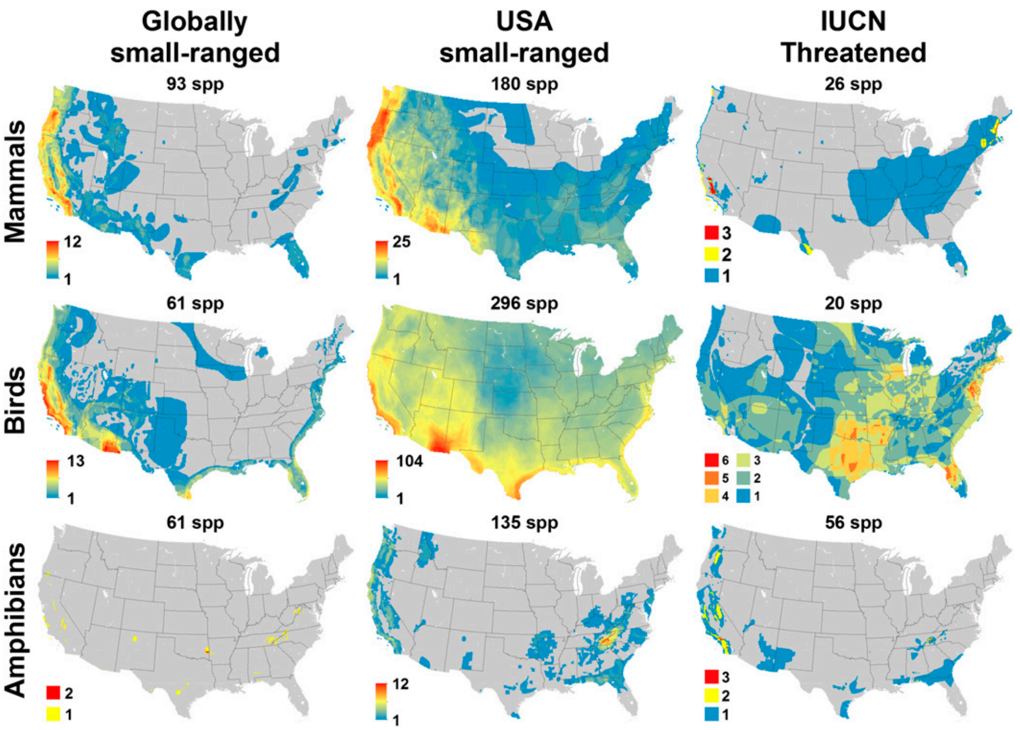

Fig. 2. Small-ranged and threatened species. Globally small-ranged are those species with ranges smaller than the global median for that taxon. USA small-ranged are those species with ranges smaller than the median for the species in the lower 48 states. IUCN Threatened are species considered vulnerable, endangered, or critically endangered on the IUCN Red List.

novel patterns. Other plant taxa would be particularly informative because diversity patterns for trees likely differ from those of plants that predominate in grasslands and other nonforest ecosystems. For invertebrates, which are almost certainly more diverse than vertebrates or plants, butterflies might be the best candidate for a nationwide database. Butterflies are diverse, charismatic, and data rich compared with other invertebrates.

Another area for possible improvement is the range maps themselves. Such maps have an inherent tendency for commission errors, including areas that species once occupied but currently do not, or areas that once had habitat but have since lost it (25). For shorter-term planning, it would certainly be useful to document better what part of a species range has habitat and whether it is occupied (26). Importantly, however, species may reoccupy currently vacant areas, and habitats can potentially recover, at least in the long term. For long-term conservation, basing decisions solely on currently occupied habitat would discount the possibility of habitat recovery or of species reoccupying currently unoccupied areas.

In addition to individual species, there is the possibility of using other measures of biodiversity or geophysical proxies. For example, using maps of ecosystems (1, 27, 28), or geophysical features such as elevation and soils (3), are other approaches for evaluating the representativeness of a protected area system.

How well does the United States protect biodiversity? Only 7.8% of the lower 48 states is within an IUCN categorized protected area (Fig. 3*A*), below the global average of 10.3% (29). Approximately 6% is in stricter IUCN categories of I to IV, about average for the globe (29). The United States employs a broadly comparable system of management categories through the Gap Analysis Program (GAP) (30). The best-protected areas—GAP Status 1 and 2—show a similar rate of 7.1% (Fig. S1 and *SI Results*).

These percentages mask a strong geographic bias. Most protected areas are in the west, which tends to be less suitable for agriculture and development and where a large fraction of the land is in federal ownership (Fig. 3*B*). Much of the publicly owned land (i.e., federal, state, and local), however, has no assigned IUCN category and/or is GAP status 3, indicating that it is to be maintained as a particular land cover but is subject to extractive use (e.g., logging, mining, grazing). Some of these public lands may have limited protection with respect to conservation, such as by the National Forest Management Act or the Endangered Species Act if they contain a federally protected species. For some individual species, these legal protections may be significant, though we do not consider them further here. Nevertheless, most of the non-IUCN ranked public lands are also in the west, matching the pattern for IUCN-ranked areas.

Most land in the center and east of the country is unprotected and privately owned. A major instrument for conservation on private land is easements. While a complete national inventory of easements is still underway (31), the partial data suggest that much of the land thus far protected is not ideally positioned for biodiversity conservation. More than 22.6% of the documented easement area is in Maine and Montana, states that together cover 6% of the total area of the lower 48 states, but have almost no endemism or small-ranged species. Florida and California, states with substantial biodiversity, reassuringly are third and fourth in easement area with more than 6% of the total each, in 1.9% and 5.3% of the total area, respectively. However, endemic-rich states in the Southeast (Tennessee, Kentucky, North Carolina, South Carolina, Mississippi, Alabama, Georgia), which make up 10.7% of the total land area of the lower 48 states, collectively contain only 7.8% of the easement area. In other words, these biodiverse states that are mostly private land, and which should be a focus of easement efforts, have less area protected than if easements were randomly distributed across the country. It appears that private land protection efforts, similar to public protected areas, are not prioritizing the most endemic-rich areas of the country, or at least are having less success in those areas.

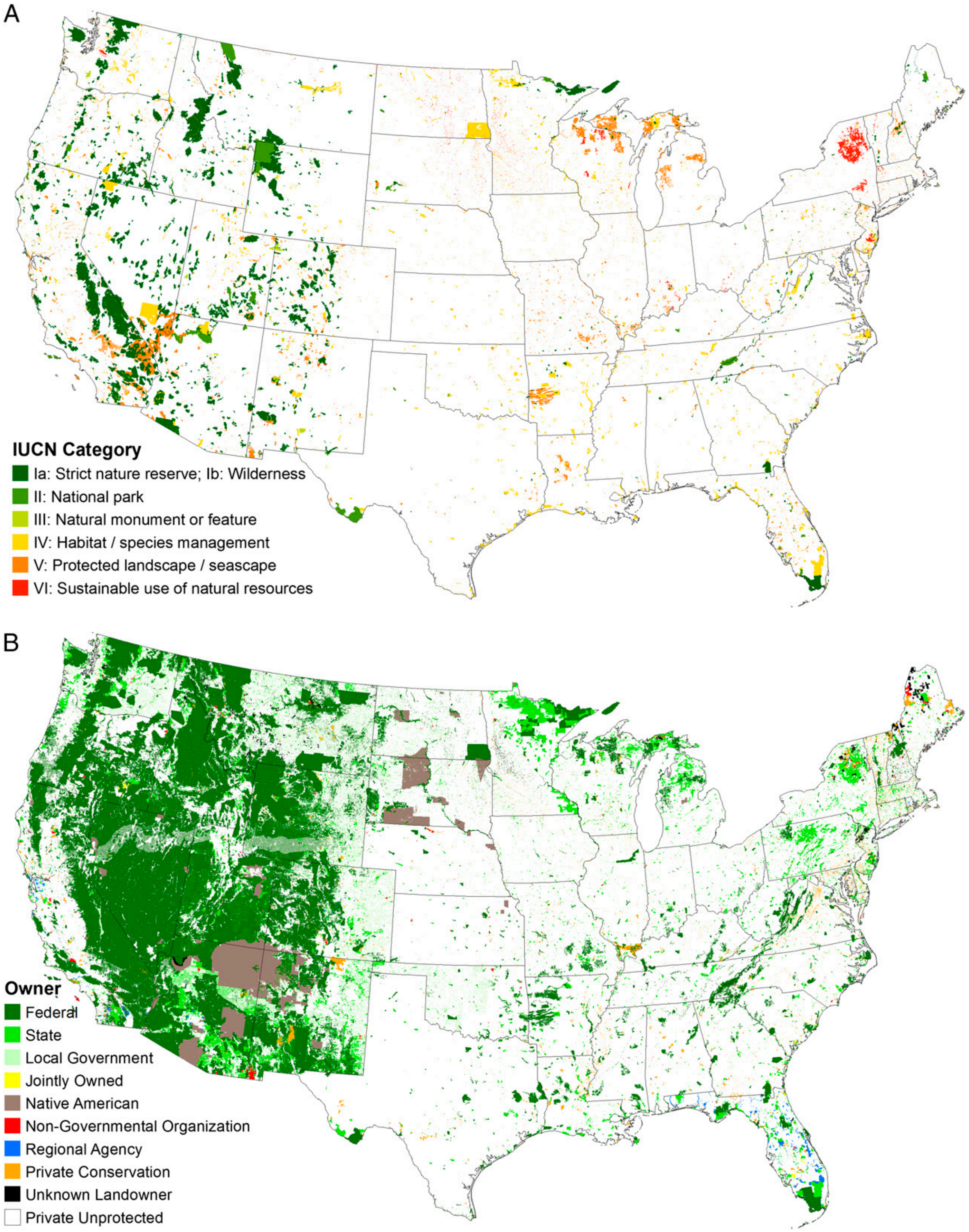

Fig. 3. Protection status and ownership of lands in the lower 48 states. (*A*) Existing protected areas colored by IUCN category (41). (*B*) Ownership status of public, private, and Native American lands.

Where might the United States efficiently expand protection for biodiversity? To prioritize lands for future conservation, we focused on the >1,200 endemic species, as their survival depends almost entirely on actions within the country. For each species, we calculated a priority score equal to the proportion of the species' range that is unprotected (i.e., not in IUCN I to VI protected areas) divided by the area of the species' range. This score increases as range size decreases, in accordance with the well-established relationship between range area and extinction risk (20–22). Conversely, if a large proportion of the species' range is within protected areas, the score accordingly decreases. Priority maps sum scores across all endemic species in a taxonomic group (Fig. 1) and across all taxonomic groups (Fig. 4).

Priorities for individual taxa vary substantially, although areas in the Southeast and California tend to have higher priority (Fig. 1). These priorities reflect both the concentration of endemics in these regions and the low rate of protection in the Southeast. Importantly, high-priority areas for individual taxa largely do not overlap. For example, although amphibians and reptiles have similar patterns for endemism, their highest priority areas are markedly different, although both are in the Southeast (Fig. 1).

Summing the priority scores across all taxa, the highest-priority areas are mostly in the Southeast, California, and Texas (Fig. 4). These areas cover a relatively small portion of the country, but are inordinately important for biodiversity. They are largely unprotected, although there are exceptions such as Great Smoky Mountains National Park and the Sequoia, Kings Canyon, Yosemite complex in California. Some priority areas likely have already lost habitat. Range maps largely do not reflect contemporary habitat losses. As a result, local conservation actions will need further guidance by using refined biodiversity maps (32–35). Nevertheless, our analysis indicates that remaining habitat in these areas, and potential for restoring habitat, is a top priority for biodiversity conservation.

To improve the coverage of biodiversity, we recommend nine foci, labeled in Fig. 4 and described below. Some priorities remain in public land although with insufficient protection to earn an IUCN ranking. A prime example is the Blue Ridge Mountains along the Tennessee, North Carolina, and Virginia border (labeled 1 in Fig. 4). Much of this region has substantial biodiversity value, but is inadequately protected under its current classification as National Forest. Raising the protection level of these lands, emphasizing ecosystem protection and low-impact recreation over extractive uses, would be a major conservation gain. More difficult may be the priority areas that are mostly private land, where current protection is likely even more limited or nonexistent, and conservation options may be more limited and costly.

Substantial progress in protecting the nation's biodiversity will require improving conservation on both public and private land. On private lands, local and state land trusts are essential, possibly through land purchases, conservation easements, and similar instruments. To save biodiversity, conservation actors must focus greater attention to biodiversity priorities, through analyses such as ours. Failure to do so could mean the extinction of the country's unique species.

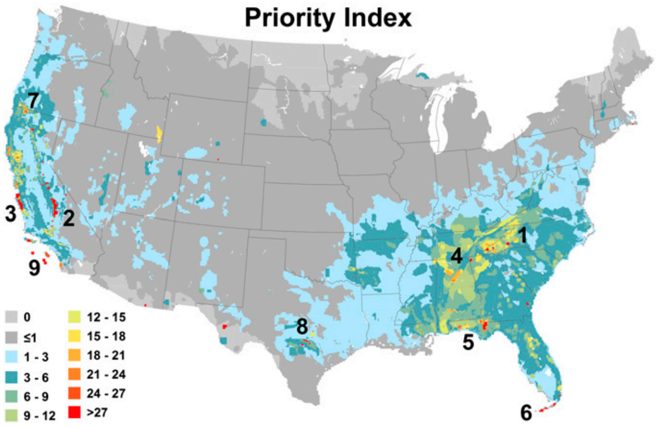

Fig. 4. Summed priority scores across all taxa and recommended priority areas to expand conservation: 1, Middle to southern Blue Ridge Mountains; 2, Sierra Nevada Mountains, particularly the southern section; 3, California Coast Ranges; 4, Tennessee, Alabama, and northern Georgia watersheds; 5, Florida panhandle; 6, Florida Keys; 7, Klamath Mountains, primarily along the border of Oregon and California; 8) South-Central Texas around Austin and San Antonio; 9, Channel Islands of California.

Recommended Priority Areas (See Locations in Fig. 4)

1) *Blue Ridge Mountains*: Particularly the middle to southern sections, including the Cherokee, Nantahala, Pisgah, and Jefferson National Forests. This region is a major priority for amphibians, mainly because of salamanders, and for fish and trees. Much of the area is federal land.
2) *Sierra Nevada Mountains*: Particularly the southern section. This region is a priority mainly because of amphibians and trees. Much of the area is federal land.
3) *California Coast Ranges*: This region is a priority mainly because of trees, amphibians, and mammals. Substantial portions are federal land.
4) *Tennessee, Alabama, northern Georgia watersheds*: This region is a priority mainly because of its exceptional fish diversity, for which it is globally significant. There is also substantial reptile and amphibian diversity in some areas. Most of the region is privately owned.
5) *Florida panhandle*: This region is a priority mainly because of trees, fish, and reptiles. Almost none of the region is within IUCN ranked protected areas. Most of the region is privately owned, but with some federal and state lands.
6) *Florida Keys*: A priority mostly because of trees. A moderate amount of the Keys is within IUCN ranked protected areas and other public lands.
7) *Klamath Mountains*: Primarily along the border of Oregon and California. This priority is mainly because of trees, and somewhat for amphibians and fish. Much of the area is federal land.
8) *South-Central Texas around Austin and San Antonio*: This area represents a cluster of sites that are priorities mainly because of amphibians, but also fish and reptiles. The region is nearly all privately owned.
9) *Channel Islands of California*: The Channel Islands are priorities mainly because of trees, reptiles, and mammals. Significant portions of the islands are within IUCN ranked protected areas, or are federal land.

Results are available in GIS format at BiodiversityMapping.org.

Methods

We mapped diversity by overlaying range maps for terrestrial vertebrates, freshwater fish, and trees, the taxa for which spatial data were sufficient. Range maps for birds were from BirdLife International (36), for amphibians and mammals from IUCN (37), for reptiles and freshwater fish from NatureServe (38, 39), and for trees from the US Geological Survey (40). Some species in the original tree dataset are presently considered subspecies. We merged those into the parent species. Original tree data are available online at: esp.cr.usgs.gov/data/little/.

For all species, we excluded extinct and nonnative species when indicated in the data and parts of species' ranges considered transitory/migratory or outside the native range. For birds, ranges included breeding and nonbreeding range. We excluded seabirds. We also removed the Bachman's Warbler (*Vermivora bachmanii*) and Ivory-billed Woodpecker (*Campephilus principalis*), because they are generally regarded to be extinct.

In selecting species endemic to the study area, we used a 20-km buffer around the Natural Earth (www.naturalearthdata.com) definition of land, including islands. This buffer is to account for inconsistencies between mapped land boundaries and the delimited polygon ranges for terrestrial species. Thus, our definition of species endemic to the study area is somewhat liberal. For birds, we based endemism on the combined breeding and nonbreeding range because our goal is to identify species whose future wholly depends on actions in the United States. There are additional species that are restricted to the study area based on only their breeding (10 species) or nonbreeding (8 species) range. For freshwater fish, we removed some species as endemics based on other sources that indicate their distributions ranged outside the study area (*Strongylura marina*, *Trinectes maculatus*, *Dormitator maculatus*, *Ariopsis felis*, *Acipenser oxyrinchus*, *Lampetra ayresii*, *Spirinchus thaleichthys*, *Thaleichthys pacificus*). For trees, we also checked Kew Botanical Gardens, Tropicos, Global Biodiversity Information Facility, and other online sources for evidence that a species' native range extended outside the United States. We revised databases for taxonomic revisions where feasible.

Data on protected areas were from the PAD-US database (30). We used ArcGIS 10 for maps and analyses. Maps use the Albers Equal Area Conic projection.

ACKNOWLEDGMENTS. We thank Anupam Anand for collating tree-species data and Robert Dunn and Nick Haddad for critical discussions about this study. C.N.J. was supported by the Brazilian agency Coordenação de Aperfeiçoamento de Pessoal de Nivel Superior (CAPES) through Ciência Sem Fronteiras Program A025_2013.

1. Aycrigg JL, et al. (2013) Representation of ecological systems within the protected areas network of the continental United States. *PLoS ONE* 8(1):e54689.
2. Scott JM (1999) A representative biological reserve system for the United States. *Soc Conserv Biol Newsl* 6(2):1–9.
3. Scott JM, et al. (2001) Nature reserves: Do they capture the full range of America's biological diversity? *Ecol Appl* 11(4):999–1007.
4. Rouget M, Richardson DM, Cowling RM (2003) The current configuration of protected areas in the Cape Floristic Region, South Africa—reservation bias and representation of biodiversity patterns and processes. *Biol Conserv* 112(1-2):129–145.
5. Ceballos G, Ehrlich PR, Soberón J, Salazar I, Fay JP (2005) Global mammal conservation: What must we manage? *Science* 309(5734):603–607.
6. Rodrigues ASL, et al. (2004) Effectiveness of the global protected area network in representing species diversity. *Nature* 428(6983):640–643.
7. Rodrigues ASL, et al. (2004) Global gap analysis: Priority regions for expanding the global protected-area network. *Bioscience* 54(12):1092–1100.
8. Araújo MB, Lobo JM, Moreno JC (2007) The effectiveness of Iberian protected areas in conserving terrestrial biodiversity. *Conserv Biol* 21(6):1423–1432.
9. Brooks T, Da Fonseca GAB, Rodrigues ASL (2004) Species, data, and conservation planning. *Conserv Biol* 18(6):1682–1688.
10. Pimm SL, et al. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344(6187):1246752.
11. Dobson AP, Rodriguez JP, Roberts WM, Wilcove DS (1997) Geographic distribution of endangered species in the United States. *Science* 275(5299):550–553.
12. Rutledge DT, Lepczyk CA, Xie J, Liu J (2001) Spatiotemporal dynamics of endangered species hotspots in the United States. *Conserv Biol* 15(2):475–487.
13. Flather CH, Knowles MS, McNees J (2008) Geographic patterns of at-risk species: A technical document supporting the USDA Forest Service Interim Update of the 2000 RPA Assessment. Gen. Tech. Rep. RMRS-GTR-211. (US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO).
14. Stein BA, Scott C, Benton N (2008) Federal lands and endangered species: The role of military and other federal lands in sustaining biodiversity. *Bioscience* 58(4):339–347.
15. Stein BA, Kutner LS (2000) *Precious Heritage: The Status of Biodiversity in the United States*, ed Adams JS (Oxford Univ Press, New York).
16. Hurlbert AH, Jetz W (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proc Natl Acad Sci USA* 104(33):13384–13389.
17. Rondinini C, Wilson KA, Boitani L, Grantham H, Possingham HP (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecol Lett* 9(10):1136–1145.
18. Jetz W, Sekercioglu CH, Watson JEM (2008) Ecological correlates and conservation implications of overestimating species geographic ranges. *Conserv Biol* 22(1):110–119.
19. Colwell RK, Lees DC (2000) The mid-domain effect: Geometric constraints on the geography of species richness. *Trends Ecol Evol* 15(2):70–76.
20. Purvis A, Gittleman JL, Cowlishaw G, Mace GM (2000) Predicting extinction risk in declining species. *Proc Biol Sci* 267(1456):1947–1952.
21. Manne LL, Pimm SL (2001) Beyond eight forms of rarity: Which species are threatened and which will be next. *Anim Conserv* 4:221–229.
22. Manne LL, Brooks TM, Pimm SL (1999) Relative risk of extinction of passerine birds on continents and islands. *Nature* 399(6733):258–261.
23. Jenkins CN, Pimm SL, Joppa LN (2013) Global patterns of terrestrial vertebrate diversity and conservation. *Proc Natl Acad Sci USA* 110(28):E2602–E2610.
24. Stuart SN, et al. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306(5702):1783–1786.
25. Van Houtan KS, Halley JM, Van Aarde R, Pimm SL (2009) Achieving success with small, translocated mammal populations. *Conserv Lett* 2(6):254–262.
26. Alves MAS, et al. (2008) Mapping and exploring the distribution of the Vulnerable grey-winged cotinga Tijuca condita. *Oryx* 42(4):562–566.
27. Scott JM, et al. (2001) Representation of natural vegetation in protected areas: Capturing the geographic range. *Biodivers Conserv* 10:1297–1301.
28. Dietz RW, Czech B (2005) Conservation deficits for the continental United States: An ecosystem gap analysis. *Conserv Biol* 19(5):1478–1487.
29. Jenkins CN, Joppa L (2009) Expansion of the global terrestrial protected area system. *Biol Conserv* 142(10):2166–2174.
30. US Geological Survey, Gap Analysis Program (2012) Protected Areas Database of the United States (PADUS), version 1.3 Combined Feature Class. Accessed July 14, 2013.
31. National Conservation Easement Database (2014) Available at: conservationeasement.us. Accessed August 17, 2014.
32. Jenkins CN, Pimm SL, Alves MAdosS (2011) How conservation GIS leads to Rio de Janeiro, Brazil. *Nat Conserv* 9(2):152–159.
33. Rondinini C, et al. (2011) Global habitat suitability models of terrestrial mammals. *Philos Trans R Soc Lond B Biol Sci* 366(1578):2633–2641.
34. Harris GM, Jenkins CN, Pimm SL (2005) Refining biodiversity conservation priorities. *Conserv Biol* 19(6):1957–1968.
35. Jetz W, Wilcove DS, Dobson AP (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol* 5(6):e157.
36. BirdLife International and NatureServe (2013) *Bird Species Distribution Maps of the World. Version 3.0.* (BirdLife International, Cambridge, UK, and NatureServe, Arlington, VA.).
37. IUCN (2012) *IUCN Red List of Threatened Species*. Version 2012.1. Available at www.iucnredlist.org. Accessed November 21, 2013.
38. NatureServe (2008) *Digital Distribution Maps of the Reptiles of the United States and Canada*. Available at www.natureserve.org. Accessed November 21, 2013.
39. NatureServe (2010) *Digital Distribution Maps of the Freshwater Fishes in the Conterminous United States*. Version 3.0. Available at www.natureserve.org. Accessed November 21, 2013.
40. US Geological Survey (1999) Digital representation of "Atlas of United States Trees" by Elbert L. Little, Jr. Available at gec.cr.usgs.gov/data/little. Accessed September 3, 2013.
41. IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1* (IUCN, Gland, Switzerland).

What Is Conservation Science?

PETER KAREIVA AND MICHELLE MARVIER

In 1985, Michael Soulé asked, "What is conservation biology?" We revisit this question more than 25 years later and offer a revised set of core principles in light of the changed global context for conservation. Most notably, scientists now widely acknowledge that we live in a world dominated by humans, and therefore, the scientific underpinnings of conservation must include a consideration of the role of humans. Today's conservation science incorporates conservation biology into a broader interdisciplinary field that explicitly recognizes the tight coupling of social and natural systems. Emerging priorities include pursuing conservation within working landscapes, rebuilding public support, working with the corporate sector, and paying better attention to human rights and equity. We argue that in conservation, strategies must be promoted that simultaneously maximize the preservation of biodiversity and the improvement of human well-being.

Keywords: conservation science, Anthropocene, biodiversity, ecosystem resilience, ecosystem services

Soulé (1985) helped define the emerging field of conservation biology with an essay that has been read by generations of students and that is now a science citation classic. However, a lot has happened in the world since 1985, and conservation, like any professional and scientific endeavor, needs to continually refresh its intellectual and academic framework to accommodate new ideas and information.

When Soulé wrote his now classic essay, the Society for Conservation Biology (SCB) did not exist, and the journal *Conservation Biology* had not yet been published. Today SCB boasts more than 10,000 members and has grown from an essentially North American society to one that is increasingly global. With over 25 years having passed since the publication of Soulé's foundational essay, it is worth exploring how his early vision for conservation biology might be updated in light of recent developments. In particular, Soulé envisioned the emerging field of conservation biology as the application of biological science to address the problems of species, communities, and ecosystems perturbed by humans. Today, one of the most important intellectual developments is the recognition that ecological dynamics cannot be separated from human dynamics (e.g., Liu et al. 2007, Folke et al. 2011). Therefore, Soulé's original delineation of conservation biology is in need of a broader framework that we label *conservation science* to distinguish it from an enterprise concerned solely with the welfare of nonhuman nature. Unlike conservation biology, conservation science has as a key goal the improvement of human well-being through the management of the environment. If managing the environment to provide human health and safety were the only goal of conservation science, we would probably label it *environmental science*. The distinguishing feature is that in conservation science, strategies to jointly maximize benefits to people and to biodiversity are pursued; it is a discipline that requires the application of both natural and social sciences to the dynamics of coupled human–natural systems.

Still a crisis discipline but evidence based

Soulé (1985) argued that conservation biology differs from many other scientific endeavors because it is a "crisis discipline." According to this line of reasoning, conservation biologists, like medical doctors, are often called on to act rapidly and without complete knowledge of the situation. We agree. However, since Soulé's essay, medicine has undergone a revolution whereby its practitioners increasingly rely on systematically accumulated evidence and meta-analyses of collections of studies rather than on personal experience and word of mouth (Evidence-Based Medicine Working Group 1992). A similar revolution is starting to take hold in conservation (Stewart et al. 2005). For example, in a systematic review of 68 case studies, Waylen and colleagues (2010) identified features of local culture that are associated with the success of community-based conservation efforts. And so, although conservationists continue to face crises, they can increasingly look to a growing body of quantitative evidence for best practices. Unfortunately, in conservation courses and training, the importance of rigorously assembling and weighing evidence is rarely emphasized. Just as modern students of medicine, dentistry, and nutrition take courses in evidence-based practice, so, too, should modern

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BioScience 62: 962–969. ISSN 0006-3568, electronic ISSN 1525-3244. doi:10.1525/bio.2012.62.11.5

students of conservation. Evidence can sometimes yield surprising answers, and relying on evidence rather than on anecdotes or conventional wisdom will make conservation more successful and more cost effective.

Another important development is that conservationists increasingly use data-based decision science to identify which actions in which places will yield the greatest impacts under the constraint of limited resources (Wilson et al. 2007). The application of systematic conservation planning and formal priority setting is now foundational to conservation (Margules and Pressey 2000) and has evolved from a focus almost exclusively on biodiversity to one on multiobjective planning and priority setting (e.g., Nelson E et al. 2009).

Humans and conservation science

In our view, the major shortcoming of Soulé's framing of conservation is its inattention to human well-being. In the traditional view of conservation, people play one of two roles: The vast majority of people are a threat to biodiversity, and a relatively small number—mostly Western biologists—act as biodiversity's protectors and, one hopes, saviors (e.g., Janzen 1986). Looking back on the last 25 years of conservation successes and failures, we see a much richer set of roles for people in conservation. First, conservation is fundamentally an expression of human values (Sarkar 2005). For better or worse, people's attitudes and actions help to shape and reshape the world that will be left behind for future generations. Therefore, the psychology and ethical reasoning that underlie people's actions and views of nature are a key but too often neglected dimension of conservation. Second, biodiversity is not the only entity affected by conservation actions and policies: People's lives and livelihoods also hang in the balance. As a direct result of conservation, economic well-being has, in some instances, been harmed, and there are well-documented instances of human communities having been unjustly displaced and disrupted for the creation of protected areas (Dowie 2009). Clearly, conservation can also benefit people, but the fact that it may disadvantage them highlights the need for paying more attention to the nexus of conservation and human society.

Conservation science that is focused primarily on biology is likely to misdiagnose problems and arrive at ill-conceived solutions. Today, we need a more integrative approach in which the centrality of humans is recognized in the conservation agenda. Although modern conservation science will continue to rely heavily on the biological disciplines, it must also embrace economics, psychology, political science, ethics, business management, marketing, anthropology, and other disciplines spanning the social sciences and humanities (figure 1).

Soulé's guiding principles

To help guide the then-nascent discipline of conservation biology, Soulé laid out four core principles, which he called *functional postulates*, and four core values, or *normative postulates* (see box 1). Soulé's functional postulates are no less true today than they were in 1985, but they are not necessarily what one would consider the essential principles for conservation in today's world. For example, the emphasis on coevolution and natural communities might seem misplaced, given that all around the world, there is now a preponderance of novel ecosystems and assemblages of species that have had little opportunity to coevolve (Hobbs et al. 2009). Thresholds and ecological tipping points certainly remain an important idea, but equally important is the recovery of ecosystems from environmental insults and degradation that in 1985 would have been viewed as irreparably damaging. Conservationists continue to observe the perils of small populations and the loss of genetic variation, but there have also been examples of successful captive breeding programs and the recovery of species from situations that once seemed insurmountable (e.g., Cade and Burnham 2003, Smith and Ferguson 2005). Strict nature reserves still command a great deal of conservation attention, but their sustainability has come into question (Mascia and Pailler 2011), and conservation attention is increasingly aimed at integrating human uses into conservation areas (Brechin et al. 2003) and working in

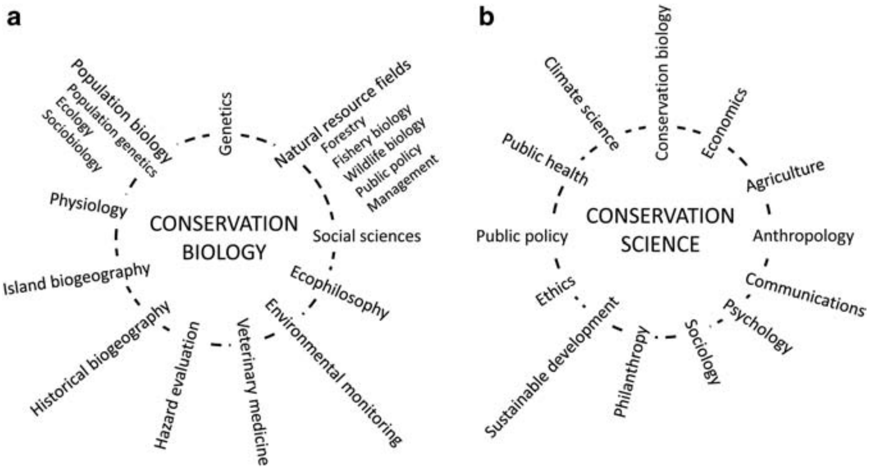

Figure 1. (a) Fields contributing to conservation biology and (b) those contributing to conservation science. In panel (a) is Soulé's (1985) depiction of the synthetic, multidisciplinary nature of conservation biology. Panel (b) depicts an updated view of conservation science, in which the many dimensions of conservation biology are part of a broader and more interdisciplinary endeavor to protect nature. As in Soulé's (1985) original figure, the dashed line indicates that the fields contributing to conservation span the boundaries between "basic" and "applied" research.

Box 1. Functional and normative postulates for the field of conservation biology (Soulé 1985).

Functional postulates

Many of the species that constitute natural communities are the products of coevolutionary processes.

Many, if not all, ecological processes have thresholds below and above which they become discontinuous, chaotic, or suspended.

Genetic and demographic processes have thresholds below which nonadaptive, random forces begin to prevail over adaptive, deterministic forces within populations.

Nature reserves are inherently disequilibrial for large, rare organisms.

Normative postulates

Diversity of organisms is good.

Ecological complexity is good.

Evolution is good.

Biotic diversity has intrinsic value, irrespective of its instrumental or utilitarian value.

landscapes outside of protected-area boundaries (Daily et al. 2003, Polasky et al. 2005).

Similarly, Soulé's normative postulates are not necessarily the leading values among contemporary conservationists. Missing is any mention of ecosystem services, which are now emerging as a primary motivation for conservation. Moreover, human rights and questions about equity and who is responsible for paying for conservation are given scant attention in Soulé's normative statements, whereas such questions of fairness are now at the forefront. Before providing our own updated functional and normative postulates, it is worth summarizing how the context for conservation has changed in the last 25-plus years.

How the global context for conservation has changed since 1985

In 1985, the global human population was 4.8 billion people. Last year, in 2011, the population raced past 7 billion—an increase of more than 40% in one human generation. Pertinent to conservation, this population growth has been and will continue to be most rapid in the very areas of the planet that harbor the highest levels of biodiversity (Cincotta et al. 2000). Therefore, the challenge of accommodating people and biodiversity has escalated dramatically since 1985 and is certain to continue to grow.

Consumption has also increased: Per capita energy use was 1420 kilograms (kg) of oil equivalent in 1985 compared with nearly 1800 kg in 2009 (*http://data.worldbank.org/indicator*). Over roughly the same period, the amount of atmospheric carbon dioxide measured at Mauna Loa increased to 391.6 parts per million (ppm) in 2011 from only 346 ppm in 1985 (NOAA 2012), and in part as a result of rising levels of carbon dioxide and other greenhouse gases, the global mean temperature has increased by approximately 0.5 degrees Celsius over the last 25 years (NASA 2012). Managed ecosystems increasingly dominate the planet. Nearly 40% of Earth's ice-free land has been converted to pastures or croplands to feed people (Ramankutty et al. 2008).

On the positive side, the amount of land under some form of conservation protection has more than doubled since 1985, from a bit more than 6.5 million square kilometers (km^2) to more than 16 million km^2 (IUCN and UNEP-WCMC 2012). Marine protected areas, which constituted less than 1 million km^2 in 1985, now cover some 8.1 million km^2 of marine habitat (*www.wdpa.org*). Therefore, conservation can boast of real success over the past couple of decades, but protected areas alone are not enough to protect biodiversity in the face of increasing human pressures (Mascia and Pailler 2011). Moreover, trends in public attitudes foreshadow a potential crisis in political will for conservation. Evidence of declining public support includes the response to a Gallup poll (*www.gallup.com/poll/1615/environment.aspx*) question that asked respondents to decide whether "protection of the environment should be given priority, even at the risk of curbing economic growth, or [whether] economic growth should be given priority, even if the environment suffers to some extent." In September 1984, 61% of the survey respondents prioritized the environment over the economy. In March 2011, the percentage favoring the environment was only 36%. With the public becoming increasingly indifferent to environmental issues and the environment ranking lower than most other voter priorities, US national policies have become less and less proenvironment (Nordhaus and Shellenberger 2007). On a global scale, the trends are complicated by an overall positive relationship between environmental concern and wealth, but some of the wealthier economies, such as Japan and Germany, are showing stable or declining environmental concern despite economic growth (Franzen and Meyer 2010).

One additional change since 1985 is a generational shift in the experience that children have with nature, largely due to urbanization, less outdoor play, and the dominance of computers and video games in their daily lives. Richard Louv, author of the best-selling book *Last Child in the Woods*, has started a movement to counter this trend, but the data reveal that children are continuing to become less engaged with nature and less knowledgeable about it (Miller 2005, Pergams and Zaradic 2008). For example, kids recognize hundreds of corporate logos but fewer than 10 native plant species (references in Miller 2005). Even children's books reveal the increased detachment of youth from nature; a study of 286 Caldecott Prize–winning children's books since 1938 (and 8036 images therein) showed a steady decline in the frequency with which natural environments and wild animals appeared in these books, to the point that natural environments "have all but disappeared" (Williams et al. 2012, p. 155). With early experiences of nature affecting lifetime support for conservation (Zaradic et al. 2009), the lack of nature experiences for our youth does not bode well.

New postulates for conservation science

As Soulé (1985) did in his essay, we offer a set of fundamental axioms about nature. These axioms help define the context within which conservation science must work.

Functional postulates. First, “pristine nature,” untouched by human influences, does not exist. Scientific assessments of the planet have shown that the effects of human activities are utterly pervasive (Sanderson et al. 2002, Halpern et al. 2008). Birds, fish, and whales in remote arctic oceans have flesh contaminated with chemical pesticides (e.g., Corsolini et al. 2006). The nitrogen and hydrological cycles are dominated by humans; human activities produce 60% of the fixed nitrogen deposited on land each year (Kaiser 2001), and people appropriate more than half of the annual accessible runoff (Postel et al. 1996), leaving little freshwater for other species. Human modifications of habitats include deforestation; the draining of wetlands; the impoundment of rivers; urbanization; pollution; species introductions; climate change; and the overharvest of plants, fish, and other wildlife. Scientists have coined a name for this era, the *Anthropocene*, to emphasize that we have entered a new geological era in which human influences on landcover, biogeochemical cycling, water quality and availability, and other major features of the world now rival or even surpass those attributable to nonanthropogenic forces (Steffen et al. 2007). Of course, pervasive human influence is not a new development; even the supposedly “virgin” rainforests of South America, Asia, and sub-Saharan Africa have, in fact, been subjected to a long history of slash-and-burn agriculture and were once dotted with surprisingly large human settlements (Willis et al. 2004). What has changed is that human domination is now so widespread and profound that it can no longer be ignored in any conservation decision.

In Western conservation, lands and waters relatively untouched by humans have historically been given high priority for protection. The creation of protected areas through the displacement and exclusion of human communities—what some people term *fortress conservation* (Wilshusen et al. 2002)—is an important manifestation of this attachment to places free of human influences. However, given the extensive human effects on the planet and the reality that protecting so-called wilderness may first require moving people out of the area, conservation centered on areas free of people is socially unjust and often scientifically misguided (Guha 1989, Nelson MP and Callicott 2008). Although protected areas will continue to be an important part of conservation, future conservation efforts will, by necessity, be focused increasingly on areas that have been and that will likely continue to be affected by human activities. Moreover, in the face of climate change and species introductions, protected areas will increasingly require active intervention to maintain the feeling of wilderness or other conservation values desired by people (Botkin 1990).

Second, the fate of nature and that of people are deeply intertwined. Human health and well-being depend on clean air, clean water, and an adequate supply of natural resources for food and shelter. Many of the activities that harm biodiversity also harm human well-being. Chemical pollution of air and water is an obvious example in which both human and nonhuman life are harmed. Less obvious, however, is that the destruction of mangrove forests can exacerbate the loss of human life caused by tsunamis or hurricanes (Das and Vincent 2009). Similarly, deforestation in mountainous regions is linked to more severe downstream flooding (Bradshaw et al. 2007). Perversely, attempts to control flooding by creating levees, which often facilitates home building on floodplains, can worsen the damage that floods cause to human lives and livelihoods (Opperman et al. 2009). Clearing tropical forest harms more than just lianas and butterflies; it also destroys an important carbon store and, therefore, contributes to global climate change, with myriad impacts on human food production and safety. All people need functioning, unpolluted ecosystems for everything from food and materials to medicines and protection from natural disasters. The ecosystems that provide these services to humanity are the same ecosystems on which many other species also depend.

Conservation as Soulé framed it was all about protecting biodiversity because species have inherent value. We do not wish to undermine the ethical motivations for conservation action. We argue that nature also merits conservation for very practical and more self-centered reasons concerning what nature and healthy ecosystems provide to humanity. The Millennium Ecosystem Assessment (2005) was the first and largest effort to date in which global trends were assessed in terms of the many products and services that natural ecosystems provide to people. The main conclusion of the assessment was that human activities have, over the last 50 years, reduced nature’s ability to provide two-thirds of the world’s ecosystem services. This should serve as a call to conservation action. It is not just biodiversity that is at risk; it is also human health and happiness.

Third, nature can be surprisingly resilient. Nature is often portrayed as fragile, and conservationists routinely talk about damages as catastrophic and irreparable (e.g., a Google Scholar search on 3 April 2012 for *ecosystem* and either *irreparable* or *irreversible* returned more than 40,000 hits). The reality, however, is that nature often rebounds from even severe perturbations (Jones and Schmitz 2009). For example, many marine ecosystems have recovered completely after severe oil spills. Similarly, lakes can undergo surprising recovery following eutrophication if the excessive phosphorous inputs are curtailed. The near-total deforestation of Puerto Rico offers another example of nature’s resilience. On the basis of species–area curves (an approach recently shown to be flawed; He and Hubbell 2011), one would predict that the denuding of Puerto Rican forests should have caused forest birds to dwindle to only one or two species. However, the bird fauna remained almost completely intact, because many species found refuge in coffee plantations and because the forests regrew before the bird species declined to extinction (Lugo 1988). Marine ecosystems are proving equally resilient. Even in the once highly overfished Baltic Sea, cod is making a surprisingly fast comeback (Cardinale and Svedäng 2011), and the Bikini Atoll, which was vaporized by a hydrogen bomb in 1954, today harbors a greater diversity of coral species than it did before the explosion (Richards et al. 2008).

The ability of nature to recover from many types of insult does not provide humans license to inflict unfettered environmental damage. Recovery occurs only after humans stop polluting, overfishing, and clearcutting, and even then, nature might rebound in ways that are unexpected and novel. Moreover, nature is not universally resilient; in some cases, ecosystems can undergo a state change from which recovery is unlikely on timescales relevant to humans. Nonetheless, the prevalence of recovery is a very different story from the apocalyptic collapse of ecosystems that environmentalists commonly herald, and conservationists should take advantage of the natural resilience of ecosystems.

Fourth, human communities can avoid the tragedy of the commons. Hardin (1968) profoundly influenced how conservationists view the world. According to Hardin, any unregulated commonly shared resource such as fisheries, forests, or water will be overexploited, because individuals will invariably act in their own short-term self-interest. If one accepts the inevitability of the tragedy of the commons, the only ways to practice conservation are to enact strict regulations and restrictions or to simply buy and protect the resource directly.

Analyses by Nobel-prize winning economist Elinor Ostrom (2009) challenged the inevitability of the tragedy of the commons. Specifically, Ostrom discovered that communities will impose costs to themselves to sustainably manage resources when the benefits of such management are transparent and the potential for cheating is sufficiently reduced. The implications of these findings for conservation are profound. Instead of relying on national governments to impose restrictions or on the endless involvement of nongovernmental organizations, sustainable conservation can be achieved by empowering local people to make decisions for themselves.

Finally, the "flat world" (*sensu* Friedman 2005) means that local conservation efforts are deeply connected to global forces. The meme of thinking globally and acting locally is no longer sufficient. No matter how effectively a nation or community reduces its carbon emissions, climate change may still take its toll if the rest of the world continues to spew carbon dioxide. The long-range transport of air pollutants similarly links continents in ways never before anticipated (National Research Council 2009). Global trade and the demand for food or biofuels can drive massive conversion of forests to meet agricultural demands (Pearce 2012) or poaching of African rhinos and elephants to meet demands in China (Milner-Gulland 1993, Naylor 2005). Therefore, conservationists need to worry as much about deliberations of the World Trade Organization as they do about designing networks of protected areas.

Normative postulates for conservation science. Soulé's normative postulates were statements of values and tenets of a potential ecological philosophy meant to guide conservation actions. We deviate from this approach and, instead, offer practical statements of what conservation should do in order to succeed.

First, conservation must occur within human-altered landscapes. Ecosystems that have undergone extensive human modification have traditionally been neglected by conservationists. However, the desire to focus efforts solely on pristine places is becoming increasingly unrealistic. Because of anthropogenic climate change, extensive conversion of habitats for human use, and a flood of introduced species, the world increasingly consists of novel ecosystems and working landscapes.

That no place is free of human influence does not mean that a large, mature forest has the same conservation value as a plantation or an urban playground. However, when conservationists do place a high priority on landscapes perceived to be the least impacted by humans, it is key that they recognize that people have nonetheless probably been a part of the history of these systems and that humans are also likely to inhabit and make a living from some of the world's wildest places. In these places, protection should protect the people as well as the biodiversity.

The strategy of moving people off of their land has sometimes backfired for conservation, because human activities such as setting fires, grazing livestock, or hunting were responsible for maintaining the conservation value of the landscape (Martinez 2003). For example, a ban on livestock grazing in India's Keoladeo Ghana National Park led to a serious decline in the park's habitat quality (Vijayan 1987, Lewis 2003). Many existing protected areas are working well, and the protected-areas strategy should certainly not be abandoned. However, there are many places where removing people or banning their activities simply will not work. The good news is that even highly modified ecosystems can offer significant conservation value in terms of both biodiversity and ecosystem services (e.g., Daily et al. 2003). Conservation needs complementary strategies that simultaneously maximize the protection of nature and that of human well-being in the areas where people hunt, harvest, and live.

Second, conservation will be a durable success only if people support conservation goals. As Nordhaus and Shellenberger (2007) noted, Martin Luther King Jr.'s famous "I have a dream" speech would have led nowhere if he had framed his message as "I have a nightmare," yet this is exactly the sort of message of hopelessness that conservationists too often deliver (Miller 2005). Because the success or failure of conservation depends heavily on whether human behaviors can be changed (Mascia et al. 2003, Ehrlich and Kennedy 2005), conservationists should pay greater attention to human psychology and the impact of their messages on people. One strategy to increase support for conservation would be focused on children and reconnecting them with nature. Another strategy is to broaden the concerns of conservation beyond biodiversity and also to pay attention to economic development, jobs, poverty, and environmental justice. However, conservationists often reject activities aimed at poverty reduction and economic development as mission drift (Salafsky 2011). We do not agree with accusations of mission drift; we see poverty alleviation as a central concern, because conservation can succeed only if people embrace its mission.

Third, conservationists must work with corporations. A small number of global corporations have a huge impact on land conversion, mining, energy extraction, and consumer choices. In essence, corporations are the "keystone species" of global ecosystems. Obviously, corporate practices, just like the actions of individuals, governments, and even religions, can be damaging to the environment, but there is a simple reality that must be faced: Through the resources that they use and the wastes that they produce, corporations drive much of what happens to our lands and waters. One cannot expect corporations to go away, nor would anyone who cared about people's lives want them to; therefore, part of the solution is to work with corporations to improve their practices. However, conservationists are prone to vilifying large corporations and rejecting attempts by conservation organizations to work with them (Choudry 2003).

We do not view working with corporations as merely a necessary evil; in fact, corporations can be a positive force in conservation. In 1997, Unilever, one of the world's largest consumer goods corporations, and the World Wildlife Fund jointly launched the Marine Stewardship Council (MSC), a program that certifies sustainably harvested fisheries. In 2010, 12% of the global harvest of wild seafood for human consumption was MSC certified (Howes 2010). More challenging, perhaps, are corporations involved in mining and resource extraction, for which, it would seem, negative impacts on the environment are inevitable, but even here, there are bright spots. For example, in 2004, Rio Tinto adopted the corporate goal that its operations should yield no net loss of biodiversity (Rio Tinto 2008). Although Rio Tinto's goals may seem unrealistic, the company has undertaken an ambitious monitoring program to track its net impacts, which is more than can be said of most conservation nongovernmental organizations.

Greenwashing, whereby corporations provide mere lip service to sustainability but continue their environmentally destructive practices, is a real threat. This does not mean that conservationists should turn away from working with corporations; the influences of corporations on the natural world are simply too large to neglect. It does mean, however, that conservationists need to be savvy about how they engage with corporations.

Fourth, only by seeking to jointly maximize conservation and economic objectives is conservation likely to succeed. Win–win outcomes for people and nature are possible, and discovering their preconditions should be a focus of research (Kareiva et al. 2008). In other cases, there may be trade-offs between conservation and economic development, but actively seeking to optimize both conservation and economic goals can minimize those trade-offs (Kareiva 2012). Modern advances in trade-off analyses and multiobjective planning approaches have integrated social science, business practices, and economics with planning approaches that were formerly focused only on biodiversity (Planning Evolution Team 2011). In addition, although they are not yet a feature of conservation strategy development, conservation could benefit greatly from systematic bright-spot analyses as a way of accelerating progress (Heath and Heath 2010). This approach, which involves looking for rare successes and trying to duplicate the conditions associated with success, is common in public health and business but largely absent from conservation practice.

Finally, conservation must not infringe on human rights and must embrace the principles of fairness and gender equity. The people who have been pushed off their lands and hunting grounds in the name of conservation overwhelmingly tend to be poor and politically marginalized. This is, quite simply, unacceptable. Obviously, life is not always fair, but conservationists should not make it less so. If there are costs to conservation, conservationists must find ways to ensure that those costs are borne by people who can afford them. In addition, women in much of the world have few rights and little input into decisions. Although this might not seem relevant to conservation, research reveals that when women are involved in resource decisions, those decisions are more likely to support sustainable resource management than if men alone control the resources (Shandra et al. 2008, Agarwal 2009).

People deserve a voice in their own fates as well as in the fates of the lands and waters they rely on. Not only is this arguably the right thing to do from an ethical perspective, it will probably improve conservation outcomes. When communities self-organize to manage their local resources, their efforts are more effective than top-down approaches (Ostrom and Nagendra 2006).

Conclusions

In the concluding paragraph of his essay, Soulé acknowledged that we cannot reverse history and restore the world to a prelapsarian past. He suggested that conservation can potentially reduce the rate of extinction, improve the management of wildlands, and mitigate the impacts of technologies. *Conservation* as it was defined by Soulé is reactive and on the defensive; its goal is to minimize losses and, to the extent that this is possible, to maintain the world as it once was. Although we share Soulé's nostalgia and similarly hope that majestic species such as the wolves and grizzly bears of the United States will not be lost to extinction, we are also relatively certain that these species will never be as abundant and widespread as they once were. Some realism is in order. Given the magnitude of human impacts and change, conservation cannot look only to the past. Instead, it must be about choosing a future for people and nature. Forward-looking conservation protects natural habitats where people live and extract resources and works with corporations to find mixes of economic and conservation activities that blend development with a concern for nature. It also seeks value in novel ecosystems and remains open to some of nature's modern experiments, such as the recent evolution of large coyotes in North America that have received genes from wolves that make them bigger and more capable of taking down deer and even elk (Levy 2012). Increasingly, conservation will entail grand restoration projects on the scale of whole ecosystems—an ambition every bit as necessary as creating networks of protected areas. Our vision of conservation science differs from earlier framings of conservation biology in large part because we believe that nature can prosper so long as people see conservation as something that sustains and enriches their own lives. In summary, we are advocating conservation *for* people rather than *from* people.

Acknowledgments

We are grateful to Sahotra Sarkar for his helpful review and suggestions and to the many conservation scientists at The Nature Conservancy, who have opened our eyes to where the future lies for conservation science.

References cited

Agarwal B. 2009. Gender and forest conservation: The impact of women's participation in community forest governance. Ecological Economics 68: 2785–2799.

Botkin DB. 1990. Discordant Harmonies: A New Ecology for the Twenty-First Century. Oxford University Press.

Bradshaw CJA, Sodhi NS, Peh KS-H, Brook BW. 2007. Global evidence that deforestation amplifies flood risk and severity in the developing world. Global Change Biology 13: 2379–2395.

Brechin SR, Wilshusen PR, Fortwangler CL, West PC, eds. 2003. Contested Nature: Promoting International Biodiversity with Social Justice in the Twenty-First Century. State University of New York Press.

Cade TJ, Burnham W. 2003. Return of the Peregrine: A North American Saga of Tenacity and Teamwork. The Peregrine Fund.

Cardinale M, Svedäng H. 2011. The beauty of simplicity in science: Baltic cod stock improves rapidly in a 'cod hostile' ecosystem state. Marine Ecology Progress Series 425: 297–301.

Choudry A. 2003. Conservation International: Privatizing nature, plundering biodiversity. Seedling (October 2003): 17–21.

Cincotta RP, Wisnewski J, Engelman R. 2000. Human populations in the biodiversity hotspots. Nature 404: 990–992.

Corsolini S, Covaci A, Ademollo N, Focardi S, Schepens P. 2006. Occurrence of organochlorine pesticides (OCPs) and their enantiomeric signatures, and concentrations of polybrominated diphenyl ethers (PBDEs) in the Adélie penguin food web, Antarctica. Environmental Pollution 140: 371–382.

Daily GC, Ceballos G, Pacheco J, Suzán G, Sánchez-Azofeifa A. 2003. Countryside biogeography of Neotropical mammals: Conservation opportunities in agricultural landscapes of Costa Rica. Conservation Biology 17: 1814–1826.

Das S, Vincent JR. 2009. Mangroves protected villages and reduced death toll during Indian super cyclone. Proceedings of the National Academy of Sciences 106: 7357–7360.

Dowie M. 2009. Conservation Refugees: The Hundred-Year Conflict between Global Conservation and Native Peoples. MIT Press.

Ehrlich PR, Kennedy D. 2005. Millennium assessment of human behavior. Science 309: 562–563.

Evidence-Based Medicine Working Group. 1992. Evidence-based medicine: A new approach to teaching the practice of medicine. Journal of the American Medical Association 268: 2420–2425.

Folke C, et al. 2011. Reconnecting to the biosphere. Ambio 40: 719–738.

Franzen A, Meyer R. 2010. Environmental attitudes in cross-national perspective: A multilevel analysis of the ISSP 1993 and 2000. European Sociological Review 26: 219–234.

Friedman T. 2005. The World Is Flat: A Brief History of the Twenty-First Century. Farrar, Straus and Giroux.

Guha R. 1989. Radical American environmentalism and wilderness preservation: A third world critique. Environmental Ethics 11: 71–83.

Halpern BS, et al. 2008. A global map of human impact on marine ecosystems. Science 319: 948–952.

Hardin G. 1968. The tragedy of the commons. Science 162: 1243–1248.

He F, Hubbell SP. 2011. Species–area relationships always overestimate extinction rates from habitat loss. Nature 473: 368–371.

Heath C, Heath D. 2010. Switch: How to Change Things When Change Is Hard. Crown Business.

Hobbs RJ, Higgs E, Harris JA. 2009. Novel ecosystems: Implications for conservation and restoration. Trends in Ecology and Evolution 24: 599–605.

Howes R. 2010. Building a market for sustainable fisheries. McKinsey and Company. (25 August 2012; *http://voices.mckinseyonsociety.com/building-a-market-for-sustainable-fisheries/*)

[IUCN and UNEP-WCMC] International Union for Conservation of Nature and United Nations Environment Programme World Conservation Monitoring Centre. 2012. The World Database on Protected Areas (WDPA): February 2012. (25 August 2012; *www.wdpa.org/resources/statistics/2012WDPA_Growth_Chart_Extent.xlsx*)

Janzen DH. 1986. The future of tropical ecology. Annual Review of Ecology and Systematics 17: 305–324.

Jones HP, Schmitz OJ. 2009. Rapid recovery of damaged ecosystems. PLOS ONE 4 (art. e5653). doi:10.1371/journal.pone.0005653

Kaiser J. 2001. The other global pollutant: Nitrogen proves tough to curb. Science 294: 1268–1269.

Kareiva P. 2012. Dam choices: Analyses for multiple needs. Proceedings of the National Academy of Sciences 109: 5553–5554. doi:10.1073/pnas.1203263109

Kareiva P, Chang A, Marvier M. 2008. Development and conservation goals in World Bank projects. Science 321: 1638–1639.

Levy S. 2012. Rise of the coyote: The new top dog. Nature 485: 296–297.

Lewis M. 2003. Cattle and conservation at Bharatpur: A case study in science and advocacy. Conservation and Society 1: 1–21.

Liu J, et al. 2007. Complexity of coupled human and natural systems. Science 317: 1513–1516.

Lugo AE. 1988. Estimating reductions in the diversity of tropical forest species. Pages 58–70 in Wilson EO, Peter FM, eds. Biodiversity. National Academies Press.

Margules CR, Pressey RL. 2000. Systematic conservation planning. Nature 405: 243–253.

Martinez D. 2003. Protected areas, indigenous peoples, and the Western idea of nature. Ecological Restoration 21: 247–250.

Mascia MB, Pailler S. 2011. Protected area downgrading, downsizing, and degazettement (PADDD) and its conservation implications. Conservation Letters 4: 9–20.

Mascia MB, Brosius JP, Dobson TA, Forbes BC, Horowitz L, McKean MA, Turner NJ. 2003. Conservation and the social sciences. Conservation Biology 17: 649–650.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-being: Synthesis. Island Press.

Miller JR. 2005. Biodiversity conservation and the extinction of experience. Trends in Ecology and Evolution 20: 430–434.

Milner-Gulland EJ. 1993. An econometric analysis of consumer demand for ivory and rhino horn. Environmental and Resource Economics 3: 73–95.

NASA. 2012. GISS Surface Temperature Analysis. NASA. (21 August 2012; *http://data.giss.nasa.gov/gistemp*)

National Research Council. 2009. Global Sources of Local Pollution: An Assessment of Long-Range Transport of Key Air Pollutants to and from the United States. National Academies Press.

Naylor RT. 2005. The underworld of ivory. Crime, Law and Social Change 42: 261–295.

Nelson E, et al. 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Frontiers in Ecology and the Environment 7: 4–11.

Nelson MP, Callicott JB, eds. 2008. The Wilderness Debate Rages On: Continuing the Great New Wilderness Debate. University of Georgia Press.

[NOAA] National Oceanic and Atmospheric Administration. 2012. ESRL data. (April 3, 2012 *ftp://ftp.cmdl.noaa.gov/ccg/co2/trends/co2_annmean_mlo.txt*)

Nordhaus T, Shellenberger M. 2007. Break Through: From the Death of Environmentalism to the Politics of Possibility. Houghton Mifflin.

Opperman JJ, Galloway GE, Fargione J, Mount JF, Richter BD, Secchi S. 2009. Sustainable floodplains through large-scale reconnection to rivers. Science 326: 1487–1488.

Ostrom E. 2009. A general framework for analyzing sustainability of social-ecological systems. Science 325: 419–422.

Ostrom E, Nagendra H. 2006. Insights on linking forests, trees, and people from the air, on the ground, and in the laboratory. Proceedings of the National Academy of Sciences 103: 19224–19231.

Pearce F. 2012. The Land Grabbers: The New Fight over Who Owns the Earth. Beacon Press.

Pergams ORW, Zaradic PA. 2008. Evidence for a fundamental and pervasive shift away from nature-based recreation. Proceedings of the National Academy of Sciences 105: 2295–2300.

Planning Evolution Team. 2011. Planning for Tomorrow's Challenges: Recommendations of the Planning Evolution Team. The Nature Conservancy. (21 August 2012; *www.conservationgateway.org/file/report-planning-tomorrow%E2%80%99s-challenges-recommendations-planning-evolution-team*)

Polasky S, Nelson E, Lonsdorf E, Fackler P, Starfield A. 2005. Conserving species in a working landscape: Land use with biological and economic objectives. Ecological Applications 15: 1387–1401.

Postel SL, Daily GC, Ehrlich PR. 1996. Human appropriation of renewable fresh water. Science 271: 785–788.

Ramankutty N, Evan AT, Monfreda C, Foley JA. 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. Global Biogeochemical Cycles 22 (art. GB1003). doi:10.1029/2007GB002952

Richards ZT, Beger M, Pinca S, Wallace CC. 2008. Bikini Atoll coral biodiversity resilience five decades after nuclear testing. Marine Pollution Bulletin 56: 503–515.

Rio Tinto. 2008. Rio Tinto and Biodiversity: Achieving Results on the Ground. Rio Tinto. (21 August 2012; *www.riotinto.com/documents/ReportsPublications/RTBidoversitystrategyfinal.pdf*)

Salafsky N. 2011. Integrating development with conservation: A means to a conservation end, or a mean end to conservation? Biological Conservation 144: 973–978.

Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wennebo AV, Woolmer G. 2002. The human footprint and the last of the wild. BioScience 52: 891–904.

Sarkar S. 2005. Biodiversity and Environmental Philosophy: An Introduction. Cambridge University Press.

Shandra JM, Shandra CL, London B. 2008. Women, non-governmental organizations and deforestation: A cross-national study. Population and Environment 30: 48–72.

Smith DW, Ferguson G. 2005. Decade of the Wolf: Returning the Wild to Yellowstone. Lyons Press.

Soulé ME. 1985. What is conservation biology? BioScience 35: 727–734.

Steffen W, Crutzen PJ, McNeill JR. 2007. The Anthropocene: Are humans now overwhelming the great forces of nature? Ambio 36: 614–621.

Stewart GB, Coles CF, Pullin AS. 2005. Applying evidence-based practice in conservation management: Lessons from the first systematic review and dissemination projects. Biological Conservation 126: 270–278.

Vijayan VS. 1987. Keoladeo National Park Ecology Study: Report Jan to June 1987. Bombay Natural History Society.

Waylen KA, Fischer A, McGowan PJK, Thirgood SJ, Milner-Gulland EJ. 2010. Effect of local cultural context on the success of community-based conservation interventions. Conservation Biology 24: 1119–1129.

Williams JA Jr, Podeschi C, Palmer N, Schwadel P, Meyler D. 2012. The human-environment dialog in award-winning children's picture books. Sociological Inquiry 82: 145–159.

Willis KJ, Gillson L, Brncic TM. 2004. How "virgin" is virgin rainforest? Science 304: 402–403.

Wilshusen PR, Brechin SR, Fortwangler CL, West PC. 2002. Reinventing a square wheel: Critique of a resurgent "protection paradigm" in international biodiversity conservation. Society and Natural Resources 15: 17–40.

Wilson KA, et al. 2007. Conserving biodiversity efficiently: What to do, where, and when. PLOS Biology 5 (art. e223): 1850–1861. doi:10.1371/journal.pbio.0050223

World Bank. 2012. World Development Indicators. (25 August 2012; *http://data.worldbank.org/indicator/EG.USE.PCAP.KG.OE*)

Zaradic PA, Pergams ORW, Kareiva P. 2009. The impact of nature experience on willingness to support conservation. PLOS ONE 4 (art. e7367). doi:10.1371/journal.pone.0007367

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The Tragedy of the Commons
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Source: *Science*, New Series, Vol. 162, No. 3859 (Dec. 13, 1968), pp. 1243-1248
Published by: American Association for the Advancement of Science
Stable URL: http://www.jstor.org/stable/1724745
Accessed: 27-08-2014 01:23 UTC

The Tragedy of the Commons

The population problem has no technical solution; it requires a fundamental extension in morality.

Garrett Hardin

At the end of a thoughtful article on the future of nuclear war, Wiesner and York (*1*) concluded that: "Both sides in the arms race are . . . confronted by the dilemma of steadily increasing military power and steadily decreasing national security. *It is our considered professional judgment that this dilemma has no technical solution.* If the great powers continue to look for solutions in the area of science and technology only, the result will be to worsen the situation."

I would like to focus your attention not on the subject of the article (national security in a nuclear world) but on the kind of conclusion they reached, namely that there is no technical solution to the problem. An implicit and almost universal assumption of discussions published in professional and semipopular scientific journals is that the problem under discussion has a technical solution. A technical solution may be defined as one that requires a change only in the techniques of the natural sciences, demanding little or nothing in the way of change in human values or ideas of morality.

In our day (though not in earlier times) technical solutions are always welcome. Because of previous failures in prophecy, it takes courage to assert that a desired technical solution is not possible. Wiesner and York exhibited this courage; publishing in a science journal, they insisted that the solution to the problem was not to be found in the natural sciences. They cautiously qualified their statement with the phrase, "It is our considered professional judgment. . . ." Whether they were right or not is not the concern of the present article. Rather, the concern here is with the important concept of a class of human problems which can be called "no technical solution problems," and, more specifically, with the identification and discussion of one of these.

It is easy to show that the class is not a null class. Recall the game of tick-tack-toe. Consider the problem, "How can I win the game of tick-tack-toe?" It is well known that I cannot, if I assume (in keeping with the conventions of game theory) that my opponent understands the game perfectly. Put another way, there is no "technical solution" to the problem. I can win only by giving a radical meaning to the word "win." I can hit my opponent over the head; or I can drug him; or I can falsify the records. Every way in which I "win" involves, in some sense, an abandonment of the game, as we intuitively understand it. (I can also, of course, openly abandon the game—refuse to play it. This is what most adults do.)

The class of "No technical solution problems" has members. My thesis is that the "population problem," as conventionally conceived, is a member of this class. How it is conventionally conceived needs some comment. It is fair to say that most people who anguish over the population problem are trying to find a way to avoid the evils of overpopulation without relinquishing any of the privileges they now enjoy. They think that farming the seas or developing new strains of wheat will solve the problem—technologically. I try to show here that the solution they seek cannot be found. The population problem cannot be solved in a technical way, any more than can the problem of winning the game of tick-tack-toe.

What Shall We Maximize?

Population, as Malthus said, naturally tends to grow "geometrically," or, as we would now say, exponentially. In a finite world this means that the per capita share of the world's goods must steadily decrease. Is ours a finite world?

A fair defense can be put forward for the view that the world is infinite; or that we do not know that it is not. But, in terms of the practical problems that we must face in the next few generations with the foreseeable technology, it is clear that we will greatly increase human misery if we do not, during the immediate future, assume that the world available to the terrestrial human population is finite. "Space" is no escape (*2*).

A finite world can support only a finite population; therefore, population growth must eventually equal zero. (The case of perpetual wide fluctuations above and below zero is a trivial variant that need not be discussed.) When this condition is met, what will be the situation of mankind? Specifically, can Bentham's goal of "the greatest good for the greatest number" be realized?

No—for two reasons, each sufficient by itself. The first is a theoretical one. It is not mathematically possible to maximize for two (or more) variables at the same time. This was clearly stated by von Neumann and Morgenstern (*3*), but the principle is implicit in the theory of partial differential equations, dating back at least to D'Alembert (1717–1783).

The second reason springs directly from biological facts. To live, any organism must have a source of energy (for example, food). This energy is utilized for two purposes: mere maintenance and work. For man, maintenance of life requires about 1600 kilocalories a day ("maintenance calories"). Anything that he does over and above merely staying alive will be defined as work, and is supported by "work calories" which he takes in. Work calories are used not only for what we call work in common speech; they are also required for all forms of enjoyment, from swimming and automobile racing to playing music and writing poetry. If our goal is to maximize population it is obvious what we must do: We must make the work calories per person approach as close to zero as possible. No gourmet meals, no vacations, no sports, no music, no literature, no art. . . . I think that everyone will grant, without

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The author is professor of biology, University of California, Santa Barbara. This article is based on a presidential address presented before the meeting of the Pacific Division of the American Association for the Advancement of Science at Utah State University, Logan, 25 June 1968.

argument or proof, that maximizing population does not maximize goods. Bentham's goal is impossible.

In reaching this conclusion I have made the usual assumption that it is the acquisition of energy that is the problem. The appearance of atomic energy has led some to question this assumption. However, given an infinite source of energy, population growth still produces an inescapable problem. The problem of the acquisition of energy is replaced by the problem of its dissipation, as J. H. Fremlin has so wittily shown (*4*). The arithmetic signs in the analysis are, as it were, reversed; but Bentham's goal is still unobtainable.

The optimum population is, then, less than the maximum. The difficulty of defining the optimum is enormous; so far as I know, no one has seriously tackled this problem. Reaching an acceptable and stable solution will surely require more than one generation of hard analytical work—and much persuasion.

We want the maximum good per person; but what is good? To one person it is wilderness, to another it is ski lodges for thousands. To one it is estuaries to nourish ducks for hunters to shoot; to another it is factory land. Comparing one good with another is, we usually say, impossible because goods are incommensurable. Incommensurables cannot be compared.

Theoretically this may be true; but in real life incommensurables *are* commensurable. Only a criterion of judgment and a system of weighting are needed. In nature the criterion is survival. Is it better for a species to be small and hideable, or large and powerful? Natural selection commensurates the incommensurables. The compromise achieved depends on a natural weighting of the values of the variables.

Man must imitate this process. There is no doubt that in fact he already does, but unconsciously. It is when the hidden decisions are made explicit that the arguments begin. The problem for the years ahead is to work out an acceptable theory of weighting. Synergistic effects, nonlinear variation, and difficulties in discounting the future make the intellectual problem difficult, but not (in principle) insoluble.

Has any cultural group solved this practical problem at the present time, even on an intuitive level? One simple fact proves that none has: there is no prosperous population in the world today that has, and has had for some time, a growth rate of zero. Any people that has intuitively identified its optimum point will soon reach it, after which its growth rate becomes and remains zero.

Of course, a positive growth rate might be taken as evidence that a population is below its optimum. However, by any reasonable standards, the most rapidly growing populations on earth today are (in general) the most miserable. This association (which need not be invariable) casts doubt on the optimistic assumption that the positive growth rate of a population is evidence that it has yet to reach its optimum.

We can make little progress in working toward optimum poulation size until we explicitly exorcize the spirit of Adam Smith in the field of practical demography. In economic affairs, *The Wealth of Nations* (1776) popularized the "invisible hand," the idea that an individual who "intends only his own gain," is, as it were, "led by an invisible hand to promote . . . the public interest" (*5*). Adam Smith did not assert that this was invariably true, and perhaps neither did any of his followers. But he contributed to a dominant tendency of thought that has ever since interfered with positive action based on rational analysis, namely, the tendency to assume that decisions reached individually will, in fact, be the best decisions for an entire society. If this assumption is correct it justifies the continuance of our present policy of laissez-faire in reproduction. If it is correct we can assume that men will control their individual fecundity so as to produce the optimum population. If the assumption is not correct, we need to reexamine our individual freedoms to see which ones are defensible.

Tragedy of Freedom in a Commons

The rebuttal to the invisible hand in population control is to be found in a scenario first sketched in a little-known pamphlet (*6*) in 1833 by a mathematical amateur named William Forster Lloyd (1794–1852). We may well call it "the tragedy of the commons," using the word "tragedy" as the philosopher Whitehead used it (*7*): "The essence of dramatic tragedy is not unhappiness. It resides in the solemnity of the remorseless working of things." He then goes on to say, "This inevitableness of destiny can only be illustrated in terms of human life by incidents which in fact involve unhappiness. For it is only by them that the futility of escape can be made evident in the drama."

The tragedy of the commons develops in this way. Picture a pasture open to all. It is to be expected that each herdsman will try to keep as many cattle as possible on the commons. Such an arrangement may work reasonably satisfactorily for centuries because tribal wars, poaching, and disease keep the numbers of both man and beast well below the carrying capacity of the land. Finally, however, comes the day of reckoning, that is, the day when the long-desired goal of social stability becomes a reality. At this point, the inherent logic of the commons remorselessly generates tragedy.

As a rational being, each herdsman seeks to maximize his gain. Explicitly or implicitly, more or less consciously, he asks, "What is the utility *to me* of adding one more animal to my herd?" This utility has one negative and one positive component.

1) The positive component is a function of the increment of one animal. Since the herdsman receives all the proceeds from the sale of the additional animal, the positive utility is nearly +1.

2) The negative component is a function of the additional overgrazing created by one more animal. Since, however, the effects of overgrazing are shared by all the herdsmen, the negative utility for any particular decision-making herdsman is only a fraction of −1.

Adding together the component partial utilities, the rational herdsman concludes that the only sensible course for him to pursue is to add another animal to his herd. And another; and another. . . . But this is the conclusion reached by each and every rational herdsman sharing a commons. Therein is the tragedy. Each man is locked into a system that compels him to increase his herd without limit—in a world that is limited. Ruin is the destination toward which all men rush, each pursuing his own best interest in a society that believes in the freedom of the commons. Freedom in a commons brings ruin to all.

Some would say that this is a platitude. Would that it were! In a sense, it was learned thousands of years ago, but natural selection favors the forces of psychological denial (*8*). The individual benefits as an individual from his ability to deny the truth even though society as a whole, of which he is a part, suffers.

Education can counteract the natural tendency to do the wrong thing, but the inexorable succession of generations requires that the basis for this knowledge be constantly refreshed.

A simple incident that occurred a few years ago in Leominster, Massachusetts, shows how perishable the knowledge is. During the Christmas shopping season the parking meters downtown were covered with plastic bags that bore tags reading: "Do not open until after Christmas. Free parking courtesy of the mayor and city council." In other words, facing the prospect of an increased demand for already scarce space, the city fathers reinstituted the system of the commons. (Cynically, we suspect that they gained more votes than they lost by this retrogressive act.)

In an approximate way, the logic of the commons has been understood for a long time, perhaps since the discovery of agriculture or the invention of private property in real estate. But it is understood mostly only in special cases which are not sufficiently generalized. Even at this late date, cattlemen leasing national land on the western ranges demonstrate no more than an ambivalent understanding, in constantly pressuring federal authorities to increase the head count to the point where overgrazing produces erosion and weed-dominance. Likewise, the oceans of the world continue to suffer from the survival of the philosophy of the commons. Maritime nations still respond automatically to the shibboleth of the "freedom of the seas." Professing to believe in the "inexhaustible resources of the oceans," they bring species after species of fish and whales closer to extinction (*9*).

The National Parks present another instance of the working out of the tragedy of the commons. At present, they are open to all, without limit. The parks themselves are limited in extent—there is only one Yosemite Valley—whereas population seems to grow without limit. The values that visitors seek in the parks are steadily eroded. Plainly, we must soon cease to treat the parks as commons or they will be of no value to anyone.

What shall we do? We have several options. We might sell them off as private property. We might keep them as public property, but allocate the right to enter them. The allocation might be on the basis of wealth, by the use of an auction system. It might be on the basis of merit, as defined by some agreed-upon standards. It might be by lottery. Or it might be on a first-come, first-served basis, administered to long queues. These, I think, are all the reasonable possibilities. They are all objectionable. But we must choose—or acquiesce in the destruction of the commons that we call our National Parks.

Pollution

In a reverse way, the tragedy of the commons reappears in problems of pollution. Here it is not a question of taking something out of the commons, but of putting something in—sewage, or chemical, radioactive, and heat wastes into water; noxious and dangerous fumes into the air; and distracting and unpleasant advertising signs into the line of sight. The calculations of utility are much the same as before. The rational man finds that his share of the cost of the wastes he discharges into the commons is less than the cost of purifying his wastes before releasing them. Since this is true for everyone, we are locked into a system of "fouling our own nest," so long as we behave only as independent, rational, free-enterprisers.

The tragedy of the commons as a food basket is averted by private property, or something formally like it. But the air and waters surrounding us cannot readily be fenced, and so the tragedy of the commons as a cesspool must be prevented by different means, by coercive laws or taxing devices that make it cheaper for the polluter to treat his pollutants than to discharge them untreated. We have not progressed as far with the solution of this problem as we have with the first. Indeed, our particular concept of private property, which deters us from exhausting the positive resources of the earth, favors pollution. The owner of a factory on the bank of a stream—whose property extends to the middle of the stream—often has difficulty seeing why it is not his natural right to muddy the waters flowing past his door. The law, always behind the times, requires elaborate stitching and fitting to adapt it to this newly perceived aspect of the commons.

The pollution problem is a consequence of population. It did not much matter how a lonely American frontiersman disposed of his waste. "Flowing water purifies itself every 10 miles," my grandfather used to say, and the myth was near enough to the truth when he was a boy, for there were not too many people. But as population became denser, the natural chemical and biological recycling processes became overloaded, calling for a redefinition of property rights.

How To Legislate Temperance?

Analysis of the pollution problem as a function of population density uncovers a not generally recognized principle of morality, namely: *the morality of an act is a function of the state of the system at the time it is performed* (*10*). Using the commons as a cesspool does not harm the general public under frontier conditions, because there is no public; the same behavior in a metropolis is unbearable. A hundred and fifty years ago a plainsman could kill an American bison, cut out only the tongue for his dinner, and discard the rest of the animal. He was not in any important sense being wasteful. Today, with only a few thousand bison left, we would be appalled at such behavior.

In passing, it is worth noting that the morality of an act cannot be determined from a photograph. One does not know whether a man killing an elephant or setting fire to the grassland is harming others until one knows the total system in which his act appears. "One picture is worth a thousand words," said an ancient Chinese; but it may take 10,000 words to validate it. It is as tempting to ecologists as it is to reformers in general to try to persuade others by way of the photographic shortcut. But the essense of an argument cannot be photographed: it must be presented rationally—in words.

That morality is system-sensitive escaped the attention of most codifiers of ethics in the past. "Thou shalt not . . ." is the form of traditional ethical directives which make no allowance for particular circumstances. The laws of our society follow the pattern of ancient ethics, and therefore are poorly suited to governing a complex, crowded, changeable world. Our epicyclic solution is to augment statutory law with administrative law. Since it is practically impossible to spell out all the conditions under which it is safe to burn trash in the back yard or to run an automobile without smog-control, by law we delegate the details to bureaus. The result is administrative law, which is rightly feared for an ancient reason—*Quis custodiet ipsos custodes?*—"Who shall watch the watchers themselves?" John Adams said that we must have "a government of laws and not men." Bureau administrators, trying to evaluate the morality of acts in the total system, are singularly liable to corruption, producing a government by men, not laws.

Prohibition is easy to legislate (though not necessarily to enforce); but how do we legislate temperance? Experience indicates that it can be accomplished best through the mediation of administrative law. We limit possibilities unnecessarily if we suppose that the sentiment of *Quis custodiet* denies us the use of administrative law. We should rather retain the phrase as a perpetual reminder of fearful dangers we cannot avoid. The great challenge facing us now is to invent the corrective feedbacks that are needed to keep custodians honest. We must find ways to legitimate the needed authority of both the custodians and the corrective feedbacks.

Freedom To Breed Is Intolerable

The tragedy of the commons is involved in population problems in another way. In a world governed solely by the principle of "dog eat dog"—if indeed there ever was such a world—how many children a family had would not be a matter of public concern. Parents who bred too exuberantly would leave fewer descendants, not more, because they would be unable to care adequately for their children. David Lack and others have found that such a negative feedback demonstrably controls the fecundity of birds (*11*). But men are not birds, and have not acted like them for millenniums, at least.

If each human family were dependent only on its own resources; *if* the children of improvident parents starved to death; *if*, thus, overbreeding brought its own "punishment" to the germ line—*then* there would be no public interest in controlling the breeding of families. But our society is deeply committed to the welfare state (*12*), and hence is confronted with another aspect of the tragedy of the commons.

In a welfare state, how shall we deal with the family, the religion, the race, or the class (or indeed any distinguishable and cohesive group) that adopts overbreeding as a policy to secure its own aggrandizement (*13*)? To couple the concept of freedom to breed with the belief that everyone born has an equal right to the commons is to lock the world into a tragic course of action.

Unfortunately this is just the course of action that is being pursued by the United Nations. In late 1967, some 30 nations agreed to the following (*14*):

> The Universal Declaration of Human Rights describes the family as the natural and fundamental unit of society. It follows that any choice and decision with regard to the size of the family must irrevocably rest with the family itself, and cannot be made by anyone else.

It is painful to have to deny categorically the validity of this right; denying it, one feels as uncomfortable as a resident of Salem, Massachusetts, who denied the reality of witches in the 17th century. At the present time, in liberal quarters, something like a taboo acts to inhibit criticism of the United Nations. There is a feeling that the United Nations is "our last and best hope," that we shouldn't find fault with it; we shouldn't play into the hands of the archconservatives. However, let us not forget what Robert Louis Stevenson said: "The truth that is suppressed by friends is the readiest weapon of the enemy." If we love the truth we must openly deny the validity of the Universal Declaration of Human Rights, even though it is promoted by the United Nations. We should also join with Kingsley Davis (*15*) in attempting to get Planned Parenthood-World Population to see the error of its ways in embracing the same tragic ideal.

Conscience Is Self-Eliminating

It is a mistake to think that we can control the breeding of mankind in the long run by an appeal to conscience. Charles Galton Darwin made this point when he spoke on the centennial of the publication of his grandfather's great book. The argument is straightforward and Darwinian.

People vary. Confronted with appeals to limit breeding, some people will undoubtedly respond to the plea more than others. Those who have more children will produce a larger fraction of the next generation than those with more susceptible consciences. The difference will be accentuated, generation by generation.

In C. G. Darwin's words: "It may well be that it would take hundreds of generations for the progenitive instinct to develop in this way, but if it should do so, nature would have taken her revenge, and the variety *Homo contracipiens* would become extinct and would be replaced by the variety *Homo progenitivus*" (*16*).

The argument assumes that conscience or the desire for children (no matter which) is hereditary—but hereditary only in the most general formal sense. The result will be the same whether the attitude is transmitted through germ cells, or exosomatically, to use A. J. Lotka's term. (If one denies the latter possibility as well as the former, then what's the point of education?) The argument has here been stated in the context of the population problem, but it applies equally well to any instance in which society appeals to an individual exploiting a commons to restrain himself for the general good—by means of his conscience. To make such an appeal is to set up a selective system that works toward the elimination of conscience from the race.

Pathogenic Effects of Conscience

The long-term disadvantage of an appeal to conscience should be enough to condemn it; but has serious short-term disadvantages as well. If we ask a man who is exploiting a commons to desist "in the name of conscience," what are we saying to him? What does he hear?—not only at the moment but also in the wee small hours of the night when, half asleep, he remembers not merely the words we used but also the nonverbal communication cues we gave him unawares? Sooner or later, consciously or subconsciously, he senses that he has received two communications, and that they are contradictory: (i) (intended communication) "If you don't do as we ask, we will openly condemn you for not acting like a responsible citizen"; (ii) (the unintended communication) "If you *do* behave as we ask, we will secretly condemn you for a simpleton who can be shamed into standing aside while the rest of us exploit the commons."

Everyman then is caught in what Bateson has called a "double bind." Bateson and his co-workers have made a plausible case for viewing the double bind as an important causative factor in the genesis of schizophrenia (*17*). The double bind may not always be so damaging, but it always endangers the mental health of anyone to whom it is applied. "A bad conscience," said Nietzsche, "is a kind of illness."

To conjure up a conscience in others

is tempting to anyone who wishes to extend his control beyond the legal limits. Leaders at the highest level succumb to this temptation. Has any President during the past generation failed to call on labor unions to moderate voluntarily their demands for higher wages, or to steel companies to honor voluntary guidelines on prices? I can recall none. The rhetoric used on such occasions is designed to produce feelings of guilt in noncooperators.

For centuries it was assumed without proof that guilt was a valuable, perhaps even an indispensable, ingredient of the civilized life. Now, in this post-Freudian world, we doubt it.

Paul Goodman speaks from the modern point of view when he says: "No good has ever come from feeling guilty, neither intelligence, policy, nor compassion. The guilty do not pay attention to the object but only to themselves, and not even to their own interests, which might make sense, but to their anxieties" (*18*).

One does not have to be a professional psychiatrist to see the consequences of anxiety. We in the Western world are just emerging from a dreadful two-centuries-long Dark Ages of Eros that was sustained partly by prohibition laws, but perhaps more effectively by the anxiety-generating mechanisms of education. Alex Comfort has told the story well in *The Anxiety Makers* (*19*); it is not a pretty one.

Since proof is difficult, we may even concede that the results of anxiety may sometimes, from certain points of view, be desirable. The larger question we should ask is whether, as a matter of policy, we should ever encourage the use of a technique the tendency (if not the intention) of which is psychologically pathogenic. We hear much talk these days of responsible parenthood; the coupled words are incorporated into the titles of some organizations devoted to birth control. Some people have proposed massive propaganda campaigns to instill responsibility into the nation's (or the world's) breeders. But what is the meaning of the word responsibility in this context? Is it not merely a synonym for the word conscience? When we use the word responsibility in the absence of substantial sanctions are we not trying to browbeat a free man in a commons into acting against his own interest? Responsibility is a verbal counterfeit for a substantial *quid pro quo*. It is an attempt to get something for nothing.

If the word responsibility is to be used at all, I suggest that it be in the sense Charles Frankel uses it (*20*). "Responsibility," says this philosopher, "is the product of definite social arrangements." Notice that Frankel calls for social arrangements—not propaganda.

Mutual Coercion Mutually Agreed upon

The social arrangements that produce responsibility are arrangements that create coercion, of some sort. Consider bank-robbing. The man who takes money from a bank acts as if the bank were a commons. How do we prevent such action? Certainly not by trying to control his behavior solely by a verbal appeal to his sense of responsibility. Rather than rely on propaganda we follow Frankel's lead and insist that a bank is not a commons; we seek the definite social arrangements that will keep it from becoming a commons. That we thereby infringe on the freedom of would-be robbers we neither deny nor regret.

The morality of bank-robbing is particularly easy to understand because we accept complete prohibition of this activity. We are willing to say "Thou shalt not rob banks," without providing for exceptions. But temperance also can be created by coercion. Taxing is a good coercive device. To keep downtown shoppers temperate in their use of parking space we introduce parking meters for short periods, and traffic fines for longer ones. We need not actually forbid a citizen to park as long as he wants to; we need merely make it increasingly expensive for him to do so. Not prohibition, but carefully biased options are what we offer him. A Madison Avenue man might call this persuasion; I prefer the greater candor of the word coercion.

Coercion is a dirty word to most liberals now, but it need not forever be so. As with the four-letter words, its dirtiness can be cleansed away by exposure to the light, by saying it over and over without apology or embarrassment. To many, the word coercion implies arbitrary decisions of distant and irresponsible bureaucrats; but this is not a necessary part of its meaning. The only kind of coercion I recommend is mutual coercion, mutually agreed upon by the majority of the people affected.

To say that we mutually agree to coercion is not to say that we are required to enjoy it, or even to pretend we enjoy it. Who enjoys taxes? We all grumble about them. But we accept compulsory taxes because we recognize that voluntary taxes would favor the conscienceless. We institute and (grumblingly) support taxes and other coercive devices to escape the horror of the commons.

An alternative to the commons need not be perfectly just to be preferable. With real estate and other material goods, the alternative we have chosen is the institution of private property coupled with legal inheritance. Is this system perfectly just? As a genetically trained biologist I deny that it is. It seems to me that, if there are to be differences in individual inheritance, legal possession should be perfectly correlated with biological inheritance—that those who are biologically more fit to be the custodians of property and power should legally inherit more. But genetic recombination continually makes a mockery of the doctrine of "like father, like son" implicit in our laws of legal inheritance. An idiot can inherit millions, and a trust fund can keep his estate intact. We must admit that our legal system of private property plus inheritance is unjust—but we put up with it because we are not convinced, at the moment, that anyone has invented a better system. The alternative of the commons is too horrifying to contemplate. Injustice is preferable to total ruin.

It is one of the peculiarities of the warfare between reform and the status quo that it is thoughtlessly governed by a double standard. Whenever a reform measure is proposed it is often defeated when its opponents triumphantly discover a flaw in it. As Kingsley Davis has pointed out (*21*), worshippers of the status quo sometimes imply that no reform is possible without unanimous agreement, an implication contrary to historical fact. As nearly as I can make out, automatic rejection of proposed reforms is based on one of two unconscious assumptions: (i) that the status quo is perfect; or (ii) that the choice we face is between reform and no action; if the proposed reform is imperfect, we presumably should take no action at all, while we wait for a perfect proposal.

But we can never do nothing. That which we have done for thousands of years is also action. It also produces evils. Once we are aware that the status quo is action, we can then compare its discoverable advantages and disadvantages with the predicted advantages and disadvantages of the proposed reform, discounting as best we can for our lack of experience. On the basis of such a comparison, we can make a rational decision which will not involve the unworkable assumption that only perfect systems are tolerable.

Recognition of Necessity

Perhaps the simplest summary of this analysis of man's population problems is this: the commons, if justifiable at all, is justifiable only under conditions of low-population density. As the human population has increased, the commons has had to be abandoned in one aspect after another.

First we abandoned the commons in food gathering, enclosing farm land and restricting pastures and hunting and fishing areas. These restrictions are still not complete throughout the world.

Somewhat later we saw that the commons as a place for waste disposal would also have to be abandoned. Restrictions on the disposal of domestic sewage are widely accepted in the Western world; we are still struggling to close the commons to pollution by automobiles, factories, insecticide sprayers, fertilizing operations, and atomic energy installations.

In a still more embryonic state is our recognition of the evils of the commons in matters of pleasure. There is almost no restriction on the propagation of sound waves in the public medium. The shopping public is assaulted with mindless music, without its consent. Our government is paying out billions of dollars to create supersonic transport which will disturb 50,000 people for every one person who is whisked from coast to coast 3 hours faster. Advertisers muddy the airwaves of radio and television and pollute the view of travelers. We are a long way from outlawing the commons in matters of pleasure. Is this because our Puritan inheritance makes us view pleasure as something of a sin, and pain (that is, the pollution of advertising) as the sign of virtue?

Every new enclosure of the commons involves the infringement of somebody's personal liberty. Infringements made in the distant past are accepted because no contemporary complains of a loss. It is the newly proposed infringements that we vigorously oppose; cries of "rights" and "freedom" fill the air. But what does "freedom" mean? When men mutually agreed to pass laws against robbing, mankind became more free, not less so. Individuals locked into the logic of the commons are free only to bring on universal ruin; once they see the necessity of mutual coercion, they become free to pursue other goals. I believe it was Hegel who said, "Freedom is the recognition of necessity."

The most important aspect of necessity that we must now recognize, is the necessity of abandoning the commons in breeding. No technical solution can rescue us from the misery of overpopulation. Freedom to breed will bring ruin to all. At the moment, to avoid hard decisions many of us are tempted to propagandize for conscience and responsible parenthood. The temptation must be resisted, because an appeal to independently acting consciences selects for the disappearance of all conscience in the long run, and an increase in anxiety in the short.

The only way we can preserve and nurture other and more precious freedoms is by relinquishing the freedom to breed, and that very soon. "Freedom is the recognition of necessity"—and it is the role of education to reveal to all the necessity of abandoning the freedom to breed. Only so, can we put an end to this aspect of the tragedy of the commons.

References

1. J. B. Wiesner and H. F. York, *Sci. Amer.* **211** (No. 4), 27 (1964).
2. G. Hardin, *J. Hered.* **50**, 68 (1959); S. von Hoernor, *Science* **137**, 18 (1962).
3. J. von Neumann and O. Morgenstern, *Theory of Games and Economic Behavior* (Princeton Univ. Press, Princeton, N.J., 1947), p. 11.
4. J. H. Fremlin, *New Sci.*, No. 415 (1964), p. 285.
5. A. Smith, *The Wealth of Nations* (Modern Library, New York, 1937), p. 423.
6. W. F. Lloyd, *Two Lectures on the Checks to Population* (Oxford Univ. Press, Oxford, England, 1833), reprinted (in part) in *Population, Evolution, and Birth Control*, G. Hardin, Ed. (Freeman, San Francisco, 1964), p. 37.
7. A. N. Whitehead, *Science and the Modern World* (Mentor, New York, 1948), p. 17.
8. G. Hardin, Ed. *Population, Evolution, and Birth Control* (Freeman, San Francisco, 1964), p. 56.
9. S. McVay, *Sci. Amer.* **216** (No. 8), 13 (1966).
10. J. Fletcher, *Situation Ethics* (Westminster, Philadelphia, 1966).
11. D. Lack, *The Natural Regulation of Animal Numbers* (Clarendon Press, Oxford, 1954).
12. H. Girvetz, *From Wealth to Welfare* (Stanford Univ. Press, Stanford, Calif., 1950).
13. G. Hardin, *Perspec. Biol. Med.* **6**, 366 (1963).
14. U. Thant, *Int. Planned Parenthood News*, No. 168 (February 1968), p. 3.
15. K. Davis, *Science* **158**, 730 (1967).
16. S. Tax, Ed., *Evolution after Darwin* (Univ. of Chicago Press, Chicago, 1960), vol. 2, p. 469.
17. G. Bateson, D. D. Jackson, J. Haley, J. Weakland, *Behav. Sci.* **1**, 251 (1956).
18. P. Goodman, *New York Rev. Books* **10**(8), 22 (23 May 1968).
19. A. Comfort, *The Anxiety Makers* (Nelson, London, 1967).
20. C. Frankel, *The Case for Modern Man* (Harper, New York, 1955), p. 203.
21. J. D. Roslansky, *Genetics and the Future of Man* (Appleton-Century-Crofts, New York, 1966), p. 177.

The Holy See

ENCYCLICAL LETTER
LAUDATO SI'
OF THE HOLY FATHER
FRANCIS
ON CARE FOR OUR COMMON HOME

1. *"LAUDATO SI', mi' Signore" – "Praise be to you, my Lord".* In the words of this beautiful canticle, Saint Francis of Assisi reminds us that our common home is like a sister with whom we share our life and a beautiful mother who opens her arms to embrace us. "Praise be to you, my Lord, through our Sister, Mother Earth, who sustains and governs us, and who produces various fruit with coloured flowers and herbs".[1]

2. This sister now cries out to us because of the harm we have inflicted on her by our irresponsible use and abuse of the goods with which God has endowed her. We have come to see ourselves as her lords and masters, entitled to plunder her at will. The violence present in our hearts, wounded by sin, is also reflected in the symptoms of sickness evident in the soil, in the water, in the air and in all forms of life. This is why the earth herself, burdened and laid waste, is among the most abandoned and maltreated of our poor; she "groans in travail" (*Rom* 8:22). We have forgotten that we ourselves are dust of the earth (cf. *Gen* 2:7); our very bodies are made up of her elements, we breathe her air and we receive life and refreshment from her waters.

Nothing in this world is indifferent to us

3. More than fifty years ago, with the world teetering on the brink of nuclear crisis, Pope Saint John XXIII wrote an Encyclical which not only rejected war but offered a proposal for peace. He addressed his message *Pacem in Terris* to the entire "Catholic world" and indeed "to all men and women of good will". Now, faced as we are with global environmental deterioration, I wish to

address every person living on this planet. In my Apostolic Exhortation *Evangelii Gaudium*, I wrote to all the members of the Church with the aim of encouraging ongoing missionary renewal. In this Encyclical, I would like to enter into dialogue with all people about our common home.

4. In 1971, eight years after *Pacem in Terris*, Blessed Pope Paul VI referred to the ecological concern as “a tragic consequence” of unchecked human activity: “Due to an ill-considered exploitation of nature, humanity runs the risk of destroying it and becoming in turn a victim of this degradation”.[2] He spoke in similar terms to the Food and Agriculture Organization of the United Nations about the potential for an “ecological catastrophe under the effective explosion of industrial civilization”, and stressed “the urgent need for a radical change in the conduct of humanity”, inasmuch as “the most extraordinary scientific advances, the most amazing technical abilities, the most astonishing economic growth, unless they are accompanied by authentic social and moral progress, will definitively turn against man”.[3]

5. Saint John Paul II became increasingly concerned about this issue. In his first Encyclical he warned that human beings frequently seem “to see no other meaning in their natural environment than what serves for immediate use and consumption”.[4] Subsequently, he would call for a global ecological *conversion*.[5] At the same time, he noted that little effort had been made to “safeguard the moral conditions for an authentic *human ecology*”.[6] The destruction of the human environment is extremely serious, not only because God has entrusted the world to us men and women, but because human life is itself a gift which must be defended from various forms of debasement. Every effort to protect and improve our world entails profound changes in “lifestyles, models of production and consumption, and the established structures of power which today govern societies”.[7] Authentic human development has a moral character. It presumes full respect for the human person, but it must also be concerned for the world around us and “take into account the nature of each being and of its mutual connection in an ordered system”.[8] Accordingly, our human ability to transform reality must proceed in line with God’s original gift of all that is.[9]

6. My predecessor Benedict XVI likewise proposed “eliminating the structural causes of the dysfunctions of the world economy and correcting models of growth which have proved incapable of ensuring respect for the environment”.[10] He observed that the world cannot be analyzed by isolating only one of its aspects, since “the book of nature is one and indivisible”, and includes the environment, life, sexuality, the family, social relations, and so forth. It follows that “the deterioration of nature is closely connected to the culture which shapes human coexistence”.[11] Pope Benedict asked us to recognize that the natural environment has been gravely damaged by our irresponsible behaviour. The social environment has also suffered damage. Both are ultimately due to the same evil: the notion that there are no indisputable truths to guide our lives, and hence human freedom is limitless. We have forgotten that “man is not only a freedom which he creates for himself. Man does not create himself. He is spirit and will, but also nature”.[12] With paternal concern, Benedict urged us to realize that creation is harmed “where we ourselves have the final

word, where everything is simply our property and we use it for ourselves alone. The misuse of creation begins when we no longer recognize any higher instance than ourselves, when we see nothing else but ourselves".[13]

United by the same concern

7. These statements of the Popes echo the reflections of numerous scientists, philosophers, theologians and civic groups, all of which have enriched the Church's thinking on these questions. Outside the Catholic Church, other Churches and Christian communities – and other religions as well – have expressed deep concern and offered valuable reflections on issues which all of us find disturbing. To give just one striking example, I would mention the statements made by the beloved Ecumenical Patriarch Bartholomew, with whom we share the hope of full ecclesial communion.

8. Patriarch Bartholomew has spoken in particular of the need for each of us to repent of the ways we have harmed the planet, for "inasmuch as we all generate small ecological damage", we are called to acknowledge "our contribution, smaller or greater, to the disfigurement and destruction of creation".[14] He has repeatedly stated this firmly and persuasively, challenging us to acknowledge our sins against creation: "For human beings… to destroy the biological diversity of God's creation; for human beings to degrade the integrity of the earth by causing changes in its climate, by stripping the earth of its natural forests or destroying its wetlands; for human beings to contaminate the earth's waters, its land, its air, and its life – these are sins".[15] For "to commit a crime against the natural world is a sin against ourselves and a sin against God".[16]

9. At the same time, Bartholomew has drawn attention to the ethical and spiritual roots of environmental problems, which require that we look for solutions not only in technology but in a change of humanity; otherwise we would be dealing merely with symptoms. He asks us to replace consumption with sacrifice, greed with generosity, wastefulness with a spirit of sharing, an asceticism which "entails learning to give, and not simply to give up. It is a way of loving, of moving gradually away from what I want to what God's world needs. It is liberation from fear, greed and compulsion".[17] As Christians, we are also called "to accept the world as a sacrament of communion, as a way of sharing with God and our neighbours on a global scale. It is our humble conviction that the divine and the human meet in the slightest detail in the seamless garment of God's creation, in the last speck of dust of our planet".[18]

Saint Francis of Assisi

10. I do not want to write this Encyclical without turning to that attractive and compelling figure, whose name I took as my guide and inspiration when I was elected Bishop of Rome. I believe that Saint Francis is the example par excellence of care for the vulnerable and of an integral ecology lived out joyfully and authentically. He is the patron saint of all who study and work in the area of ecology, and he is also much loved by non-Christians. He was particularly concerned for God's

creation and for the poor and outcast. He loved, and was deeply loved for his joy, his generous self-giving, his openheartedness. He was a mystic and a pilgrim who lived in simplicity and in wonderful harmony with God, with others, with nature and with himself. He shows us just how inseparable the bond is between concern for nature, justice for the poor, commitment to society, and interior peace.

11. Francis helps us to see that an integral ecology calls for openness to categories which transcend the language of mathematics and biology, and take us to the heart of what it is to be human. Just as happens when we fall in love with someone, whenever he would gaze at the sun, the moon or the smallest of animals, he burst into song, drawing all other creatures into his praise. He communed with all creation, even preaching to the flowers, inviting them "to praise the Lord, just as if they were endowed with reason".[19] His response to the world around him was so much more than intellectual appreciation or economic calculus, for to him each and every creature was a sister united to him by bonds of affection. That is why he felt called to care for all that exists. His disciple Saint Bonaventure tells us that, "from a reflection on the primary source of all things, filled with even more abundant piety, he would call creatures, no matter how small, by the name of 'brother' or 'sister'".[20] Such a conviction cannot be written off as naive romanticism, for it affects the choices which determine our behaviour. If we approach nature and the environment without this openness to awe and wonder, if we no longer speak the language of fraternity and beauty in our relationship with the world, our attitude will be that of masters, consumers, ruthless exploiters, unable to set limits on their immediate needs. By contrast, if we feel intimately united with all that exists, then sobriety and care will well up spontaneously. The poverty and austerity of Saint Francis were no mere veneer of asceticism, but something much more radical: a refusal to turn reality into an object simply to be used and controlled.

12. What is more, Saint Francis, faithful to Scripture, invites us to see nature as a magnificent book in which God speaks to us and grants us a glimpse of his infinite beauty and goodness. "Through the greatness and the beauty of creatures one comes to know by analogy their maker" (*Wis* 13:5); indeed, "his eternal power and divinity have been made known through his works since the creation of the world" (*Rom* 1:20). For this reason, Francis asked that part of the friary garden always be left untouched, so that wild flowers and herbs could grow there, and those who saw them could raise their minds to God, the Creator of such beauty.[21] Rather than a problem to be solved, the world is a joyful mystery to be contemplated with gladness and praise.

My appeal

13. The urgent challenge to protect our common home includes a concern to bring the whole human family together to seek a sustainable and integral development, for we know that things can change. The Creator does not abandon us; he never forsakes his loving plan or repents of having created us. Humanity still has the ability to work together in building our common home. Here I want to recognize, encourage and thank all those striving in countless ways to guarantee

the protection of the home which we share. Particular appreciation is owed to those who tirelessly seek to resolve the tragic effects of environmental degradation on the lives of the world's poorest. Young people demand change. They wonder how anyone can claim to be building a better future without thinking of the environmental crisis and the sufferings of the excluded.

14. I urgently appeal, then, for a new dialogue about how we are shaping the future of our planet. We need a conversation which includes everyone, since the environmental challenge we are undergoing, and its human roots, concern and affect us all. The worldwide ecological movement has already made considerable progress and led to the establishment of numerous organizations committed to raising awareness of these challenges. Regrettably, many efforts to seek concrete solutions to the environmental crisis have proved ineffective, not only because of powerful opposition but also because of a more general lack of interest. Obstructionist attitudes, even on the part of believers, can range from denial of the problem to indifference, nonchalant resignation or blind confidence in technical solutions. We require a new and universal solidarity. As the bishops of Southern Africa have stated: "Everyone's talents and involvement are needed to redress the damage caused by human abuse of God's creation". [22] All of us can cooperate as instruments of God for the care of creation, each according to his or her own culture, experience, involvements and talents.

15. It is my hope that this Encyclical Letter, which is now added to the body of the Church's social teaching, can help us to acknowledge the appeal, immensity and urgency of the challenge we face. I will begin by briefly reviewing several aspects of the present ecological crisis, with the aim of drawing on the results of the best scientific research available today, letting them touch us deeply and provide a concrete foundation for the ethical and spiritual itinerary that follows. I will then consider some principles drawn from the Judaeo-Christian tradition which can render our commitment to the environment more coherent. I will then attempt to get to the roots of the present situation, so as to consider not only its symptoms but also its deepest causes. This will help to provide an approach to ecology which respects our unique place as human beings in this world and our relationship to our surroundings. In light of this reflection, I will advance some broader proposals for dialogue and action which would involve each of us as individuals, and also affect international policy. Finally, convinced as I am that change is impossible without motivation and a process of education, I will offer some inspired guidelines for human development to be found in the treasure of Christian spiritual experience.

16. Although each chapter will have its own subject and specific approach, it will also take up and re-examine important questions previously dealt with. This is particularly the case with a number of themes which will reappear as the Encyclical unfolds. As examples, I will point to the intimate relationship between the poor and the fragility of the planet, the conviction that everything in the world is connected, the critique of new paradigms and forms of power derived from technology, the call to seek other ways of understanding the economy and progress, the value proper to each creature, the human meaning of ecology, the need for forthright and honest debate, the serious

responsibility of international and local policy, the throwaway culture and the proposal of a new lifestyle. These questions will not be dealt with once and for all, but reframed and enriched again and again.

CHAPTER ONE

WHAT IS HAPPENING TO OUR COMMON HOME

17. Theological and philosophical reflections on the situation of humanity and the world can sound tiresome and abstract, unless they are grounded in a fresh analysis of our present situation, which is in many ways unprecedented in the history of humanity. So, before considering how faith brings new incentives and requirements with regard to the world of which we are a part, I will briefly turn to what is happening to our common home.

18. The continued acceleration of changes affecting humanity and the planet is coupled today with a more intensified pace of life and work which might be called “rapidification”. Although change is part of the working of complex systems, the speed with which human activity has developed contrasts with the naturally slow pace of biological evolution. Moreover, the goals of this rapid and constant change are not necessarily geared to the common good or to integral and sustainable human development. Change is something desirable, yet it becomes a source of anxiety when it causes harm to the world and to the quality of life of much of humanity.

19. Following a period of irrational confidence in progress and human abilities, some sectors of society are now adopting a more critical approach. We see increasing sensitivity to the environment and the need to protect nature, along with a growing concern, both genuine and distressing, for what is happening to our planet. Let us review, however cursorily, those questions which are troubling us today and which we can no longer sweep under the carpet. Our goal is not to amass information or to satisfy curiosity, but rather to become painfully aware, to dare to turn what is happening to the world into our own personal suffering and thus to discover what each of us can do about it.

I. POLLUTION AND CLIMATE CHANGE

Pollution, waste and the throwaway culture

20. Some forms of pollution are part of people’s daily experience. Exposure to atmospheric pollutants produces a broad spectrum of health hazards, especially for the poor, and causes millions of premature deaths. People take sick, for example, from breathing high levels of smoke from fuels used in cooking or heating. There is also pollution that affects everyone, caused by transport, industrial fumes, substances which contribute to the acidification of soil and water, fertilizers, insecticides, fungicides, herbicides and agrotoxins in general. Technology, which, linked

to business interests, is presented as the only way of solving these problems, in fact proves incapable of seeing the mysterious network of relations between things and so sometimes solves one problem only to create others.

21. Account must also be taken of the pollution produced by residue, including dangerous waste present in different areas. Each year hundreds of millions of tons of waste are generated, much of it non-biodegradable, highly toxic and radioactive, from homes and businesses, from construction and demolition sites, from clinical, electronic and industrial sources. The earth, our home, is beginning to look more and more like an immense pile of filth. In many parts of the planet, the elderly lament that once beautiful landscapes are now covered with rubbish. Industrial waste and chemical products utilized in cities and agricultural areas can lead to bioaccumulation in the organisms of the local population, even when levels of toxins in those places are low. Frequently no measures are taken until after people's health has been irreversibly affected.

22. These problems are closely linked to a throwaway culture which affects the excluded just as it quickly reduces things to rubbish. To cite one example, most of the paper we produce is thrown away and not recycled. It is hard for us to accept that the way natural ecosystems work is exemplary: plants synthesize nutrients which feed herbivores; these in turn become food for carnivores, which produce significant quantities of organic waste which give rise to new generations of plants. But our industrial system, at the end of its cycle of production and consumption, has not developed the capacity to absorb and reuse waste and by-products. We have not yet managed to adopt a circular model of production capable of preserving resources for present and future generations, while limiting as much as possible the use of non-renewable resources, moderating their consumption, maximizing their efficient use, reusing and recycling them. A serious consideration of this issue would be one way of counteracting the throwaway culture which affects the entire planet, but it must be said that only limited progress has been made in this regard.

Climate as a common good

23. The climate is a common good, belonging to all and meant for all. At the global level, it is a complex system linked to many of the essential conditions for human life. A very solid scientific consensus indicates that we are presently witnessing a disturbing warming of the climatic system. In recent decades this warming has been accompanied by a constant rise in the sea level and, it would appear, by an increase of extreme weather events, even if a scientifically determinable cause cannot be assigned to each particular phenomenon. Humanity is called to recognize the need for changes of lifestyle, production and consumption, in order to combat this warming or at least the human causes which produce or aggravate it. It is true that there are other factors (such as volcanic activity, variations in the earth's orbit and axis, the solar cycle), yet a number of scientific studies indicate that most global warming in recent decades is due to the great concentration of greenhouse gases (carbon dioxide, methane, nitrogen oxides and others)

released mainly as a result of human activity. Concentrated in the atmosphere, these gases do not allow the warmth of the sun's rays reflected by the earth to be dispersed in space. The problem is aggravated by a model of development based on the intensive use of fossil fuels, which is at the heart of the worldwide energy system. Another determining factor has been an increase in changed uses of the soil, principally deforestation for agricultural purposes.

24. Warming has effects on the carbon cycle. It creates a vicious circle which aggravates the situation even more, affecting the availability of essential resources like drinking water, energy and agricultural production in warmer regions, and leading to the extinction of part of the planet's biodiversity. The melting in the polar ice caps and in high altitude plains can lead to the dangerous release of methane gas, while the decomposition of frozen organic material can further increase the emission of carbon dioxide. Things are made worse by the loss of tropical forests which would otherwise help to mitigate climate change. Carbon dioxide pollution increases the acidification of the oceans and compromises the marine food chain. If present trends continue, this century may well witness extraordinary climate change and an unprecedented destruction of ecosystems, with serious consequences for all of us. A rise in the sea level, for example, can create extremely serious situations, if we consider that a quarter of the world's population lives on the coast or nearby, and that the majority of our megacities are situated in coastal areas.

25. Climate change is a global problem with grave implications: environmental, social, economic, political and for the distribution of goods. It represents one of the principal challenges facing humanity in our day. Its worst impact will probably be felt by developing countries in coming decades. Many of the poor live in areas particularly affected by phenomena related to warming, and their means of subsistence are largely dependent on natural reserves and ecosystemic services such as agriculture, fishing and forestry. They have no other financial activities or resources which can enable them to adapt to climate change or to face natural disasters, and their access to social services and protection is very limited. For example, changes in climate, to which animals and plants cannot adapt, lead them to migrate; this in turn affects the livelihood of the poor, who are then forced to leave their homes, with great uncertainty for their future and that of their children. There has been a tragic rise in the number of migrants seeking to flee from the growing poverty caused by environmental degradation. They are not recognized by international conventions as refugees; they bear the loss of the lives they have left behind, without enjoying any legal protection whatsoever. Sadly, there is widespread indifference to such suffering, which is even now taking place throughout our world. Our lack of response to these tragedies involving our brothers and sisters points to the loss of that sense of responsibility for our fellow men and women upon which all civil society is founded.

26. Many of those who possess more resources and economic or political power seem mostly to be concerned with masking the problems or concealing their symptoms, simply making efforts to reduce some of the negative impacts of climate change. However, many of these symptoms indicate that such effects will continue to worsen if we continue with current models of production

and consumption. There is an urgent need to develop policies so that, in the next few years, the emission of carbon dioxide and other highly polluting gases can be drastically reduced, for example, substituting for fossil fuels and developing sources of renewable energy. Worldwide there is minimal access to clean and renewable energy. There is still a need to develop adequate storage technologies. Some countries have made considerable progress, although it is far from constituting a significant proportion. Investments have also been made in means of production and transportation which consume less energy and require fewer raw materials, as well as in methods of construction and renovating buildings which improve their energy efficiency. But these good practices are still far from widespread.

II. THE ISSUE OF WATER

27. Other indicators of the present situation have to do with the depletion of natural resources. We all know that it is not possible to sustain the present level of consumption in developed countries and wealthier sectors of society, where the habit of wasting and discarding has reached unprecedented levels. The exploitation of the planet has already exceeded acceptable limits and we still have not solved the problem of poverty.

28. Fresh drinking water is an issue of primary importance, since it is indispensable for human life and for supporting terrestrial and aquatic ecosystems. Sources of fresh water are necessary for health care, agriculture and industry. Water supplies used to be relatively constant, but now in many places demand exceeds the sustainable supply, with dramatic consequences in the short and long term. Large cities dependent on significant supplies of water have experienced periods of shortage, and at critical moments these have not always been administered with sufficient oversight and impartiality. Water poverty especially affects Africa where large sectors of the population have no access to safe drinking water or experience droughts which impede agricultural production. Some countries have areas rich in water while others endure drastic scarcity.

29. One particularly serious problem is the quality of water available to the poor. Every day, unsafe water results in many deaths and the spread of water-related diseases, including those caused by microorganisms and chemical substances. Dysentery and cholera, linked to inadequate hygiene and water supplies, are a significant cause of suffering and of infant mortality. Underground water sources in many places are threatened by the pollution produced in certain mining, farming and industrial activities, especially in countries lacking adequate regulation or controls. It is not only a question of industrial waste. Detergents and chemical products, commonly used in many places of the world, continue to pour into our rivers, lakes and seas.

30. Even as the quality of available water is constantly diminishing, in some places there is a growing tendency, despite its scarcity, to privatize this resource, turning it into a commodity subject to the laws of the market. Yet *access to safe drinkable water is a basic and universal*

human right, since it is essential to human survival and, as such, is a condition for the exercise of other human rights. Our world has a grave social debt towards the poor who lack access to drinking water, because *they are denied the right to a life consistent with their inalienable dignity*. This debt can be paid partly by an increase in funding to provide clean water and sanitary services among the poor. But water continues to be wasted, not only in the developed world but also in developing countries which possess it in abundance. This shows that the problem of water is partly an educational and cultural issue, since there is little awareness of the seriousness of such behaviour within a context of great inequality.

31. Greater scarcity of water will lead to an increase in the cost of food and the various products which depend on its use. Some studies warn that an acute water shortage may occur within a few decades unless urgent action is taken. The environmental repercussions could affect billions of people; it is also conceivable that the control of water by large multinational businesses may become a major source of conflict in this century.[23]

III. LOSS OF BIODIVERSITY

32. The earth's resources are also being plundered because of short-sighted approaches to the economy, commerce and production. The loss of forests and woodlands entails the loss of species which may constitute extremely important resources in the future, not only for food but also for curing disease and other uses. Different species contain genes which could be key resources in years ahead for meeting human needs and regulating environmental problems.

33. It is not enough, however, to think of different species merely as potential "resources" to be exploited, while overlooking the fact that they have value in themselves. Each year sees the disappearance of thousands of plant and animal species which we will never know, which our children will never see, because they have been lost for ever. The great majority become extinct for reasons related to human activity. Because of us, thousands of species will no longer give glory to God by their very existence, nor convey their message to us. We have no such right.

34. It may well disturb us to learn of the extinction of mammals or birds, since they are more visible. But the good functioning of ecosystems also requires fungi, algae, worms, insects, reptiles and an innumerable variety of microorganisms. Some less numerous species, although generally unseen, nonetheless play a critical role in maintaining the equilibrium of a particular place. Human beings must intervene when a geosystem reaches a critical state. But nowadays, such intervention in nature has become more and more frequent. As a consequence, serious problems arise, leading to further interventions; human activity becomes ubiquitous, with all the risks which this entails. Often a vicious circle results, as human intervention to resolve a problem further aggravates the situation. For example, many birds and insects which disappear due to synthetic agrotoxins are helpful for agriculture: their disappearance will have to be compensated for by yet other techniques which may well prove harmful. We must be grateful for the praiseworthy efforts

being made by scientists and engineers dedicated to finding solutions to man-made problems. But a sober look at our world shows that the degree of human intervention, often in the service of business interests and consumerism, is actually making our earth less rich and beautiful, ever more limited and grey, even as technological advances and consumer goods continue to abound limitlessly. We seem to think that we can substitute an irreplaceable and irretrievable beauty with something which we have created ourselves.

35. In assessing the environmental impact of any project, concern is usually shown for its effects on soil, water and air, yet few careful studies are made of its impact on biodiversity, as if the loss of species or animals and plant groups were of little importance. Highways, new plantations, the fencing-off of certain areas, the damming of water sources, and similar developments, crowd out natural habitats and, at times, break them up in such a way that animal populations can no longer migrate or roam freely. As a result, some species face extinction. Alternatives exist which at least lessen the impact of these projects, like the creation of biological corridors, but few countries demonstrate such concern and foresight. Frequently, when certain species are exploited commercially, little attention is paid to studying their reproductive patterns in order to prevent their depletion and the consequent imbalance of the ecosystem.

36. Caring for ecosystems demands far-sightedness, since no one looking for quick and easy profit is truly interested in their preservation. But the cost of the damage caused by such selfish lack of concern is much greater than the economic benefits to be obtained. Where certain species are destroyed or seriously harmed, the values involved are incalculable. We can be silent witnesses to terrible injustices if we think that we can obtain significant benefits by making the rest of humanity, present and future, pay the extremely high costs of environmental deterioration.

37. Some countries have made significant progress in establishing sanctuaries on land and in the oceans where any human intervention is prohibited which might modify their features or alter their original structures. In the protection of biodiversity, specialists insist on the need for particular attention to be shown to areas richer both in the number of species and in endemic, rare or less protected species. Certain places need greater protection because of their immense importance for the global ecosystem, or because they represent important water reserves and thus safeguard other forms of life.

38. Let us mention, for example, those richly biodiverse lungs of our planet which are the Amazon and the Congo basins, or the great aquifers and glaciers. We know how important these are for the entire earth and for the future of humanity. The ecosystems of tropical forests possess an enormously complex biodiversity which is almost impossible to appreciate fully, yet when these forests are burned down or levelled for purposes of cultivation, within the space of a few years countless species are lost and the areas frequently become arid wastelands. A delicate balance has to be maintained when speaking about these places, for we cannot overlook the huge global economic interests which, under the guise of protecting them, can undermine the sovereignty of

individual nations. In fact, there are “proposals to internationalize the Amazon, which only serve the economic interests of transnational corporations”.[24] We cannot fail to praise the commitment of international agencies and civil society organizations which draw public attention to these issues and offer critical cooperation, employing legitimate means of pressure, to ensure that each government carries out its proper and inalienable responsibility to preserve its country’s environment and natural resources, without capitulating to spurious local or international interests.

39. The replacement of virgin forest with plantations of trees, usually monocultures, is rarely adequately analyzed. Yet this can seriously compromise a biodiversity which the new species being introduced does not accommodate. Similarly, wetlands converted into cultivated land lose the enormous biodiversity which they formerly hosted. In some coastal areas the disappearance of ecosystems sustained by mangrove swamps is a source of serious concern.

40. Oceans not only contain the bulk of our planet’s water supply, but also most of the immense variety of living creatures, many of them still unknown to us and threatened for various reasons. What is more, marine life in rivers, lakes, seas and oceans, which feeds a great part of the world’s population, is affected by uncontrolled fishing, leading to a drastic depletion of certain species. Selective forms of fishing which discard much of what they collect continue unabated. Particularly threatened are marine organisms which we tend to overlook, like some forms of plankton; they represent a significant element in the ocean food chain, and species used for our food ultimately depend on them.

41. In tropical and subtropical seas, we find coral reefs comparable to the great forests on dry land, for they shelter approximately a million species, including fish, crabs, molluscs, sponges and algae. Many of the world’s coral reefs are already barren or in a state of constant decline. “Who turned the wonderworld of the seas into underwater cemeteries bereft of colour and life?”[25] This phenomenon is due largely to pollution which reaches the sea as the result of deforestation, agricultural monocultures, industrial waste and destructive fishing methods, especially those using cyanide and dynamite. It is aggravated by the rise in temperature of the oceans. All of this helps us to see that every intervention in nature can have consequences which are not immediately evident, and that certain ways of exploiting resources prove costly in terms of degradation which ultimately reaches the ocean bed itself.

42. Greater investment needs to be made in research aimed at understanding more fully the functioning of ecosystems and adequately analyzing the different variables associated with any significant modification of the environment. Because all creatures are connected, each must be cherished with love and respect, for all of us as living creatures are dependent on one another. Each area is responsible for the care of this family. This will require undertaking a careful inventory of the species which it hosts, with a view to developing programmes and strategies of protection with particular care for safeguarding species heading towards extinction.

IV. DECLINE IN THE QUALITY OF HUMAN LIFE AND THE BREAKDOWN OF SOCIETY

43. Human beings too are creatures of this world, enjoying a right to life and happiness, and endowed with unique dignity. So we cannot fail to consider the effects on people's lives of environmental deterioration, current models of development and the throwaway culture.

44. Nowadays, for example, we are conscious of the disproportionate and unruly growth of many cities, which have become unhealthy to live in, not only because of pollution caused by toxic emissions but also as a result of urban chaos, poor transportation, and visual pollution and noise. Many cities are huge, inefficient structures, excessively wasteful of energy and water. Neighbourhoods, even those recently built, are congested, chaotic and lacking in sufficient green space. We were not meant to be inundated by cement, asphalt, glass and metal, and deprived of physical contact with nature.

45. In some places, rural and urban alike, the privatization of certain spaces has restricted people's access to places of particular beauty. In others, "ecological" neighbourhoods have been created which are closed to outsiders in order to ensure an artificial tranquillity. Frequently, we find beautiful and carefully manicured green spaces in so-called "safer" areas of cities, but not in the more hidden areas where the disposable of society live.

46. The social dimensions of global change include the effects of technological innovations on employment, social exclusion, an inequitable distribution and consumption of energy and other services, social breakdown, increased violence and a rise in new forms of social aggression, drug trafficking, growing drug use by young people, and the loss of identity. These are signs that the growth of the past two centuries has not always led to an integral development and an improvement in the quality of life. Some of these signs are also symptomatic of real social decline, the silent rupture of the bonds of integration and social cohesion.

47. Furthermore, when media and the digital world become omnipresent, their influence can stop people from learning how to live wisely, to think deeply and to love generously. In this context, the great sages of the past run the risk of going unheard amid the noise and distractions of an information overload. Efforts need to be made to help these media become sources of new cultural progress for humanity and not a threat to our deepest riches. True wisdom, as the fruit of self-examination, dialogue and generous encounter between persons, is not acquired by a mere accumulation of data which eventually leads to overload and confusion, a sort of mental pollution. Real relationships with others, with all the challenges they entail, now tend to be replaced by a type of internet communication which enables us to choose or eliminate relationships at whim, thus giving rise to a new type of contrived emotion which has more to do with devices and displays than with other people and with nature. Today's media do enable us to communicate and to share our knowledge and affections. Yet at times they also shield us from direct contact with the pain, the fears and the joys of others and the complexity of their personal experiences. For this reason,

we should be concerned that, alongside the exciting possibilities offered by these media, a deep and melancholic dissatisfaction with interpersonal relations, or a harmful sense of isolation, can also arise.

V. GLOBAL INEQUALITY

48. The human environment and the natural environment deteriorate together; we cannot adequately combat environmental degradation unless we attend to causes related to human and social degradation. In fact, the deterioration of the environment and of society affects the most vulnerable people on the planet: “Both everyday experience and scientific research show that the gravest effects of all attacks on the environment are suffered by the poorest”.[26] For example, the depletion of fishing reserves especially hurts small fishing communities without the means to replace those resources; water pollution particularly affects the poor who cannot buy bottled water; and rises in the sea level mainly affect impoverished coastal populations who have nowhere else to go. The impact of present imbalances is also seen in the premature death of many of the poor, in conflicts sparked by the shortage of resources, and in any number of other problems which are insufficiently represented on global agendas.[27]

49. It needs to be said that, generally speaking, there is little in the way of clear awareness of problems which especially affect the excluded. Yet they are the majority of the planet’s population, billions of people. These days, they are mentioned in international political and economic discussions, but one often has the impression that their problems are brought up as an afterthought, a question which gets added almost out of duty or in a tangential way, if not treated merely as collateral damage. Indeed, when all is said and done, they frequently remain at the bottom of the pile. This is due partly to the fact that many professionals, opinion makers, communications media and centres of power, being located in affluent urban areas, are far removed from the poor, with little direct contact with their problems. They live and reason from the comfortable position of a high level of development and a quality of life well beyond the reach of the majority of the world’s population. This lack of physical contact and encounter, encouraged at times by the disintegration of our cities, can lead to a numbing of conscience and to tendentious analyses which neglect parts of reality. At times this attitude exists side by side with a “green” rhetoric. Today, however, we have to realize that a true ecological approach *always* becomes a social approach; it must integrate questions of justice in debates on the environment, so as to hear *both the cry of the earth and the cry of the poor*.

50. Instead of resolving the problems of the poor and thinking of how the world can be different, some can only propose a reduction in the birth rate. At times, developing countries face forms of international pressure which make economic assistance contingent on certain policies of “reproductive health”. Yet “while it is true that an unequal distribution of the population and of available resources creates obstacles to development and a sustainable use of the environment, it must nonetheless be recognized that demographic growth is fully compatible with an integral and

shared development”.[28] To blame population growth instead of extreme and selective consumerism on the part of some, is one way of refusing to face the issues. It is an attempt to legitimize the present model of distribution, where a minority believes that it has the right to consume in a way which can never be universalized, since the planet could not even contain the waste products of such consumption. Besides, we know that approximately a third of all food produced is discarded, and “whenever food is thrown out it is as if it were stolen from the table of the poor”.[29] Still, attention needs to be paid to imbalances in population density, on both national and global levels, since a rise in consumption would lead to complex regional situations, as a result of the interplay between problems linked to environmental pollution, transport, waste treatment, loss of resources and quality of life.

51. Inequity affects not only individuals but entire countries; it compels us to consider an ethics of international relations. A true “ecological debt” exists, particularly between the global north and south, connected to commercial imbalances with effects on the environment, and the disproportionate use of natural resources by certain countries over long periods of time. The export of raw materials to satisfy markets in the industrialized north has caused harm locally, as for example in mercury pollution in gold mining or sulphur dioxide pollution in copper mining. There is a pressing need to calculate the use of environmental space throughout the world for depositing gas residues which have been accumulating for two centuries and have created a situation which currently affects all the countries of the world. The warming caused by huge consumption on the part of some rich countries has repercussions on the poorest areas of the world, especially Africa, where a rise in temperature, together with drought, has proved devastating for farming. There is also the damage caused by the export of solid waste and toxic liquids to developing countries, and by the pollution produced by companies which operate in less developed countries in ways they could never do at home, in the countries in which they raise their capital: “We note that often the businesses which operate this way are multinationals. They do here what they would never do in developed countries or the so-called first world. Generally, after ceasing their activity and withdrawing, they leave behind great human and environmental liabilities such as unemployment, abandoned towns, the depletion of natural reserves, deforestation, the impoverishment of agriculture and local stock breeding, open pits, riven hills, polluted rivers and a handful of social works which are no longer sustainable”.[30]

52. The foreign debt of poor countries has become a way of controlling them, yet this is not the case where ecological debt is concerned. In different ways, developing countries, where the most important reserves of the biosphere are found, continue to fuel the development of richer countries at the cost of their own present and future. The land of the southern poor is rich and mostly unpolluted, yet access to ownership of goods and resources for meeting vital needs is inhibited by a system of commercial relations and ownership which is structurally perverse. The developed countries ought to help pay this debt by significantly limiting their consumption of non-renewable energy and by assisting poorer countries to support policies and programmes of sustainable development. The poorest areas and countries are less capable of adopting new models for

reducing environmental impact because they lack the wherewithal to develop the necessary processes and to cover their costs. We must continue to be aware that, regarding climate change, there are *differentiated responsibilities*. As the United States bishops have said, greater attention must be given to “the needs of the poor, the weak and the vulnerable, in a debate often dominated by more powerful interests”.[31] We need to strengthen the conviction that we are one single human family. There are no frontiers or barriers, political or social, behind which we can hide, still less is there room for the globalization of indifference.

VI. WEAK RESPONSES

53. These situations have caused sister earth, along with all the abandoned of our world, to cry out, pleading that we take another course. Never have we so hurt and mistreated our common home as we have in the last two hundred years. Yet we are called to be instruments of God our Father, so that our planet might be what he desired when he created it and correspond with his plan for peace, beauty and fullness. The problem is that we still lack the culture needed to confront this crisis. We lack leadership capable of striking out on new paths and meeting the needs of the present with concern for all and without prejudice towards coming generations. The establishment of a legal framework which can set clear boundaries and ensure the protection of ecosystems has become indispensable; otherwise, the new power structures based on the techno-economic paradigm may overwhelm not only our politics but also freedom and justice.

54. It is remarkable how weak international political responses have been. The failure of global summits on the environment make it plain that our politics are subject to technology and finance. There are too many special interests, and economic interests easily end up trumping the common good and manipulating information so that their own plans will not be affected. The *Aparecida Document* urges that “the interests of economic groups which irrationally demolish sources of life should not prevail in dealing with natural resources”.[32] The alliance between the economy and technology ends up sidelining anything unrelated to its immediate interests. Consequently the most one can expect is superficial rhetoric, sporadic acts of philanthropy and perfunctory expressions of concern for the environment, whereas any genuine attempt by groups within society to introduce change is viewed as a nuisance based on romantic illusions or an obstacle to be circumvented.

55. Some countries are gradually making significant progress, developing more effective controls and working to combat corruption. People may well have a growing ecological sensitivity but it has not succeeded in changing their harmful habits of consumption which, rather than decreasing, appear to be growing all the more. A simple example is the increasing use and power of air-conditioning. The markets, which immediately benefit from sales, stimulate ever greater demand. An outsider looking at our world would be amazed at such behaviour, which at times appears self-destructive.

56. In the meantime, economic powers continue to justify the current global system where priority tends to be given to speculation and the pursuit of financial gain, which fail to take the context into account, let alone the effects on human dignity and the natural environment. Here we see how environmental deterioration and human and ethical degradation are closely linked. Many people will deny doing anything wrong because distractions constantly dull our consciousness of just how limited and finite our world really is. As a result, “whatever is fragile, like the environment, is defenceless before the interests of a deified market, which become the only rule”.[33]

57. It is foreseeable that, once certain resources have been depleted, the scene will be set for new wars, albeit under the guise of noble claims. War always does grave harm to the environment and to the cultural riches of peoples, risks which are magnified when one considers nuclear arms and biological weapons. “Despite the international agreements which prohibit chemical, bacteriological and biological warfare, the fact is that laboratory research continues to develop new offensive weapons capable of altering the balance of nature”.[34] Politics must pay greater attention to foreseeing new conflicts and addressing the causes which can lead to them. But powerful financial interests prove most resistant to this effort, and political planning tends to lack breadth of vision. What would induce anyone, at this stage, to hold on to power only to be remembered for their inability to take action when it was urgent and necessary to do so?

58. In some countries, there are positive examples of environmental improvement: rivers, polluted for decades, have been cleaned up; native woodlands have been restored; landscapes have been beautified thanks to environmental renewal projects; beautiful buildings have been erected; advances have been made in the production of non-polluting energy and in the improvement of public transportation. These achievements do not solve global problems, but they do show that men and women are still capable of intervening positively. For all our limitations, gestures of generosity, solidarity and care cannot but well up within us, since we were made for love.

59. At the same time we can note the rise of a false or superficial ecology which bolsters complacency and a cheerful recklessness. As often occurs in periods of deep crisis which require bold decisions, we are tempted to think that what is happening is not entirely clear. Superficially, apart from a few obvious signs of pollution and deterioration, things do not look that serious, and the planet could continue as it is for some time. Such evasiveness serves as a licence to carrying on with our present lifestyles and models of production and consumption. This is the way human beings contrive to feed their self-destructive vices: trying not to see them, trying not to acknowledge them, delaying the important decisions and pretending that nothing will happen.

VII. A VARIETY OF OPINIONS

60. Finally, we need to acknowledge that different approaches and lines of thought have emerged regarding this situation and its possible solutions. At one extreme, we find those who doggedly uphold the myth of progress and tell us that ecological problems will solve themselves simply with

the application of new technology and without any need for ethical considerations or deep change. At the other extreme are those who view men and women and all their interventions as no more than a threat, jeopardizing the global ecosystem, and consequently the presence of human beings on the planet should be reduced and all forms of intervention prohibited. Viable future scenarios will have to be generated between these extremes, since there is no one path to a solution. This makes a variety of proposals possible, all capable of entering into dialogue with a view to developing comprehensive solutions.

61. On many concrete questions, the Church has no reason to offer a definitive opinion; she knows that honest debate must be encouraged among experts, while respecting divergent views. But we need only take a frank look at the facts to see that our common home is falling into serious disrepair. Hope would have us recognize that there is always a way out, that we can always redirect our steps, that we can always do something to solve our problems. Still, we can see signs that things are now reaching a breaking point, due to the rapid pace of change and degradation; these are evident in large-scale natural disasters as well as social and even financial crises, for the world’s problems cannot be analyzed or explained in isolation. There are regions now at high risk and, aside from all doomsday predictions, the present world system is certainly unsustainable from a number of points of view, for we have stopped thinking about the goals of human activity. “If we scan the regions of our planet, we immediately see that humanity has disappointed God’s expectations”.[35]

CHAPTER TWO

THE GOSPEL OF CREATION

62. Why should this document, addressed to all people of good will, include a chapter dealing with the convictions of believers? I am well aware that in the areas of politics and philosophy there are those who firmly reject the idea of a Creator, or consider it irrelevant, and consequently dismiss as irrational the rich contribution which religions can make towards an integral ecology and the full development of humanity. Others view religions simply as a subculture to be tolerated. Nonetheless, science and religion, with their distinctive approaches to understanding reality, can enter into an intense dialogue fruitful for both.

I. THE LIGHT OFFERED BY FAITH

63. Given the complexity of the ecological crisis and its multiple causes, we need to realize that the solutions will not emerge from just one way of interpreting and transforming reality. Respect must also be shown for the various cultural riches of different peoples, their art and poetry, their interior life and spirituality. If we are truly concerned to develop an ecology capable of remedying the damage we have done, no branch of the sciences and no form of wisdom can be left out, and that includes religion and the language particular to it. The Catholic Church is open to dialogue

with philosophical thought; this has enabled her to produce various syntheses between faith and reason. The development of the Church's social teaching represents such a synthesis with regard to social issues; this teaching is called to be enriched by taking up new challenges.

64. Furthermore, although this Encyclical welcomes dialogue with everyone so that together we can seek paths of liberation, I would like from the outset to show how faith convictions can offer Christians, and some other believers as well, ample motivation to care for nature and for the most vulnerable of their brothers and sisters. If the simple fact of being human moves people to care for the environment of which they are a part, Christians in their turn "realize that their responsibility within creation, and their duty towards nature and the Creator, are an essential part of their faith".[36] It is good for humanity and the world at large when we believers better recognize the ecological commitments which stem from our convictions.

II. THE WISDOM OF THE BIBLICAL ACCOUNTS

65. Without repeating the entire theology of creation, we can ask what the great biblical narratives say about the relationship of human beings with the world. In the first creation account in the Book of Genesis, God's plan includes creating humanity. After the creation of man and woman, "God saw everything that he had made, and behold it was *very good*" (*Gen* 1:31). The Bible teaches that every man and woman is created out of love and made in God's image and likeness (cf. *Gen* 1:26). This shows us the immense dignity of each person, "who is not just something, but someone. He is capable of self-knowledge, of self-possession and of freely giving himself and entering into communion with other persons".[37] Saint John Paul II stated that the special love of the Creator for each human being "confers upon him or her an infinite dignity".[38] Those who are committed to defending human dignity can find in the Christian faith the deepest reasons for this commitment. How wonderful is the certainty that each human life is not adrift in the midst of hopeless chaos, in a world ruled by pure chance or endlessly recurring cycles! The Creator can say to each one of us: "Before I formed you in the womb, I knew you" (*Jer* 1:5). We were conceived in the heart of God, and for this reason "each of us is the result of a thought of God. Each of us is willed, each of us is loved, each of us is necessary".[39]

66. The creation accounts in the book of Genesis contain, in their own symbolic and narrative language, profound teachings about human existence and its historical reality. They suggest that human life is grounded in three fundamental and closely intertwined relationships: with God, with our neighbour and with the earth itself. According to the Bible, these three vital relationships have been broken, both outwardly and within us. This rupture is sin. The harmony between the Creator, humanity and creation as a whole was disrupted by our presuming to take the place of God and refusing to acknowledge our creaturely limitations. This in turn distorted our mandate to "have dominion" over the earth (cf. *Gen* 1:28), to "till it and keep it" (*Gen* 2:15). As a result, the originally harmonious relationship between human beings and nature became conflictual (cf. *Gen* 3:17-19). It is significant that the harmony which Saint Francis of Assisi experienced with all creatures was

seen as a healing of that rupture. Saint Bonaventure held that, through universal reconciliation with every creature, Saint Francis in some way returned to the state of original innocence.[40] This is a far cry from our situation today, where sin is manifest in all its destructive power in wars, the various forms of violence and abuse, the abandonment of the most vulnerable, and attacks on nature.

67. We are not God. The earth was here before us and it has been given to us. This allows us to respond to the charge that Judaeo-Christian thinking, on the basis of the Genesis account which grants man “dominion” over the earth (cf. *Gen* 1:28), has encouraged the unbridled exploitation of nature by painting him as domineering and destructive by nature. This is not a correct interpretation of the Bible as understood by the Church. Although it is true that we Christians have at times incorrectly interpreted the Scriptures, nowadays we must forcefully reject the notion that our being created in God’s image and given dominion over the earth justifies absolute domination over other creatures. The biblical texts are to be read in their context, with an appropriate hermeneutic, recognizing that they tell us to “till and keep” the garden of the world (cf. *Gen* 2:15). “Tilling” refers to cultivating, ploughing or working, while “keeping” means caring, protecting, overseeing and preserving. This implies a relationship of mutual responsibility between human beings and nature. Each community can take from the bounty of the earth whatever it needs for subsistence, but it also has the duty to protect the earth and to ensure its fruitfulness for coming generations. “The earth is the Lord’s” (*Ps* 24:1); to him belongs “the earth with all that is within it” (*Dt* 10:14). Thus God rejects every claim to absolute ownership: “The land shall not be sold in perpetuity, for the land is mine; for you are strangers and sojourners with me” (*Lev* 25:23).

68. This responsibility for God’s earth means that human beings, endowed with intelligence, must respect the laws of nature and the delicate equilibria existing between the creatures of this world, for “he commanded and they were created; and he established them for ever and ever; he fixed their bounds and he set a law which cannot pass away” (*Ps* 148:5b-6). The laws found in the Bible dwell on relationships, not only among individuals but also with other living beings. “You shall not see your brother’s donkey or his ox fallen down by the way and withhold your help… If you chance to come upon a bird’s nest in any tree or on the ground, with young ones or eggs and the mother sitting upon the young or upon the eggs; you shall not take the mother with the young” (*Dt* 22:4, 6). Along these same lines, rest on the seventh day is meant not only for human beings, but also so “that your ox and your donkey may have rest” (*Ex* 23:12). Clearly, the Bible has no place for a tyrannical anthropocentrism unconcerned for other creatures.

69. Together with our obligation to use the earth’s goods responsibly, we are called to recognize that other living beings have a value of their own in God’s eyes: “by their mere existence they bless him and give him glory”,[41] and indeed, “the Lord rejoices in all his works” (*Ps* 104:31). By virtue of our unique dignity and our gift of intelligence, we are called to respect creation and its inherent laws, for “the Lord by wisdom founded the earth” (*Prov* 3:19). In our time, the Church does not simply state that other creatures are completely subordinated to the good of human

beings, as if they have no worth in themselves and can be treated as we wish. The German bishops have taught that, where other creatures are concerned, “we can speak of the priority of *being* over that of *being useful*”.[42] The Catechism clearly and forcefully criticizes a distorted anthropocentrism: “Each creature possesses its own particular goodness and perfection… Each of the various creatures, willed in its own being, reflects in its own way a ray of God’s infinite wisdom and goodness. Man must therefore respect the particular goodness of every creature, to avoid any disordered use of things”.[43]

70. In the story of Cain and Abel, we see how envy led Cain to commit the ultimate injustice against his brother, which in turn ruptured the relationship between Cain and God, and between Cain and the earth from which he was banished. This is seen clearly in the dramatic exchange between God and Cain. God asks: “Where is Abel your brother?” Cain answers that he does not know, and God persists: “What have you done? The voice of your brother’s blood is crying to me from the ground. And now you are cursed from the ground” (*Gen* 4:9-11). Disregard for the duty to cultivate and maintain a proper relationship with my neighbour, for whose care and custody I am responsible, ruins my relationship with my own self, with others, with God and with the earth. When all these relationships are neglected, when justice no longer dwells in the land, the Bible tells us that life itself is endangered. We see this in the story of Noah, where God threatens to do away with humanity because of its constant failure to fulfil the requirements of justice and peace: “I have determined to make an end of all flesh; for the earth is filled with violence through them” (*Gen* 6:13). These ancient stories, full of symbolism, bear witness to a conviction which we today share, that everything is interconnected, and that genuine care for our own lives and our relationships with nature is inseparable from fraternity, justice and faithfulness to others.

71. Although “the wickedness of man was great in the earth” (*Gen* 6:5) and the Lord “was sorry that he had made man on the earth” (*Gen* 6:6), nonetheless, through Noah, who remained innocent and just, God decided to open a path of salvation. In this way he gave humanity the chance of a new beginning. All it takes is one good person to restore hope! The biblical tradition clearly shows that this renewal entails recovering and respecting the rhythms inscribed in nature by the hand of the Creator. We see this, for example, in the law of the Sabbath. On the seventh day, God rested from all his work. He commanded Israel to set aside each seventh day as a day of rest, a *Sabbath*, (cf. *Gen* 2:2-3; *Ex* 16:23; 20:10). Similarly, every seven years, a sabbatical year was set aside for Israel, a complete rest for the land (cf. *Lev* 25:1-4), when sowing was forbidden and one reaped only what was necessary to live on and to feed one’s household (cf. *Lev* 25:4-6). Finally, after seven weeks of years, which is to say forty-nine years, the Jubilee was celebrated as a year of general forgiveness and “liberty throughout the land for all its inhabitants” (cf. *Lev* 25:10). This law came about as an attempt to ensure balance and fairness in their relationships with others and with the land on which they lived and worked. At the same time, it was an acknowledgment that the gift of the earth with its fruits belongs to everyone. Those who tilled and kept the land were obliged to share its fruits, especially with the poor, with widows, orphans and foreigners in their midst: “When you reap the harvest of your land, you shall not reap your field to

its very border, neither shall you gather the gleanings after the harvest. And you shall not strip your vineyard bare, neither shall you gather the fallen grapes of your vineyard; you shall leave them for the poor and for the sojourner” (*Lev* 19:9-10).

72. The Psalms frequently exhort us to praise God the Creator, “who spread out the earth on the waters, for his steadfast love endures for ever” (*Ps* 136:6). They also invite other creatures to join us in this praise: “Praise him, sun and moon, praise him, all you shining stars! Praise him, you highest heavens, and you waters above the heavens! Let them praise the name of the Lord, for he commanded and they were created” (*Ps* 148:3-5). We do not only exist by God’s mighty power; we also live with him and beside him. This is why we adore him.

73. The writings of the prophets invite us to find renewed strength in times of trial by contemplating the all-powerful God who created the universe. Yet God’s infinite power does not lead us to flee his fatherly tenderness, because in him affection and strength are joined. Indeed, all sound spirituality entails both welcoming divine love and adoration, confident in the Lord because of his infinite power. In the Bible, the God who liberates and saves is the same God who created the universe, and these two divine ways of acting are intimately and inseparably connected: “Ah Lord God! It is you who made the heavens and the earth by your great power and by your outstretched arm! Nothing is too hard for you… You brought your people Israel out of the land of Egypt with signs and wonders” (*Jer* 32:17, 21). “The Lord is the everlasting God, the Creator of the ends of the earth. He does not faint or grow weary; his understanding is unsearchable. He gives power to the faint, and strengthens the powerless” (*Is* 40:28b-29).

74. The experience of the Babylonian captivity provoked a spiritual crisis which led to deeper faith in God. Now his creative omnipotence was given pride of place in order to exhort the people to regain their hope in the midst of their wretched predicament. Centuries later, in another age of trial and persecution, when the Roman Empire was seeking to impose absolute dominion, the faithful would once again find consolation and hope in a growing trust in the all-powerful God: “Great and wonderful are your deeds, O Lord God the Almighty! Just and true are your ways!” (*Rev* 15:3). The God who created the universe out of nothing can also intervene in this world and overcome every form of evil. Injustice is not invincible.

75. A spirituality which forgets God as all-powerful and Creator is not acceptable. That is how we end up worshipping earthly powers, or ourselves usurping the place of God, even to the point of claiming an unlimited right to trample his creation underfoot. The best way to restore men and women to their rightful place, putting an end to their claim to absolute dominion over the earth, is to speak once more of the figure of a Father who creates and who alone owns the world. Otherwise, human beings will always try to impose their own laws and interests on reality.

III. THE MYSTERY OF THE UNIVERSE

76. In the Judaeo-Christian tradition, the word “creation” has a broader meaning than “nature”, for it has to do with God’s loving plan in which every creature has its own value and significance. Nature is usually seen as a system which can be studied, understood and controlled, whereas creation can only be understood as a gift from the outstretched hand of the Father of all, and as a reality illuminated by the love which calls us together into universal communion.

77. “By the word of the Lord the heavens were made” (*Ps* 33:6). This tells us that the world came about as the result of a decision, not from chaos or chance, and this exalts it all the more. The creating word expresses a free choice. The universe did not emerge as the result of arbitrary omnipotence, a show of force or a desire for self-assertion. Creation is of the order of love. God’s love is the fundamental moving force in all created things: “For you love all things that exist, and detest none of the things that you have made; for you would not have made anything if you had hated it” (*Wis* 11:24). Every creature is thus the object of the Father’s tenderness, who gives it its place in the world. Even the fleeting life of the least of beings is the object of his love, and in its few seconds of existence, God enfolds it with his affection. Saint Basil the Great described the Creator as “goodness without measure”,[44] while Dante Alighieri spoke of “the love which moves the sun and the stars”.[45] Consequently, we can ascend from created things “to the greatness of God and to his loving mercy”.[46]

78. At the same time, Judaeo-Christian thought demythologized nature. While continuing to admire its grandeur and immensity, it no longer saw nature as divine. In doing so, it emphasizes all the more our human responsibility for nature. This rediscovery of nature can never be at the cost of the freedom and responsibility of human beings who, as part of the world, have the duty to cultivate their abilities in order to protect it and develop its potential. If we acknowledge the value and the fragility of nature and, at the same time, our God-given abilities, we can finally leave behind the modern myth of unlimited material progress. A fragile world, entrusted by God to human care, challenges us to devise intelligent ways of directing, developing and limiting our power.

79. In this universe, shaped by open and intercommunicating systems, we can discern countless forms of relationship and participation. This leads us to think of the whole as open to God’s transcendence, within which it develops. Faith allows us to interpret the meaning and the mysterious beauty of what is unfolding. We are free to apply our intelligence towards things evolving positively, or towards adding new ills, new causes of suffering and real setbacks. This is what makes for the excitement and drama of human history, in which freedom, growth, salvation and love can blossom, or lead towards decadence and mutual destruction. The work of the Church seeks not only to remind everyone of the duty to care for nature, but at the same time “she must above all protect mankind from self-destruction”.[47]

80. Yet God, who wishes to work with us and who counts on our cooperation, can also bring good out of the evil we have done. “The Holy Spirit can be said to possess an infinite creativity, proper

to the divine mind, which knows how to loosen the knots of human affairs, including the most complex and inscrutable”.[48] Creating a world in need of development, God in some way sought to limit himself in such a way that many of the things we think of as evils, dangers or sources of suffering, are in reality part of the pains of childbirth which he uses to draw us into the act of cooperation with the Creator.[49] God is intimately present to each being, without impinging on the autonomy of his creature, and this gives rise to the rightful autonomy of earthly affairs.[50] His divine presence, which ensures the subsistence and growth of each being, “continues the work of creation”.[51] The Spirit of God has filled the universe with possibilities and therefore, from the very heart of things, something new can always emerge: “Nature is nothing other than a certain kind of art, namely God’s art, impressed upon things, whereby those things are moved to a determinate end. It is as if a shipbuilder were able to give timbers the wherewithal to move themselves to take the form of a ship”.[52]

81. Human beings, even if we postulate a process of evolution, also possess a uniqueness which cannot be fully explained by the evolution of other open systems. Each of us has his or her own personal identity and is capable of entering into dialogue with others and with God himself. Our capacity to reason, to develop arguments, to be inventive, to interpret reality and to create art, along with other not yet discovered capacities, are signs of a uniqueness which transcends the spheres of physics and biology. The sheer novelty involved in the emergence of a personal being within a material universe presupposes a direct action of God and a particular call to life and to relationship on the part of a “Thou” who addresses himself to another “thou”. The biblical accounts of creation invite us to see each human being as a subject who can never be reduced to the status of an object.

82. Yet it would also be mistaken to view other living beings as mere objects subjected to arbitrary human domination. When nature is viewed solely as a source of profit and gain, this has serious consequences for society. This vision of “might is right” has engendered immense inequality, injustice and acts of violence against the majority of humanity, since resources end up in the hands of the first comer or the most powerful: the winner takes all. Completely at odds with this model are the ideals of harmony, justice, fraternity and peace as proposed by Jesus. As he said of the powers of his own age: “You know that the rulers of the Gentiles lord it over them, and their great men exercise authority over them. It shall not be so among you; but whoever would be great among you must be your servant” (*Mt* 20:25-26).

83. The ultimate destiny of the universe is in the fullness of God, which has already been attained by the risen Christ, the measure of the maturity of all things.[53] Here we can add yet another argument for rejecting every tyrannical and irresponsible domination of human beings over other creatures. The ultimate purpose of other creatures is not to be found in us. Rather, all creatures are moving forward with us and through us towards a common point of arrival, which is God, in that transcendent fullness where the risen Christ embraces and illumines all things. Human beings, endowed with intelligence and love, and drawn by the fullness of Christ, are called to lead

all creatures back to their Creator.

IV. THE MESSAGE OF EACH CREATURE IN THE HARMONY OF CREATION

84. Our insistence that each human being is an image of God should not make us overlook the fact that each creature has its own purpose. None is superfluous. The entire material universe speaks of God's love, his boundless affection for us. Soil, water, mountains: everything is, as it were, a caress of God. The history of our friendship with God is always linked to particular places which take on an intensely personal meaning; we all remember places, and revisiting those memories does us much good. Anyone who has grown up in the hills or used to sit by the spring to drink, or played outdoors in the neighbourhood square; going back to these places is a chance to recover something of their true selves.

85. God has written a precious book, "whose letters are the multitude of created things present in the universe".[54] The Canadian bishops rightly pointed out that no creature is excluded from this manifestation of God: "From panoramic vistas to the tiniest living form, nature is a constant source of wonder and awe. It is also a continuing revelation of the divine".[55] The bishops of Japan, for their part, made a thought-provoking observation: "To sense each creature singing the hymn of its existence is to live joyfully in God's love and hope".[56] This contemplation of creation allows us to discover in each thing a teaching which God wishes to hand on to us, since "for the believer, to contemplate creation is to hear a message, to listen to a paradoxical and silent voice".[57] We can say that "alongside revelation properly so-called, contained in sacred Scripture, there is a divine manifestation in the blaze of the sun and the fall of night".[58] Paying attention to this manifestation, we learn to see ourselves in relation to all other creatures: "I express myself in expressing the world; in my effort to decipher the sacredness of the world, I explore my own".[59]

86. The universe as a whole, in all its manifold relationships, shows forth the inexhaustible riches of God. Saint Thomas Aquinas wisely noted that multiplicity and variety "come from the intention of the first agent" who willed that "what was wanting to one in the representation of the divine goodness might be supplied by another",[60] inasmuch as God's goodness "could not be represented fittingly by any one creature".[61] Hence we need to grasp the variety of things in their multiple relationships.[62] We understand better the importance and meaning of each creature if we contemplate it within the entirety of God's plan. As the Catechism teaches: "God wills the interdependence of creatures. The sun and the moon, the cedar and the little flower, the eagle and the sparrow: the spectacle of their countless diversities and inequalities tells us that no creature is self-sufficient. Creatures exist only in dependence on each other, to complete each other, in the service of each other".[63]

87. When we can see God reflected in all that exists, our hearts are moved to praise the Lord for all his creatures and to worship him in union with them. This sentiment finds magnificent expression in the hymn of Saint Francis of Assisi:

Praised be you, my Lord, with all your creatures,
especially Sir Brother Sun,
who is the day and through whom you give us light.
And he is beautiful and radiant with great splendour;
and bears a likeness of you, Most High.
Praised be you, my Lord, through Sister Moon and the stars,
in heaven you formed them clear and precious and beautiful.
Praised be you, my Lord, through Brother Wind,
and through the air, cloudy and serene, and every kind of weather
through whom you give sustenance to your creatures.
Praised be you, my Lord, through Sister Water,
who is very useful and humble and precious and chaste.
Praised be you, my Lord, through Brother Fire,
through whom you light the night,
and he is beautiful and playful and robust and strong".[64]

88. The bishops of Brazil have pointed out that nature as a whole not only manifests God but is also a locus of his presence. The Spirit of life dwells in every living creature and calls us to enter into relationship with him.[65] Discovering this presence leads us to cultivate the "ecological virtues".[66] This is not to forget that there is an infinite distance between God and the things of this world, which do not possess his fullness. Otherwise, we would not be doing the creatures themselves any good either, for we would be failing to acknowledge their right and proper place. We would end up unduly demanding of them something which they, in their smallness, cannot give us.

V. A UNIVERSAL COMMUNION

89. The created things of this world are not free of ownership: "For they are yours, O Lord, who love the living" (*Wis* 11:26). This is the basis of our conviction that, as part of the universe, called into being by one Father, all of us are linked by unseen bonds and together form a kind of universal family, a sublime communion which fills us with a sacred, affectionate and humble respect. Here I would reiterate that "God has joined us so closely to the world around us that we can feel the desertification of the soil almost as a physical ailment, and the extinction of a species as a painful disfigurement".[67]

90. This is not to put all living beings on the same level nor to deprive human beings of their unique worth and the tremendous responsibility it entails. Nor does it imply a divinization of the earth which would prevent us from working on it and protecting it in its fragility. Such notions would end up creating new imbalances which would deflect us from the reality which challenges us.[68] At times we see an obsession with denying any pre-eminence to the human person; more zeal is shown in protecting other species than in defending the dignity which all human beings share in

equal measure. Certainly, we should be concerned lest other living beings be treated irresponsibly. But we should be particularly indignant at the enormous inequalities in our midst, whereby we continue to tolerate some considering themselves more worthy than others. We fail to see that some are mired in desperate and degrading poverty, with no way out, while others have not the faintest idea of what to do with their possessions, vainly showing off their supposed superiority and leaving behind them so much waste which, if it were the case everywhere, would destroy the planet. In practice, we continue to tolerate that some consider themselves more human than others, as if they had been born with greater rights.

91. A sense of deep communion with the rest of nature cannot be real if our hearts lack tenderness, compassion and concern for our fellow human beings. It is clearly inconsistent to combat trafficking in endangered species while remaining completely indifferent to human trafficking, unconcerned about the poor, or undertaking to destroy another human being deemed unwanted. This compromises the very meaning of our struggle for the sake of the environment. It is no coincidence that, in the canticle in which Saint Francis praises God for his creatures, he goes on to say: “Praised be you my Lord, through those who give pardon for your love”. Everything is connected. Concern for the environment thus needs to be joined to a sincere love for our fellow human beings and an unwavering commitment to resolving the problems of society.

92. Moreover, when our hearts are authentically open to universal communion, this sense of fraternity excludes nothing and no one. It follows that our indifference or cruelty towards fellow creatures of this world sooner or later affects the treatment we mete out to other human beings. We have only one heart, and the same wretchedness which leads us to mistreat an animal will not be long in showing itself in our relationships with other people. Every act of cruelty towards any creature is “contrary to human dignity”.[69] We can hardly consider ourselves to be fully loving if we disregard any aspect of reality: “Peace, justice and the preservation of creation are three absolutely interconnected themes, which cannot be separated and treated individually without once again falling into reductionism”.[70] Everything is related, and we human beings are united as brothers and sisters on a wonderful pilgrimage, woven together by the love God has for each of his creatures and which also unites us in fond affection with brother sun, sister moon, brother river and mother earth.

VI. THE COMMON DESTINATION OF GOODS

93. Whether believers or not, we are agreed today that the earth is essentially a shared inheritance, whose fruits are meant to benefit everyone. For believers, this becomes a question of fidelity to the Creator, since God created the world for everyone. Hence every ecological approach needs to incorporate a social perspective which takes into account the fundamental rights of the poor and the underprivileged. The principle of the subordination of private property to the universal destination of goods, and thus the right of everyone to their use, is a golden rule of social conduct and “the first principle of the whole ethical and social order”.[71] The Christian tradition has never

recognized the right to private property as absolute or inviolable, and has stressed the social purpose of all forms of private property. Saint John Paul II forcefully reaffirmed this teaching, stating that “God gave the earth to the whole human race for the sustenance of all its members, *without excluding or favouring anyone*”.[72] These are strong words. He noted that “a type of development which did not respect and promote human rights – personal and social, economic and political, including the rights of nations and of peoples – would not be really worthy of man”.[73] He clearly explained that “the Church does indeed defend the legitimate right to private property, but she also teaches no less clearly that there is always a social mortgage on all private property, in order that goods may serve the general purpose that God gave them”.[74] Consequently, he maintained, “it is not in accord with God’s plan that this gift be used in such a way that its benefits favour only a few”.[75] This calls into serious question the unjust habits of a part of humanity.[76]

94. The rich and the poor have equal dignity, for “the Lord is the maker of them all” (*Prov* 22:2). “He himself made both small and great” (*Wis* 6:7), and “he makes his sun rise on the evil and on the good” (*Mt* 5:45). This has practical consequences, such as those pointed out by the bishops of Paraguay: “Every *campesino* has a natural right to possess a reasonable allotment of land where he can establish his home, work for subsistence of his family and a secure life. This right must be guaranteed so that its exercise is not illusory but real. That means that apart from the ownership of property, rural people must have access to means of technical education, credit, insurance, and markets”.[77]

95. The natural environment is a collective good, the patrimony of all humanity and the responsibility of everyone. If we make something our own, it is only to administer it for the good of all. If we do not, we burden our consciences with the weight of having denied the existence of others. That is why the New Zealand bishops asked what the commandment “Thou shall not kill” means when “twenty percent of the world’s population consumes resources at a rate that robs the poor nations and future generations of what they need to survive”.[78]

VII. THE GAZE OF JESUS

96. Jesus took up the biblical faith in God the Creator, emphasizing a fundamental truth: God is Father (cf. *Mt* 11:25). In talking with his disciples, Jesus would invite them to recognize the paternal relationship God has with all his creatures. With moving tenderness he would remind them that each one of them is important in God’s eyes: “Are not five sparrows sold for two pennies? And not one of them is forgotten before God” (*Lk* 12:6). “Look at the birds of the air: they neither sow nor reap nor gather into barns, and yet your heavenly Father feeds them” (*Mt* 6:26).

97. The Lord was able to invite others to be attentive to the beauty that there is in the world because he himself was in constant touch with nature, lending it an attention full of fondness and wonder. As he made his way throughout the land, he often stopped to contemplate the beauty

sown by his Father, and invited his disciples to perceive a divine message in things: “Lift up your eyes, and see how the fields are already white for harvest” (*Jn* 4:35). “The kingdom of God is like a grain of mustard seed which a man took and sowed in his field; it is the smallest of all seeds, but once it has grown, it is the greatest of plants” (*Mt* 13:31-32).

98. Jesus lived in full harmony with creation, and others were amazed: “What sort of man is this, that even the winds and the sea obey him?” (*Mt* 8:27). His appearance was not that of an ascetic set apart from the world, nor of an enemy to the pleasant things of life. Of himself he said: “The Son of Man came eating and drinking and they say, ‘Look, a glutton and a drunkard!’” (*Mt* 11:19). He was far removed from philosophies which despised the body, matter and the things of the world. Such unhealthy dualisms, nonetheless, left a mark on certain Christian thinkers in the course of history and disfigured the Gospel. Jesus worked with his hands, in daily contact with the matter created by God, to which he gave form by his craftsmanship. It is striking that most of his life was dedicated to this task in a simple life which awakened no admiration at all: “Is not this the carpenter, the son of Mary?” (*Mk* 6:3). In this way he sanctified human labour and endowed it with a special significance for our development. As Saint John Paul II taught, “by enduring the toil of work in union with Christ crucified for us, man in a way collaborates with the Son of God for the redemption of humanity”.[79]

99. In the Christian understanding of the world, the destiny of all creation is bound up with the mystery of Christ, present from the beginning: “All things have been created though him and for him” (*Col* 1:16).[80] The prologue of the Gospel of John (1:1-18) reveals Christ’s creative work as the Divine Word (*Logos*). But then, unexpectedly, the prologue goes on to say that this same Word “became flesh” (*Jn* 1:14). One Person of the Trinity entered into the created cosmos, throwing in his lot with it, even to the cross. From the beginning of the world, but particularly through the incarnation, the mystery of Christ is at work in a hidden manner in the natural world as a whole, without thereby impinging on its autonomy.

100. The New Testament does not only tell us of the earthly Jesus and his tangible and loving relationship with the world. It also shows him risen and glorious, present throughout creation by his universal Lordship: “For in him all the fullness of God was pleased to dwell, and through him to reconcile to himself all things, whether on earth or in heaven, making peace by the blood of his cross” (*Col* 1:19-20). This leads us to direct our gaze to the end of time, when the Son will deliver all things to the Father, so that “God may be everything to every one” (*1 Cor* 15:28). Thus, the creatures of this world no longer appear to us under merely natural guise because the risen One is mysteriously holding them to himself and directing them towards fullness as their end. The very flowers of the field and the birds which his human eyes contemplated and admired are now imbued with his radiant presence.

CHAPTER THREE

THE HUMAN ROOTS OF THE ECOLOGICAL CRISIS

101. It would hardly be helpful to describe symptoms without acknowledging the human origins of the ecological crisis. A certain way of understanding human life and activity has gone awry, to the serious detriment of the world around us. Should we not pause and consider this? At this stage, I propose that we focus on the dominant technocratic paradigm and the place of human beings and of human action in the world.

I. TECHNOLOGY: CREATIVITY AND POWER

102. Humanity has entered a new era in which our technical prowess has brought us to a crossroads. We are the beneficiaries of two centuries of enormous waves of change: steam engines, railways, the telegraph, electricity, automobiles, aeroplanes, chemical industries, modern medicine, information technology and, more recently, the digital revolution, robotics, biotechnologies and nanotechnologies. It is right to rejoice in these advances and to be excited by the immense possibilities which they continue to open up before us, for “science and technology are wonderful products of a God-given human creativity”.[81] The modification of nature for useful purposes has distinguished the human family from the beginning; technology itself “expresses the inner tension that impels man gradually to overcome material limitations”.[82] Technology has remedied countless evils which used to harm and limit human beings. How can we not feel gratitude and appreciation for this progress, especially in the fields of medicine, engineering and communications? How could we not acknowledge the work of many scientists and engineers who have provided alternatives to make development sustainable?

103. Technoscience, when well directed, can produce important means of improving the quality of human life, from useful domestic appliances to great transportation systems, bridges, buildings and public spaces. It can also produce art and enable men and women immersed in the material world to “leap” into the world of beauty. Who can deny the beauty of an aircraft or a skyscraper? Valuable works of art and music now make use of new technologies. So, in the beauty intended by the one who uses new technical instruments and in the contemplation of such beauty, a quantum leap occurs, resulting in a fulfilment which is uniquely human.

104. Yet it must also be recognized that nuclear energy, biotechnology, information technology, knowledge of our DNA, and many other abilities which we have acquired, have given us tremendous power. More precisely, they have given those with the knowledge, and especially the economic resources to use them, an impressive dominance over the whole of humanity and the entire world. Never has humanity had such power over itself, yet nothing ensures that it will be used wisely, particularly when we consider how it is currently being used. We need but think of the nuclear bombs dropped in the middle of the twentieth century, or the array of technology which Nazism, Communism and other totalitarian regimes have employed to kill millions of people, to say nothing of the increasingly deadly arsenal of weapons available for modern warfare. In whose

hands does all this power lie, or will it eventually end up? It is extremely risky for a small part of humanity to have it.

105. There is a tendency to believe that every increase in power means “an increase of ‘progress’ itself”, an advance in “security, usefulness, welfare and vigour; …an assimilation of new values into the stream of culture”,[83] as if reality, goodness and truth automatically flow from technological and economic power as such. The fact is that “contemporary man has not been trained to use power well”,[84] because our immense technological development has not been accompanied by a development in human responsibility, values and conscience. Each age tends to have only a meagre awareness of its own limitations. It is possible that we do not grasp the gravity of the challenges now before us. “The risk is growing day by day that man will not use his power as he should”; in effect, “power is never considered in terms of the responsibility of choice which is inherent in freedom” since its “only norms are taken from alleged necessity, from either utility or security”.[85] But human beings are not completely autonomous. Our freedom fades when it is handed over to the blind forces of the unconscious, of immediate needs, of self-interest, and of violence. In this sense, we stand naked and exposed in the face of our ever-increasing power, lacking the wherewithal to control it. We have certain superficial mechanisms, but we cannot claim to have a sound ethics, a culture and spirituality genuinely capable of setting limits and teaching clear-minded self-restraint.

II. THE GLOBALIZATION OF THE TECHNOCRATIC PARADIGM

106. The basic problem goes even deeper: it is the way that humanity has taken up technology and its development *according to an undifferentiated and one-dimensional paradigm*. This paradigm exalts the concept of a subject who, using logical and rational procedures, progressively approaches and gains control over an external object. This subject makes every effort to establish the scientific and experimental method, which in itself is already a technique of possession, mastery and transformation. It is as if the subject were to find itself in the presence of something formless, completely open to manipulation. Men and women have constantly intervened in nature, but for a long time this meant being in tune with and respecting the possibilities offered by the things themselves. It was a matter of receiving what nature itself allowed, as if from its own hand. Now, by contrast, we are the ones to lay our hands on things, attempting to extract everything possible from them while frequently ignoring or forgetting the reality in front of us. Human beings and material objects no longer extend a friendly hand to one another; the relationship has become confrontational. This has made it easy to accept the idea of infinite or unlimited growth, which proves so attractive to economists, financiers and experts in technology. It is based on the lie that there is an infinite supply of the earth’s goods, and this leads to the planet being squeezed dry beyond every limit. It is the false notion that “an infinite quantity of energy and resources are available, that it is possible to renew them quickly, and that the negative effects of the exploitation of the natural order can be easily absorbed”.[86]

107. It can be said that many problems of today's world stem from the tendency, at times unconscious, to make the method and aims of science and technology an epistemological paradigm which shapes the lives of individuals and the workings of society. The effects of imposing this model on reality as a whole, human and social, are seen in the deterioration of the environment, but this is just one sign of a reductionism which affects every aspect of human and social life. We have to accept that technological products are not neutral, for they create a framework which ends up conditioning lifestyles and shaping social possibilities along the lines dictated by the interests of certain powerful groups. Decisions which may seem purely instrumental are in reality decisions about the kind of society we want to build.

108. The idea of promoting a different cultural paradigm and employing technology as a mere instrument is nowadays inconceivable. The technological paradigm has become so dominant that it would be difficult to do without its resources and even more difficult to utilize them without being dominated by their internal logic. It has become countercultural to choose a lifestyle whose goals are even partly independent of technology, of its costs and its power to globalize and make us all the same. Technology tends to absorb everything into its ironclad logic, and those who are surrounded with technology "know full well that it moves forward in the final analysis neither for profit nor for the well-being of the human race", that "in the most radical sense of the term power is its motive – a lordship over all".[87] As a result, "man seizes hold of the naked elements of both nature and human nature".[88] Our capacity to make decisions, a more genuine freedom and the space for each one's alternative creativity are diminished.

109. The technocratic paradigm also tends to dominate economic and political life. The economy accepts every advance in technology with a view to profit, without concern for its potentially negative impact on human beings. Finance overwhelms the real economy. The lessons of the global financial crisis have not been assimilated, and we are learning all too slowly the lessons of environmental deterioration. Some circles maintain that current economics and technology will solve all environmental problems, and argue, in popular and non-technical terms, that the problems of global hunger and poverty will be resolved simply by market growth. They are less concerned with certain economic theories which today scarcely anybody dares defend, than with their actual operation in the functioning of the economy. They may not affirm such theories with words, but nonetheless support them with their deeds by showing no interest in more balanced levels of production, a better distribution of wealth, concern for the environment and the rights of future generations. Their behaviour shows that for them maximizing profits is enough. Yet by itself the market cannot guarantee integral human development and social inclusion.[89] At the same time, we have "a sort of 'superdevelopment' of a wasteful and consumerist kind which forms an unacceptable contrast with the ongoing situations of dehumanizing deprivation",[90] while we are all too slow in developing economic institutions and social initiatives which can give the poor regular access to basic resources. We fail to see the deepest roots of our present failures, which have to do with the direction, goals, meaning and social implications of technological and economic growth.

110. The specialization which belongs to technology makes it difficult to see the larger picture. The fragmentation of knowledge proves helpful for concrete applications, and yet it often leads to a loss of appreciation for the whole, for the relationships between things, and for the broader horizon, which then becomes irrelevant. This very fact makes it hard to find adequate ways of solving the more complex problems of today's world, particularly those regarding the environment and the poor; these problems cannot be dealt with from a single perspective or from a single set of interests. A science which would offer solutions to the great issues would necessarily have to take into account the data generated by other fields of knowledge, including philosophy and social ethics; but this is a difficult habit to acquire today. Nor are there genuine ethical horizons to which one can appeal. Life gradually becomes a surrender to situations conditioned by technology, itself viewed as the principal key to the meaning of existence. In the concrete situation confronting us, there are a number of symptoms which point to what is wrong, such as environmental degradation, anxiety, a loss of the purpose of life and of community living. Once more we see that "realities are more important than ideas".[91]

111. Ecological culture cannot be reduced to a series of urgent and partial responses to the immediate problems of pollution, environmental decay and the depletion of natural resources. There needs to be a distinctive way of looking at things, a way of thinking, policies, an educational programme, a lifestyle and a spirituality which together generate resistance to the assault of the technocratic paradigm. Otherwise, even the best ecological initiatives can find themselves caught up in the same globalized logic. To seek only a technical remedy to each environmental problem which comes up is to separate what is in reality interconnected and to mask the true and deepest problems of the global system.

112. Yet we can once more broaden our vision. We have the freedom needed to limit and direct technology; we can put it at the service of another type of progress, one which is healthier, more human, more social, more integral. Liberation from the dominant technocratic paradigm does in fact happen sometimes, for example, when cooperatives of small producers adopt less polluting means of production, and opt for a non-consumerist model of life, recreation and community. Or when technology is directed primarily to resolving people's concrete problems, truly helping them live with more dignity and less suffering. Or indeed when the desire to create and contemplate beauty manages to overcome reductionism through a kind of salvation which occurs in beauty and in those who behold it. An authentic humanity, calling for a new synthesis, seems to dwell in the midst of our technological culture, almost unnoticed, like a mist seeping gently beneath a closed door. Will the promise last, in spite of everything, with all that is authentic rising up in stubborn resistance?

113. There is also the fact that people no longer seem to believe in a happy future; they no longer have blind trust in a better tomorrow based on the present state of the world and our technical abilities. There is a growing awareness that scientific and technological progress cannot be equated with the progress of humanity and history, a growing sense that the way to a better future

lies elsewhere. This is not to reject the possibilities which technology continues to offer us. But humanity has changed profoundly, and the accumulation of constant novelties exalts a superficiality which pulls us in one direction. It becomes difficult to pause and recover depth in life. If architecture reflects the spirit of an age, our megastructures and drab apartment blocks express the spirit of globalized technology, where a constant flood of new products coexists with a tedious monotony. Let us refuse to resign ourselves to this, and continue to wonder about the purpose and meaning of everything. Otherwise we would simply legitimate the present situation and need new forms of escapism to help us endure the emptiness.

114. All of this shows the urgent need for us to move forward in a bold cultural revolution. Science and technology are not neutral; from the beginning to the end of a process, various intentions and possibilities are in play and can take on distinct shapes. Nobody is suggesting a return to the Stone Age, but we do need to slow down and look at reality in a different way, to appropriate the positive and sustainable progress which has been made, but also to recover the values and the great goals swept away by our unrestrained delusions of grandeur.

III. THE CRISIS AND EFFECTS OF MODERN ANTHROPOCENTRISM

115. Modern anthropocentrism has paradoxically ended up prizing technical thought over reality, since “the technological mind sees nature as an insensate order, as a cold body of facts, as a mere ‘given’, as an object of utility, as raw material to be hammered into useful shape; it views the cosmos similarly as a mere ‘space’ into which objects can be thrown with complete indifference”.[92] The intrinsic dignity of the world is thus compromised. When human beings fail to find their true place in this world, they misunderstand themselves and end up acting against themselves: “Not only has God given the earth to man, who must use it with respect for the original good purpose for which it was given, but, man too is God’s gift to man. He must therefore respect the natural and moral structure with which he has been endowed”.[93]

116. Modernity has been marked by an excessive anthropocentrism which today, under another guise, continues to stand in the way of shared understanding and of any effort to strengthen social bonds. The time has come to pay renewed attention to reality and the limits it imposes; this in turn is the condition for a more sound and fruitful development of individuals and society. An inadequate presentation of Christian anthropology gave rise to a wrong understanding of the relationship between human beings and the world. Often, what was handed on was a Promethean vision of mastery over the world, which gave the impression that the protection of nature was something that only the faint-hearted cared about. Instead, our “dominion” over the universe should be understood more properly in the sense of responsible stewardship.[94]

117. Neglecting to monitor the harm done to nature and the environmental impact of our decisions is only the most striking sign of a disregard for the message contained in the structures of nature itself. When we fail to acknowledge as part of reality the worth of a poor person, a human embryo,

a person with disabilities – to offer just a few examples – it becomes difficult to hear the cry of nature itself; everything is connected. Once the human being declares independence from reality and behaves with absolute dominion, the very foundations of our life begin to crumble, for "instead of carrying out his role as a cooperator with God in the work of creation, man sets himself up in place of God and thus ends up provoking a rebellion on the part of nature".[95]

118. This situation has led to a constant schizophrenia, wherein a technocracy which sees no intrinsic value in lesser beings coexists with the other extreme, which sees no special value in human beings. But one cannot prescind from humanity. There can be no renewal of our relationship with nature without a renewal of humanity itself. There can be no ecology without an adequate anthropology. When the human person is considered as simply one being among others, the product of chance or physical determinism, then "our overall sense of responsibility wanes".[96] A misguided anthropocentrism need not necessarily yield to "biocentrism", for that would entail adding yet another imbalance, failing to solve present problems and adding new ones. Human beings cannot be expected to feel responsibility for the world unless, at the same time, their unique capacities of knowledge, will, freedom and responsibility are recognized and valued.

119. Nor must the critique of a misguided anthropocentrism underestimate the importance of interpersonal relations. If the present ecological crisis is one small sign of the ethical, cultural and spiritual crisis of modernity, we cannot presume to heal our relationship with nature and the environment without healing all fundamental human relationships. Christian thought sees human beings as possessing a particular dignity above other creatures; it thus inculcates esteem for each person and respect for others. Our openness to others, each of whom is a "thou" capable of knowing, loving and entering into dialogue, remains the source of our nobility as human persons. A correct relationship with the created world demands that we not weaken this social dimension of openness to others, much less the transcendent dimension of our openness to the "Thou" of God. Our relationship with the environment can never be isolated from our relationship with others and with God. Otherwise, it would be nothing more than romantic individualism dressed up in ecological garb, locking us into a stifling immanence.

120. Since everything is interrelated, concern for the protection of nature is also incompatible with the justification of abortion. How can we genuinely teach the importance of concern for other vulnerable beings, however troublesome or inconvenient they may be, if we fail to protect a human embryo, even when its presence is uncomfortable and creates difficulties? "If personal and social sensitivity towards the acceptance of the new life is lost, then other forms of acceptance that are valuable for society also wither away".[97]

121. We need to develop a new synthesis capable of overcoming the false arguments of recent centuries. Christianity, in fidelity to its own identity and the rich deposit of truth which it has received from Jesus Christ, continues to reflect on these issues in fruitful dialogue with changing

historical situations. In doing so, it reveals its eternal newness.[98]

Practical relativism

122. A misguided anthropocentrism leads to a misguided lifestyle. In the Apostolic Exhortation *Evangelii Gaudium,* I noted that the practical relativism typical of our age is "even more dangerous than doctrinal relativism".[99] When human beings place themselves at the centre, they give absolute priority to immediate convenience and all else becomes relative. Hence we should not be surprised to find, in conjunction with the omnipresent technocratic paradigm and the cult of unlimited human power, the rise of a relativism which sees everything as irrelevant unless it serves one's own immediate interests. There is a logic in all this whereby different attitudes can feed on one another, leading to environmental degradation and social decay.

123. The culture of relativism is the same disorder which drives one person to take advantage of another, to treat others as mere objects, imposing forced labour on them or enslaving them to pay their debts. The same kind of thinking leads to the sexual exploitation of children and abandonment of the elderly who no longer serve our interests. It is also the mindset of those who say: Let us allow the invisible forces of the market to regulate the economy, and consider their impact on society and nature as collateral damage. In the absence of objective truths or sound principles other than the satisfaction of our own desires and immediate needs, what limits can be placed on human trafficking, organized crime, the drug trade, commerce in blood diamonds and the fur of endangered species? Is it not the same relativistic logic which justifies buying the organs of the poor for resale or use in experimentation, or eliminating children because they are not what their parents wanted? This same "use and throw away" logic generates so much waste, because of the disordered desire to consume more than what is really necessary. We should not think that political efforts or the force of law will be sufficient to prevent actions which affect the environment because, when the culture itself is corrupt and objective truth and universally valid principles are no longer upheld, then laws can only be seen as arbitrary impositions or obstacles to be avoided.

The need to protect employment

124. Any approach to an integral ecology, which by definition does not exclude human beings, needs to take account of the value of labour, as Saint John Paul II wisely noted in his Encyclical *Laborem Exercens*. According to the biblical account of creation, God placed man and woman in the garden he had created (cf. *Gen* 2:15) not only to preserve it ("keep") but also to make it fruitful ("till"). Labourers and craftsmen thus "maintain the fabric of the world" (*Sir* 38:34). Developing the created world in a prudent way is the best way of caring for it, as this means that we ourselves become the instrument used by God to bring out the potential which he himself inscribed in things: "The Lord created medicines out of the earth, and a sensible man will not despise them" (*Sir* 38:4).

125. If we reflect on the proper relationship between human beings and the world around us, we

see the need for a correct understanding of work; if we talk about the relationship between human beings and things, the question arises as to the meaning and purpose of all human activity. This has to do not only with manual or agricultural labour but with any activity involving a modification of existing reality, from producing a social report to the design of a technological development. Underlying every form of work is a concept of the relationship which we can and must have with what is other than ourselves. Together with the awe-filled contemplation of creation which we find in Saint Francis of Assisi, the Christian spiritual tradition has also developed a rich and balanced understanding of the meaning of work, as, for example, in the life of Blessed Charles de Foucauld and his followers.

126. We can also look to the great tradition of monasticism. Originally, it was a kind of flight from the world, an escape from the decadence of the cities. The monks sought the desert, convinced that it was the best place for encountering the presence of God. Later, Saint Benedict of Norcia proposed that his monks live in community, combining prayer and spiritual reading with manual labour (*ora et labora*). Seeing manual labour as spiritually meaningful proved revolutionary. Personal growth and sanctification came to be sought in the interplay of recollection and work. This way of experiencing work makes us more protective and respectful of the environment; it imbues our relationship to the world with a healthy sobriety.

127. We are convinced that “man is the source, the focus and the aim of all economic and social life”.[100] Nonetheless, once our human capacity for contemplation and reverence is impaired, it becomes easy for the meaning of work to be misunderstood.[101] We need to remember that men and women have “the capacity to improve their lot, to further their moral growth and to develop their spiritual endowments”.[102] Work should be the setting for this rich personal growth, where many aspects of life enter into play: creativity, planning for the future, developing our talents, living out our values, relating to others, giving glory to God. It follows that, in the reality of today’s global society, it is essential that “we continue to prioritize the goal of access to steady employment for everyone”,[103] no matter the limited interests of business and dubious economic reasoning.

128. We were created with a vocation to work. The goal should not be that technological progress increasingly replace human work, for this would be detrimental to humanity. Work is a necessity, part of the meaning of life on this earth, a path to growth, human development and personal fulfilment. Helping the poor financially must always be a provisional solution in the face of pressing needs. The broader objective should always be to allow them a dignified life through work. Yet the orientation of the economy has favoured a kind of technological progress in which the costs of production are reduced by laying off workers and replacing them with machines. This is yet another way in which we can end up working against ourselves. The loss of jobs also has a negative impact on the economy “through the progressive erosion of social capital: the network of relationships of trust, dependability, and respect for rules, all of which are indispensable for any form of civil coexistence”.[104] In other words, “human costs always include economic costs, and economic dysfunctions always involve human costs”.[105] To stop investing in people, in order to

gain greater short-term financial gain, is bad business for society.

129. In order to continue providing employment, it is imperative to promote an economy which favours productive diversity and business creativity. For example, there is a great variety of small-scale food production systems which feed the greater part of the world's peoples, using a modest amount of land and producing less waste, be it in small agricultural parcels, in orchards and gardens, hunting and wild harvesting or local fishing. Economies of scale, especially in the agricultural sector, end up forcing smallholders to sell their land or to abandon their traditional crops. Their attempts to move to other, more diversified, means of production prove fruitless because of the difficulty of linkage with regional and global markets, or because the infrastructure for sales and transport is geared to larger businesses. Civil authorities have the right and duty to adopt clear and firm measures in support of small producers and differentiated production. To ensure economic freedom from which all can effectively benefit, restraints occasionally have to be imposed on those possessing greater resources and financial power. To claim economic freedom while real conditions bar many people from actual access to it, and while possibilities for employment continue to shrink, is to practise a doublespeak which brings politics into disrepute. Business is a noble vocation, directed to producing wealth and improving our world. It can be a fruitful source of prosperity for the areas in which it operates, especially if it sees the creation of jobs as an essential part of its service to the common good.

New biological technologies

130. In the philosophical and theological vision of the human being and of creation which I have presented, it is clear that the human person, endowed with reason and knowledge, is not an external factor to be excluded. While human intervention on plants and animals is permissible when it pertains to the necessities of human life, the *Catechism of the Catholic Church* teaches that experimentation on animals is morally acceptable only "if it remains within reasonable limits [and] contributes to caring for or saving human lives".[106] The *Catechism* firmly states that human power has limits and that "it is contrary to human dignity to cause animals to suffer or die needlessly".[107] All such use and experimentation "requires a religious respect for the integrity of creation".[108]

131. Here I would recall the balanced position of Saint John Paul II, who stressed the benefits of scientific and technological progress as evidence of "the nobility of the human vocation to participate responsibly in God's creative action", while also noting that "we cannot interfere in one area of the ecosystem without paying due attention to the consequences of such interference in other areas".[109] He made it clear that the Church values the benefits which result "from the study and applications of molecular biology, supplemented by other disciplines such as genetics, and its technological application in agriculture and industry".[110] But he also pointed out that this should not lead to "indiscriminate genetic manipulation"[111] which ignores the negative effects of such interventions. Human creativity cannot be suppressed. If an artist cannot be stopped from

using his or her creativity, neither should those who possess particular gifts for the advancement of science and technology be prevented from using their God-given talents for the service of others. We need constantly to rethink the goals, effects, overall context and ethical limits of this human activity, which is a form of power involving considerable risks.

132. This, then, is the correct framework for any reflection concerning human intervention on plants and animals, which at present includes genetic manipulation by biotechnology for the sake of exploiting the potential present in material reality. The respect owed by faith to reason calls for close attention to what the biological sciences, through research uninfluenced by economic interests, can teach us about biological structures, their possibilities and their mutations. Any legitimate intervention will act on nature only in order "to favour its development in its own line, that of creation, as intended by God".[112]

133. It is difficult to make a general judgement about genetic modification (GM), whether vegetable or animal, medical or agricultural, since these vary greatly among themselves and call for specific considerations. The risks involved are not always due to the techniques used, but rather to their improper or excessive application. Genetic mutations, in fact, have often been, and continue to be, caused by nature itself. Nor are mutations caused by human intervention a modern phenomenon. The domestication of animals, the crossbreeding of species and other older and universally accepted practices can be mentioned as examples. We need but recall that scientific developments in GM cereals began with the observation of natural bacteria which spontaneously modified plant genomes. In nature, however, this process is slow and cannot be compared to the fast pace induced by contemporary technological advances, even when the latter build upon several centuries of scientific progress.

134. Although no conclusive proof exists that GM cereals may be harmful to human beings, and in some regions their use has brought about economic growth which has helped to resolve problems, there remain a number of significant difficulties which should not be underestimated. In many places, following the introduction of these crops, productive land is concentrated in the hands of a few owners due to "the progressive disappearance of small producers, who, as a consequence of the loss of the exploited lands, are obliged to withdraw from direct production".[113] The most vulnerable of these become temporary labourers, and many rural workers end up moving to poverty-stricken urban areas. The expansion of these crops has the effect of destroying the complex network of ecosystems, diminishing the diversity of production and affecting regional economies, now and in the future. In various countries, we see an expansion of oligopolies for the production of cereals and other products needed for their cultivation. This dependency would be aggravated were the production of infertile seeds to be considered; the effect would be to force farmers to purchase them from larger producers.

135. Certainly, these issues require constant attention and a concern for their ethical implications. A broad, responsible scientific and social debate needs to take place, one capable of considering

all the available information and of calling things by their name. It sometimes happens that complete information is not put on the table; a selection is made on the basis of particular interests, be they politico-economic or ideological. This makes it difficult to reach a balanced and prudent judgement on different questions, one which takes into account all the pertinent variables. Discussions are needed in which all those directly or indirectly affected (farmers, consumers, civil authorities, scientists, seed producers, people living near fumigated fields, and others) can make known their problems and concerns, and have access to adequate and reliable information in order to make decisions for the common good, present and future. This is a complex environmental issue; it calls for a comprehensive approach which would require, at the very least, greater efforts to finance various lines of independent, interdisciplinary research capable of shedding new light on the problem.

136. On the other hand, it is troubling that, when some ecological movements defend the integrity of the environment, rightly demanding that certain limits be imposed on scientific research, they sometimes fail to apply those same principles to human life. There is a tendency to justify transgressing all boundaries when experimentation is carried out on living human embryos. We forget that the inalienable worth of a human being transcends his or her degree of development. In the same way, when technology disregards the great ethical principles, it ends up considering any practice whatsoever as licit. As we have seen in this chapter, a technology severed from ethics will not easily be able to limit its own power.

CHAPTER FOUR

INTEGRAL ECOLOGY

137. Since everything is closely interrelated, and today’s problems call for a vision capable of taking into account every aspect of the global crisis, I suggest that we now consider some elements of an *integral ecology*, one which clearly respects its human and social dimensions.

I. ENVIRONMENTAL, ECONOMIC AND SOCIAL ECOLOGY

138. Ecology studies the relationship between living organisms and the environment in which they develop. This necessarily entails reflection and debate about the conditions required for the life and survival of society, and the honesty needed to question certain models of development, production and consumption. It cannot be emphasized enough how everything is interconnected. Time and space are not independent of one another, and not even atoms or subatomic particles can be considered in isolation. Just as the different aspects of the planet – physical, chemical and biological – are interrelated, so too living species are part of a network which we will never fully explore and understand. A good part of our genetic code is shared by many living beings. It follows that the fragmentation of knowledge and the isolation of bits of information can actually become a form of ignorance, unless they are integrated into a broader vision of reality.

139. When we speak of the “environment”, what we really mean is a relationship existing between nature and the society which lives in it. Nature cannot be regarded as something separate from ourselves or as a mere setting in which we live. We are part of nature, included in it and thus in constant interaction with it. Recognizing the reasons why a given area is polluted requires a study of the workings of society, its economy, its behaviour patterns, and the ways it grasps reality. Given the scale of change, it is no longer possible to find a specific, discrete answer for each part of the problem. It is essential to seek comprehensive solutions which consider the interactions within natural systems themselves and with social systems. We are faced not with two separate crises, one environmental and the other social, but rather with one complex crisis which is both social and environmental. Strategies for a solution demand an integrated approach to combating poverty, restoring dignity to the excluded, and at the same time protecting nature.

140. Due to the number and variety of factors to be taken into account when determining the environmental impact of a concrete undertaking, it is essential to give researchers their due role, to facilitate their interaction, and to ensure broad academic freedom. Ongoing research should also give us a better understanding of how different creatures relate to one another in making up the larger units which today we term “ecosystems”. We take these systems into account not only to determine how best to use them, but also because they have an intrinsic value independent of their usefulness. Each organism, as a creature of God, is good and admirable in itself; the same is true of the harmonious ensemble of organisms existing in a defined space and functioning as a system. Although we are often not aware of it, we depend on these larger systems for our own existence. We need only recall how ecosystems interact in dispersing carbon dioxide, purifying water, controlling illnesses and epidemics, forming soil, breaking down waste, and in many other ways which we overlook or simply do not know about. Once they become conscious of this, many people realize that we live and act on the basis of a reality which has previously been given to us, which precedes our existence and our abilities. So, when we speak of “sustainable use”, consideration must always be given to each ecosystem’s regenerative ability in its different areas and aspects.

141. Economic growth, for its part, tends to produce predictable reactions and a certain standardization with the aim of simplifying procedures and reducing costs. This suggests the need for an “economic ecology” capable of appealing to a broader vision of reality. The protection of the environment is in fact “an integral part of the development process and cannot be considered in isolation from it”.[114] We urgently need a humanism capable of bringing together the different fields of knowledge, including economics, in the service of a more integral and integrating vision. Today, the analysis of environmental problems cannot be separated from the analysis of human, family, work-related and urban contexts, nor from how individuals relate to themselves, which leads in turn to how they relate to others and to the environment. There is an interrelation between ecosystems and between the various spheres of social interaction, demonstrating yet again that “the whole is greater than the part”.[115]

142. If everything is related, then the health of a society’s institutions has consequences for the environment and the quality of human life. “Every violation of solidarity and civic friendship harms the environment”.[116] In this sense, social ecology is necessarily institutional, and gradually extends to the whole of society, from the primary social group, the family, to the wider local, national and international communities. Within each social stratum, and between them, institutions develop to regulate human relationships. Anything which weakens those institutions has negative consequences, such as injustice, violence and loss of freedom. A number of countries have a relatively low level of institutional effectiveness, which results in greater problems for their people while benefiting those who profit from this situation. Whether in the administration of the state, the various levels of civil society, or relationships between individuals themselves, lack of respect for the law is becoming more common. Laws may be well framed yet remain a dead letter. Can we hope, then, that in such cases, legislation and regulations dealing with the environment will really prove effective? We know, for example, that countries which have clear legislation about the protection of forests continue to keep silent as they watch laws repeatedly being broken. Moreover, what takes place in any one area can have a direct or indirect influence on other areas. Thus, for example, drug use in affluent societies creates a continual and growing demand for products imported from poorer regions, where behaviour is corrupted, lives are destroyed, and the environment continues to deteriorate.

II. CULTURAL ECOLOGY

143. Together with the patrimony of nature, there is also an historic, artistic and cultural patrimony which is likewise under threat. This patrimony is a part of the shared identity of each place and a foundation upon which to build a habitable city. It is not a matter of tearing down and building new cities, supposedly more respectful of the environment yet not always more attractive to live in. Rather, there is a need to incorporate the history, culture and architecture of each place, thus preserving its original identity. Ecology, then, also involves protecting the cultural treasures of humanity in the broadest sense. More specifically, it calls for greater attention to local cultures when studying environmental problems, favouring a dialogue between scientific-technical language and the language of the people. Culture is more than what we have inherited from the past; it is also, and above all, a living, dynamic and participatory present reality, which cannot be excluded as we rethink the relationship between human beings and the environment.

144. A consumerist vision of human beings, encouraged by the mechanisms of today’s globalized economy, has a levelling effect on cultures, diminishing the immense variety which is the heritage of all humanity. Attempts to resolve all problems through uniform regulations or technical interventions can lead to overlooking the complexities of local problems which demand the active participation of all members of the community. New processes taking shape cannot always fit into frameworks imported from outside; they need to be based in the local culture itself. As life and the world are dynamic realities, so our care for the world must also be flexible and dynamic. Merely technical solutions run the risk of addressing symptoms and not the more serious underlying

problems. There is a need to respect the rights of peoples and cultures, and to appreciate that the development of a social group presupposes an historical process which takes place within a cultural context and demands the constant and active involvement of local people *from within their proper culture*. Nor can the notion of the quality of life be imposed from without, for quality of life must be understood within the world of symbols and customs proper to each human group.

145. Many intensive forms of environmental exploitation and degradation not only exhaust the resources which provide local communities with their livelihood, but also undo the social structures which, for a long time, shaped cultural identity and their sense of the meaning of life and community. The disappearance of a culture can be just as serious, or even more serious, than the disappearance of a species of plant or animal. The imposition of a dominant lifestyle linked to a single form of production can be just as harmful as the altering of ecosystems.

146. In this sense, it is essential to show special care for indigenous communities and their cultural traditions. They are not merely one minority among others, but should be the principal dialogue partners, especially when large projects affecting their land are proposed. For them, land is not a commodity but rather a gift from God and from their ancestors who rest there, a sacred space with which they need to interact if they are to maintain their identity and values. When they remain on their land, they themselves care for it best. Nevertheless, in various parts of the world, pressure is being put on them to abandon their homelands to make room for agricultural or mining projects which are undertaken without regard for the degradation of nature and culture.

III. ECOLOGY OF DAILY LIFE

147. Authentic development includes efforts to bring about an integral improvement in the quality of human life, and this entails considering the setting in which people live their lives. These settings influence the way we think, feel and act. In our rooms, our homes, our workplaces and neighbourhoods, we use our environment as a way of expressing our identity. We make every effort to adapt to our environment, but when it is disorderly, chaotic or saturated with noise and ugliness, such overstimulation makes it difficult to find ourselves integrated and happy.

148. An admirable creativity and generosity is shown by persons and groups who respond to environmental limitations by alleviating the adverse effects of their surroundings and learning to orient their lives amid disorder and uncertainty. For example, in some places, where the façades of buildings are derelict, people show great care for the interior of their homes, or find contentment in the kindness and friendliness of others. A wholesome social life can light up a seemingly undesirable environment. At times a commendable human ecology is practised by the poor despite numerous hardships. The feeling of asphyxiation brought on by densely populated residential areas is countered if close and warm relationships develop, if communities are created, if the limitations of the environment are compensated for in the interior of each person who feels held within a network of solidarity and belonging. In this way, any place can turn from being a hell

on earth into the setting for a dignified life.

149. The extreme poverty experienced in areas lacking harmony, open spaces or potential for integration, can lead to incidents of brutality and to exploitation by criminal organizations. In the unstable neighbourhoods of mega-cities, the daily experience of overcrowding and social anonymity can create a sense of uprootedness which spawns antisocial behaviour and violence. Nonetheless, I wish to insist that love always proves more powerful. Many people in these conditions are able to weave bonds of belonging and togetherness which convert overcrowding into an experience of community in which the walls of the ego are torn down and the barriers of selfishness overcome. This experience of a communitarian salvation often generates creative ideas for the improvement of a building or a neighbourhood.[117]

150. Given the interrelationship between living space and human behaviour, those who design buildings, neighbourhoods, public spaces and cities, ought to draw on the various disciplines which help us to understand people’s thought processes, symbolic language and ways of acting. It is not enough to seek the beauty of design. More precious still is the service we offer to another kind of beauty: people’s quality of life, their adaptation to the environment, encounter and mutual assistance. Here too, we see how important it is that urban planning always take into consideration the views of those who will live in these areas.

151. There is also a need to protect those common areas, visual landmarks and urban landscapes which increase our sense of belonging, of rootedness, of “feeling at home” within a city which includes us and brings us together. It is important that the different parts of a city be well integrated and that those who live there have a sense of the whole, rather than being confined to one neighbourhood and failing to see the larger city as space which they share with others. Interventions which affect the urban or rural landscape should take into account how various elements combine to form a whole which is perceived by its inhabitants as a coherent and meaningful framework for their lives. Others will then no longer be seen as strangers, but as part of a “we” which all of us are working to create. For this same reason, in both urban and rural settings, it is helpful to set aside some places which can be preserved and protected from constant changes brought by human intervention.

152. Lack of housing is a grave problem in many parts of the world, both in rural areas and in large cities, since state budgets usually cover only a small portion of the demand. Not only the poor, but many other members of society as well, find it difficult to own a home. Having a home has much to do with a sense of personal dignity and the growth of families. This is a major issue for human ecology. In some places, where makeshift shanty towns have sprung up, this will mean developing those neighbourhoods rather than razing or displacing them. When the poor live in unsanitary slums or in dangerous tenements, “in cases where it is necessary to relocate them, in order not to heap suffering upon suffering, adequate information needs to be given beforehand, with choices of decent housing offered, and the people directly involved must be part of the process”.[118] At the

same time, creativity should be shown in integrating rundown neighbourhoods into a welcoming city: “How beautiful those cities which overcome paralyzing mistrust, integrate those who are different and make this very integration a new factor of development! How attractive are those cities which, even in their architectural design, are full of spaces which connect, relate and favour the recognition of others!”[119]

153. The quality of life in cities has much to do with systems of transport, which are often a source of much suffering for those who use them. Many cars, used by one or more people, circulate in cities, causing traffic congestion, raising the level of pollution, and consuming enormous quantities of non-renewable energy. This makes it necessary to build more roads and parking areas which spoil the urban landscape. Many specialists agree on the need to give priority to public transportation. Yet some measures needed will not prove easily acceptable to society unless substantial improvements are made in the systems themselves, which in many cities force people to put up with undignified conditions due to crowding, inconvenience, infrequent service and lack of safety.

154. Respect for our dignity as human beings often jars with the chaotic realities that people have to endure in city life. Yet this should not make us overlook the abandonment and neglect also experienced by some rural populations which lack access to essential services and where some workers are reduced to conditions of servitude, without rights or even the hope of a more dignified life.

155. Human ecology also implies another profound reality: the relationship between human life and the moral law, which is inscribed in our nature and is necessary for the creation of a more dignified environment. Pope Benedict XVI spoke of an “ecology of man”, based on the fact that “man too has a nature that he must respect and that he cannot manipulate at will”.[120] It is enough to recognize that our body itself establishes us in a direct relationship with the environment and with other living beings. The acceptance of our bodies as God’s gift is vital for welcoming and accepting the entire world as a gift from the Father and our common home, whereas thinking that we enjoy absolute power over our own bodies turns, often subtly, into thinking that we enjoy absolute power over creation. Learning to accept our body, to care for it and to respect its fullest meaning, is an essential element of any genuine human ecology. Also, valuing one’s own body in its femininity or masculinity is necessary if I am going to be able to recognize myself in an encounter with someone who is different. In this way we can joyfully accept the specific gifts of another man or woman, the work of God the Creator, and find mutual enrichment. It is not a healthy attitude which would seek “to cancel out sexual difference because it no longer knows how to confront it”.[121]

IV. THE PRINCIPLE OF THE COMMON GOOD

156. An integral ecology is inseparable from the notion of the common good, a central and unifying

principle of social ethics. The common good is “the sum of those conditions of social life which allow social groups and their individual members relatively thorough and ready access to their own fulfilment”.[122]

157. Underlying the principle of the common good is respect for the human person as such, endowed with basic and inalienable rights ordered to his or her integral development. It has also to do with the overall welfare of society and the development of a variety of intermediate groups, applying the principle of subsidiarity. Outstanding among those groups is the family, as the basic cell of society. Finally, the common good calls for social peace, the stability and security provided by a certain order which cannot be achieved without particular concern for distributive justice; whenever this is violated, violence always ensues. Society as a whole, and the state in particular, are obliged to defend and promote the common good.

158. In the present condition of global society, where injustices abound and growing numbers of people are deprived of basic human rights and considered expendable, the principle of the common good immediately becomes, logically and inevitably, a summons to solidarity and a preferential option for the poorest of our brothers and sisters. This option entails recognizing the implications of the universal destination of the world’s goods, but, as I mentioned in the Apostolic Exhortation *Evangelii Gaudium*,[123] it demands before all else an appreciation of the immense dignity of the poor in the light of our deepest convictions as believers. We need only look around us to see that, today, this option is in fact an ethical imperative essential for effectively attaining the common good.

V. JUSTICE BETWEEN THE GENERATIONS

159. The notion of the common good also extends to future generations. The global economic crises have made painfully obvious the detrimental effects of disregarding our common destiny, which cannot exclude those who come after us. We can no longer speak of sustainable development apart from intergenerational solidarity. Once we start to think about the kind of world we are leaving to future generations, we look at things differently; we realize that the world is a gift which we have freely received and must share with others. Since the world has been given to us, we can no longer view reality in a purely utilitarian way, in which efficiency and productivity are entirely geared to our individual benefit. Intergenerational solidarity is not optional, but rather a basic question of justice, since the world we have received also belongs to those who will follow us. The Portuguese bishops have called upon us to acknowledge this obligation of justice: “The environment is part of a logic of receptivity. It is on loan to each generation, which must then hand it on to the next”.[124] An integral ecology is marked by this broader vision.

160. What kind of world do we want to leave to those who come after us, to children who are now growing up? This question not only concerns the environment in isolation; the issue cannot be approached piecemeal. When we ask ourselves what kind of world we want to leave behind, we

think in the first place of its general direction, its meaning and its values. Unless we struggle with these deeper issues, I do not believe that our concern for ecology will produce significant results. But if these issues are courageously faced, we are led inexorably to ask other pointed questions: What is the purpose of our life in this world? Why are we here? What is the goal of our work and all our efforts? What need does the earth have of us? It is no longer enough, then, simply to state that we should be concerned for future generations. We need to see that what is at stake is our own dignity. Leaving an inhabitable planet to future generations is, first and foremost, up to us. The issue is one which dramatically affects us, for it has to do with the ultimate meaning of our earthly sojourn.

161. Doomsday predictions can no longer be met with irony or disdain. We may well be leaving to coming generations debris, desolation and filth. The pace of consumption, waste and environmental change has so stretched the planet's capacity that our contemporary lifestyle, unsustainable as it is, can only precipitate catastrophes, such as those which even now periodically occur in different areas of the world. The effects of the present imbalance can only be reduced by our decisive action, here and now. We need to reflect on our accountability before those who will have to endure the dire consequences.

162. Our difficulty in taking up this challenge seriously has much to do with an ethical and cultural decline which has accompanied the deterioration of the environment. Men and women of our postmodern world run the risk of rampant individualism, and many problems of society are connected with today's self-centred culture of instant gratification. We see this in the crisis of family and social ties and the difficulties of recognizing the other. Parents can be prone to impulsive and wasteful consumption, which then affects their children who find it increasingly difficult to acquire a home of their own and build a family. Furthermore, our inability to think seriously about future generations is linked to our inability to broaden the scope of our present interests and to give consideration to those who remain excluded from development. Let us not only keep the poor of the future in mind, but also today's poor, whose life on this earth is brief and who cannot keep on waiting. Hence, "in addition to a fairer sense of intergenerational solidarity there is also an urgent moral need for a renewed sense of intragenerational solidarity".[125]

CHAPTER FIVE

LINES OF APPROACH AND ACTION

163. So far I have attempted to take stock of our present situation, pointing to the cracks in the planet that we inhabit as well as to the profoundly human causes of environmental degradation. Although the contemplation of this reality in itself has already shown the need for a change of direction and other courses of action, now we shall try to outline the major paths of dialogue which can help us escape the spiral of self-destruction which currently engulfs us.

I. DIALOGUE ON THE ENVIRONMENT IN THE INTERNATIONAL COMMUNITY

164. Beginning in the middle of the last century and overcoming many difficulties, there has been a growing conviction that our planet is a homeland and that humanity is one people living in a common home. An interdependent world not only makes us more conscious of the negative effects of certain lifestyles and models of production and consumption which affect us all; more importantly, it motivates us to ensure that solutions are proposed from a global perspective, and not simply to defend the interests of a few countries. Interdependence obliges us to think of *one world with a common plan*. Yet the same ingenuity which has brought about enormous technological progress has so far proved incapable of finding effective ways of dealing with grave environmental and social problems worldwide. A global consensus is essential for confronting the deeper problems, which cannot be resolved by unilateral actions on the part of individual countries. Such a consensus could lead, for example, to planning a sustainable and diversified agriculture, developing renewable and less polluting forms of energy, encouraging a more efficient use of energy, promoting a better management of marine and forest resources, and ensuring universal access to drinking water.

165. We know that technology based on the use of highly polluting fossil fuels – especially coal, but also oil and, to a lesser degree, gas – needs to be progressively replaced without delay. Until greater progress is made in developing widely accessible sources of renewable energy, it is legitimate to choose the less harmful alternative or to find short-term solutions. But the international community has still not reached adequate agreements about the responsibility for paying the costs of this energy transition. In recent decades, environmental issues have given rise to considerable public debate and have elicited a variety of committed and generous civic responses. Politics and business have been slow to react in a way commensurate with the urgency of the challenges facing our world. Although the post-industrial period may well be remembered as one of the most irresponsible in history, nonetheless there is reason to hope that humanity at the dawn of the twenty-first century will be remembered for having generously shouldered its grave responsibilities.

166. Worldwide, the ecological movement has made significant advances, thanks also to the efforts of many organizations of civil society. It is impossible here to mention them all, or to review the history of their contributions. But thanks to their efforts, environmental questions have increasingly found a place on public agendas and encouraged more far-sighted approaches. This notwithstanding, recent World Summits on the environment have not lived up to expectations because, due to lack of political will, they were unable to reach truly meaningful and effective global agreements on the environment.

167. The 1992 Earth Summit in Rio de Janeiro is worth mentioning. It proclaimed that “human beings are at the centre of concerns for sustainable development”.[126] Echoing the 1972 Stockholm Declaration, it enshrined international cooperation to care for the ecosystem of the

entire earth, the obligation of those who cause pollution to assume its costs, and the duty to assess the environmental impact of given projects and works. It set the goal of limiting greenhouse gas concentration in the atmosphere, in an effort to reverse the trend of global warming. It also drew up an agenda with an action plan and a convention on biodiversity, and stated principles regarding forests. Although the summit was a real step forward, and prophetic for its time, its accords have been poorly implemented, due to the lack of suitable mechanisms for oversight, periodic review and penalties in cases of non-compliance. The principles which it proclaimed still await an efficient and flexible means of practical implementation.

168. Among positive experiences in this regard, we might mention, for example, the Basel Convention on hazardous wastes, with its system of reporting, standards and controls. There is also the binding Convention on international trade in endangered species of wild fauna and flora, which includes on-site visits for verifying effective compliance. Thanks to the Vienna Convention for the protection of the ozone layer and its implementation through the Montreal Protocol and amendments, the problem of the layer’s thinning seems to have entered a phase of resolution.

169. As far as the protection of biodiversity and issues related to desertification are concerned, progress has been far less significant. With regard to climate change, the advances have been regrettably few. Reducing greenhouse gases requires honesty, courage and responsibility, above all on the part of those countries which are more powerful and pollute the most. The Conference of the United Nations on Sustainable Development, “Rio+20” (Rio de Janeiro 2012), issued a wide-ranging but ineffectual outcome document. International negotiations cannot make significant progress due to positions taken by countries which place their national interests above the global common good. Those who will have to suffer the consequences of what we are trying to hide will not forget this failure of conscience and responsibility. Even as this Encyclical was being prepared, the debate was intensifying. We believers cannot fail to ask God for a positive outcome to the present discussions, so that future generations will not have to suffer the effects of our ill-advised delays.

170. Some strategies for lowering pollutant gas emissions call for the internationalization of environmental costs, which would risk imposing on countries with fewer resources burdensome commitments to reducing emissions comparable to those of the more industrialized countries. Imposing such measures penalizes those countries most in need of development. A further injustice is perpetrated under the guise of protecting the environment. Here also, the poor end up paying the price. Furthermore, since the effects of climate change will be felt for a long time to come, even if stringent measures are taken now, some countries with scarce resources will require assistance in adapting to the effects already being produced, which affect their economies. In this context, there is a need for common and differentiated responsibilities. As the bishops of Bolivia have stated, “the countries which have benefited from a high degree of industrialization, at the cost of enormous emissions of greenhouse gases, have a greater responsibility for providing a solution to the problems they have caused”.[127]

171. The strategy of buying and selling “carbon credits” can lead to a new form of speculation which would not help reduce the emission of polluting gases worldwide. This system seems to provide a quick and easy solution under the guise of a certain commitment to the environment, but in no way does it allow for the radical change which present circumstances require. Rather, it may simply become a ploy which permits maintaining the excessive consumption of some countries and sectors.

172. For poor countries, the priorities must be to eliminate extreme poverty and to promote the social development of their people. At the same time, they need to acknowledge the scandalous level of consumption in some privileged sectors of their population and to combat corruption more effectively. They are likewise bound to develop less polluting forms of energy production, but to do so they require the help of countries which have experienced great growth at the cost of the ongoing pollution of the planet. Taking advantage of abundant solar energy will require the establishment of mechanisms and subsidies which allow developing countries access to technology transfer, technical assistance and financial resources, but in a way which respects their concrete situations, since “the compatibility of [infrastructures] with the context for which they have been designed is not always adequately assessed”.[128] The costs of this would be low, compared to the risks of climate change. In any event, these are primarily ethical decisions, rooted in solidarity between all peoples.

173. Enforceable international agreements are urgently needed, since local authorities are not always capable of effective intervention. Relations between states must be respectful of each other’s sovereignty, but must also lay down mutually agreed means of averting regional disasters which would eventually affect everyone. Global regulatory norms are needed to impose obligations and prevent unacceptable actions, for example, when powerful companies or countries dump contaminated waste or offshore polluting industries in other countries.

174. Let us also mention the system of governance of the oceans. International and regional conventions do exist, but fragmentation and the lack of strict mechanisms of regulation, control and penalization end up undermining these efforts. The growing problem of marine waste and the protection of the open seas represent particular challenges. What is needed, in effect, is an agreement on systems of governance for the whole range of so-called “global commons”.

175. The same mindset which stands in the way of making radical decisions to reverse the trend of global warming also stands in the way of achieving the goal of eliminating poverty. A more responsible overall approach is needed to deal with both problems: the reduction of pollution and the development of poorer countries and regions. The twenty-first century, while maintaining systems of governance inherited from the past, is witnessing a weakening of the power of nation states, chiefly because the economic and financial sectors, being transnational, tends to prevail over the political. Given this situation, it is essential to devise stronger and more efficiently organized international institutions, with functionaries who are appointed fairly by agreement

among national governments, and empowered to impose sanctions. As Benedict XVI has affirmed in continuity with the social teaching of the Church: “To manage the global economy; to revive economies hit by the crisis; to avoid any deterioration of the present crisis and the greater imbalances that would result; to bring about integral and timely disarmament, food security and peace; to guarantee the protection of the environment and to regulate migration: for all this, there is urgent need of a true world political authority, as my predecessor Blessed John XXIII indicated some years ago”.[129] Diplomacy also takes on new importance in the work of developing international strategies which can anticipate serious problems affecting us all.

II. DIALOGUE FOR NEW NATIONAL AND LOCAL POLICIES

176. There are not just winners and losers among countries, but within poorer countries themselves. Hence different responsibilities need to be identified. Questions related to the environment and economic development can no longer be approached only from the standpoint of differences between countries; they also call for greater attention to policies on the national and local levels.

177. Given the real potential for a misuse of human abilities, individual states can no longer ignore their responsibility for planning, coordination, oversight and enforcement within their respective borders. How can a society plan and protect its future amid constantly developing technological innovations? One authoritative source of oversight and coordination is the law, which lays down rules for admissible conduct in the light of the common good. The limits which a healthy, mature and sovereign society must impose are those related to foresight and security, regulatory norms, timely enforcement, the elimination of corruption, effective responses to undesired side-effects of production processes, and appropriate intervention where potential or uncertain risks are involved. There is a growing jurisprudence dealing with the reduction of pollution by business activities. But political and institutional frameworks do not exist simply to avoid bad practice, but also to promote best practice, to stimulate creativity in seeking new solutions and to encourage individual or group initiatives.

178. A politics concerned with immediate results, supported by consumerist sectors of the population, is driven to produce short-term growth. In response to electoral interests, governments are reluctant to upset the public with measures which could affect the level of consumption or create risks for foreign investment. The myopia of power politics delays the inclusion of a far-sighted environmental agenda within the overall agenda of governments. Thus we forget that “time is greater than space”,[130] that we are always more effective when we generate processes rather than holding on to positions of power. True statecraft is manifest when, in difficult times, we uphold high principles and think of the long-term common good. Political powers do not find it easy to assume this duty in the work of nation-building.

179. In some places, cooperatives are being developed to exploit renewable sources of energy

which ensure local self-sufficiency and even the sale of surplus energy. This simple example shows that, while the existing world order proves powerless to assume its responsibilities, local individuals and groups can make a real difference. They are able to instil a greater sense of responsibility, a strong sense of community, a readiness to protect others, a spirit of creativity and a deep love for the land. They are also concerned about what they will eventually leave to their children and grandchildren. These values are deeply rooted in indigenous peoples. Because the enforcement of laws is at times inadequate due to corruption, public pressure has to be exerted in order to bring about decisive political action. Society, through non-governmental organizations and intermediate groups, must put pressure on governments to develop more rigorous regulations, procedures and controls. Unless citizens control political power – national, regional and municipal – it will not be possible to control damage to the environment. Local legislation can be more effective, too, if agreements exist between neighbouring communities to support the same environmental policies.

180. There are no uniform recipes, because each country or region has its own problems and limitations. It is also true that political realism may call for transitional measures and technologies, so long as these are accompanied by the gradual framing and acceptance of binding commitments. At the same time, on the national and local levels, much still needs to be done, such as promoting ways of conserving energy. These would include favouring forms of industrial production with maximum energy efficiency and diminished use of raw materials, removing from the market products which are less energy efficient or more polluting, improving transport systems, and encouraging the construction and repair of buildings aimed at reducing their energy consumption and levels of pollution. Political activity on the local level could also be directed to modifying consumption, developing an economy of waste disposal and recycling, protecting certain species and planning a diversified agriculture and the rotation of crops. Agriculture in poorer regions can be improved through investment in rural infrastructures, a better organization of local or national markets, systems of irrigation, and the development of techniques of sustainable agriculture. New forms of cooperation and community organization can be encouraged in order to defend the interests of small producers and preserve local ecosystems from destruction. Truly, much can be done!

181. Here, continuity is essential, because policies related to climate change and environmental protection cannot be altered with every change of government. Results take time and demand immediate outlays which may not produce tangible effects within any one government’s term. That is why, in the absence of pressure from the public and from civic institutions, political authorities will always be reluctant to intervene, all the more when urgent needs must be met. To take up these responsibilities and the costs they entail, politicians will inevitably clash with the mindset of short-term gain and results which dominates present-day economics and politics. But if they are courageous, they will attest to their God-given dignity and leave behind a testimony of selfless responsibility. A healthy politics is sorely needed, capable of reforming and coordinating institutions, promoting best practices and overcoming undue pressure and bureaucratic inertia. It

should be added, though, that even the best mechanisms can break down when there are no worthy goals and values, or a genuine and profound humanism to serve as the basis of a noble and generous society.

III. DIALOGUE AND TRANSPARENCY IN DECISION-MAKING

182. An assessment of the environmental impact of business ventures and projects demands transparent political processes involving a free exchange of views. On the other hand, the forms of corruption which conceal the actual environmental impact of a given project, in exchange for favours, usually produce specious agreements which fail to inform adequately and to allow for full debate.

183. Environmental impact assessment should not come after the drawing up of a business proposition or the proposal of a particular policy, plan or programme. It should be part of the process from the beginning, and be carried out in a way which is interdisciplinary, transparent and free of all economic or political pressure. It should be linked to a study of working conditions and possible effects on people’s physical and mental health, on the local economy and on public safety. Economic returns can thus be forecast more realistically, taking into account potential scenarios and the eventual need for further investment to correct possible undesired effects. A consensus should always be reached between the different stakeholders, who can offer a variety of approaches, solutions and alternatives. The local population should have a special place at the table; they are concerned about their own future and that of their children, and can consider goals transcending immediate economic interest. We need to stop thinking in terms of “interventions” to save the environment in favour of policies developed and debated by all interested parties. The participation of the latter also entails being fully informed about such projects and their different risks and possibilities; this includes not just preliminary decisions but also various follow-up activities and continued monitoring. Honesty and truth are needed in scientific and political discussions; these should not be limited to the issue of whether or not a particular project is permitted by law.

184. In the face of possible risks to the environment which may affect the common good now and in the future, decisions must be made “based on a comparison of the risks and benefits foreseen for the various possible alternatives”.[131] This is especially the case when a project may lead to a greater use of natural resources, higher levels of emission or discharge, an increase of refuse, or significant changes to the landscape, the habitats of protected species or public spaces. Some projects, if insufficiently studied, can profoundly affect the quality of life of an area due to very different factors such as unforeseen noise pollution, the shrinking of visual horizons, the loss of cultural values, or the effects of nuclear energy use. The culture of consumerism, which prioritizes short-term gain and private interest, can make it easy to rubber-stamp authorizations or to conceal information.

185. In any discussion about a proposed venture, a number of questions need to be asked in order to discern whether or not it will contribute to genuine integral development. What will it accomplish? Why? Where? When? How? For whom? What are the risks? What are the costs? Who will pay those costs and how? In this discernment, some questions must have higher priority. For example, we know that water is a scarce and indispensable resource and a fundamental right which conditions the exercise of other human rights. This indisputable fact overrides any other assessment of environmental impact on a region.

186. The Rio Declaration of 1992 states that “where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a pretext for postponing cost-effective measures”[132] which prevent environmental degradation. This precautionary principle makes it possible to protect those who are most vulnerable and whose ability to defend their interests and to assemble incontrovertible evidence is limited. If objective information suggests that serious and irreversible damage may result, a project should be halted or modified, even in the absence of indisputable proof. Here the burden of proof is effectively reversed, since in such cases objective and conclusive demonstrations will have to be brought forward to demonstrate that the proposed activity will not cause serious harm to the environment or to those who inhabit it.

187. This does not mean being opposed to any technological innovations which can bring about an improvement in the quality of life. But it does mean that profit cannot be the sole criterion to be taken into account, and that, when significant new information comes to light, a reassessment should be made, with the involvement of all interested parties. The outcome may be a decision not to proceed with a given project, to modify it or to consider alternative proposals.

188. There are certain environmental issues where it is not easy to achieve a broad consensus. Here I would state once more that the Church does not presume to settle scientific questions or to replace politics. But I am concerned to encourage an honest and open debate so that particular interests or ideologies will not prejudice the common good.

IV. POLITICS AND ECONOMY IN DIALOGUE FOR HUMAN FULFILMENT

189. Politics must not be subject to the economy, nor should the economy be subject to the dictates of an efficiency-driven paradigm of technocracy. Today, in view of the common good, there is urgent need for politics and economics to enter into a frank dialogue in the service of life, especially human life. Saving banks at any cost, making the public pay the price, foregoing a firm commitment to reviewing and reforming the entire system, only reaffirms the absolute power of a financial system, a power which has no future and will only give rise to new crises after a slow, costly and only apparent recovery. The financial crisis of 2007-08 provided an opportunity to develop a new economy, more attentive to ethical principles, and new ways of regulating speculative financial practices and virtual wealth. But the response to the crisis did not include rethinking the outdated criteria which continue to rule the world. Production is not always rational,

and is usually tied to economic variables which assign to products a value that does not necessarily correspond to their real worth. This frequently leads to an overproduction of some commodities, with unnecessary impact on the environment and with negative results on regional economies.[133] The financial bubble also tends to be a productive bubble. The problem of the real economy is not confronted with vigour, yet it is the real economy which makes diversification and improvement in production possible, helps companies to function well, and enables small and medium businesses to develop and create employment.

190. Here too, it should always be kept in mind that “environmental protection cannot be assured solely on the basis of financial calculations of costs and benefits. The environment is one of those goods that cannot be adequately safeguarded or promoted by market forces”.[134] Once more, we need to reject a magical conception of the market, which would suggest that problems can be solved simply by an increase in the profits of companies or individuals. Is it realistic to hope that those who are obsessed with maximizing profits will stop to reflect on the environmental damage which they will leave behind for future generations? Where profits alone count, there can be no thinking about the rhythms of nature, its phases of decay and regeneration, or the complexity of ecosystems which may be gravely upset by human intervention. Moreover, biodiversity is considered at most a deposit of economic resources available for exploitation, with no serious thought for the real value of things, their significance for persons and cultures, or the concerns and needs of the poor.

191. Whenever these questions are raised, some react by accusing others of irrationally attempting to stand in the way of progress and human development. But we need to grow in the conviction that a decrease in the pace of production and consumption can at times give rise to another form of progress and development. Efforts to promote a sustainable use of natural resources are not a waste of money, but rather an investment capable of providing other economic benefits in the medium term. If we look at the larger picture, we can see that more diversified and innovative forms of production which impact less on the environment can prove very profitable. It is a matter of openness to different possibilities which do not involve stifling human creativity and its ideals of progress, but rather directing that energy along new channels.

192. For example, a path of productive development, which is more creative and better directed, could correct the present disparity between excessive technological investment in consumption and insufficient investment in resolving urgent problems facing the human family. It could generate intelligent and profitable ways of reusing, revamping and recycling, and it could also improve the energy efficiency of cities. Productive diversification offers the fullest possibilities to human ingenuity to create and innovate, while at the same time protecting the environment and creating more sources of employment. Such creativity would be a worthy expression of our most noble human qualities, for we would be striving intelligently, boldly and responsibly to promote a sustainable and equitable development within the context of a broader concept of quality of life. On the other hand, to find ever new ways of despoiling nature, purely for the sake of new

consumer items and quick profit, would be, in human terms, less worthy and creative, and more superficial.

193. In any event, if in some cases sustainable development were to involve new forms of growth, then in other cases, given the insatiable and irresponsible growth produced over many decades, we need also to think of containing growth by setting some reasonable limits and even retracing our steps before it is too late. We know how unsustainable is the behaviour of those who constantly consume and destroy, while others are not yet able to live in a way worthy of their human dignity. That is why the time has come to accept decreased growth in some parts of the world, in order to provide resources for other places to experience healthy growth. Benedict XVI has said that "technologically advanced societies must be prepared to encourage more sober lifestyles, while reducing their energy consumption and improving its efficiency".[135]

194. For new models of progress to arise, there is a need to change "models of global development";[136] this will entail a responsible reflection on "the meaning of the economy and its goals with an eye to correcting its malfunctions and misapplications".[137] It is not enough to balance, in the medium term, the protection of nature with financial gain, or the preservation of the environment with progress. Halfway measures simply delay the inevitable disaster. Put simply, it is a matter of redefining our notion of progress. A technological and economic development which does not leave in its wake a better world and an integrally higher quality of life cannot be considered progress. Frequently, in fact, people's quality of life actually diminishes – by the deterioration of the environment, the low quality of food or the depletion of resources – in the midst of economic growth. In this context, talk of sustainable growth usually becomes a way of distracting attention and offering excuses. It absorbs the language and values of ecology into the categories of finance and technocracy, and the social and environmental responsibility of businesses often gets reduced to a series of marketing and image-enhancing measures.

195. The principle of the maximization of profits, frequently isolated from other considerations, reflects a misunderstanding of the very concept of the economy. As long as production is increased, little concern is given to whether it is at the cost of future resources or the health of the environment; as long as the clearing of a forest increases production, no one calculates the losses entailed in the desertification of the land, the harm done to biodiversity or the increased pollution. In a word, businesses profit by calculating and paying only a fraction of the costs involved. Yet only when "the economic and social costs of using up shared environmental resources are recognized with transparency and fully borne by those who incur them, not by other peoples or future generations",[138] can those actions be considered ethical. An instrumental way of reasoning, which provides a purely static analysis of realities in the service of present needs, is at work whether resources are allocated by the market or by state central planning.

196. What happens with politics? Let us keep in mind the principle of subsidiarity, which grants freedom to develop the capabilities present at every level of society, while also demanding a

greater sense of responsibility for the common good from those who wield greater power. Today, it is the case that some economic sectors exercise more power than states themselves. But economics without politics cannot be justified, since this would make it impossible to favour other ways of handling the various aspects of the present crisis. The mindset which leaves no room for sincere concern for the environment is the same mindset which lacks concern for the inclusion of the most vulnerable members of society. For "the current model, with its emphasis on success and self-reliance, does not appear to favour an investment in efforts to help the slow, the weak or the less talented to find opportunities in life".[139]

197. What is needed is a politics which is far-sighted and capable of a new, integral and interdisciplinary approach to handling the different aspects of the crisis. Often, politics itself is responsible for the disrepute in which it is held, on account of corruption and the failure to enact sound public policies. If in a given region the state does not carry out its responsibilities, some business groups can come forward in the guise of benefactors, wield real power, and consider themselves exempt from certain rules, to the point of tolerating different forms of organized crime, human trafficking, the drug trade and violence, all of which become very difficult to eradicate. If politics shows itself incapable of breaking such a perverse logic, and remains caught up in inconsequential discussions, we will continue to avoid facing the major problems of humanity. A strategy for real change calls for rethinking processes in their entirety, for it is not enough to include a few superficial ecological considerations while failing to question the logic which underlies present-day culture. A healthy politics needs to be able to take up this challenge.

198. Politics and the economy tend to blame each other when it comes to poverty and environmental degradation. It is to be hoped that they can acknowledge their own mistakes and find forms of interaction directed to the common good. While some are concerned only with financial gain, and others with holding on to or increasing their power, what we are left with are conflicts or spurious agreements where the last thing either party is concerned about is caring for the environment and protecting those who are most vulnerable. Here too, we see how true it is that "unity is greater than conflict".[140]

V. RELIGIONS IN DIALOGUE WITH SCIENCE

199. It cannot be maintained that empirical science provides a complete explanation of life, the interplay of all creatures and the whole of reality. This would be to breach the limits imposed by its own methodology. If we reason only within the confines of the latter, little room would be left for aesthetic sensibility, poetry, or even reason's ability to grasp the ultimate meaning and purpose of things.[141] I would add that "religious classics can prove meaningful in every age; they have an enduring power to open new horizons… Is it reasonable and enlightened to dismiss certain writings simply because they arose in the context of religious belief?"[142] It would be quite simplistic to think that ethical principles present themselves purely in the abstract, detached from any context. Nor does the fact that they may be couched in religious language detract from their

value in public debate. The ethical principles capable of being apprehended by reason can always reappear in different guise and find expression in a variety of languages, including religious language.

200. Any technical solution which science claims to offer will be powerless to solve the serious problems of our world if humanity loses its compass, if we lose sight of the great motivations which make it possible for us to live in harmony, to make sacrifices and to treat others well. Believers themselves must constantly feel challenged to live in a way consonant with their faith and not to contradict it by their actions. They need to be encouraged to be ever open to God's grace and to draw constantly from their deepest convictions about love, justice and peace. If a mistaken understanding of our own principles has at times led us to justify mistreating nature, to exercise tyranny over creation, to engage in war, injustice and acts of violence, we believers should acknowledge that by so doing we were not faithful to the treasures of wisdom which we have been called to protect and preserve. Cultural limitations in different eras often affected the perception of these ethical and spiritual treasures, yet by constantly returning to their sources, religions will be better equipped to respond to today's needs.

201. The majority of people living on our planet profess to be believers. This should spur religions to dialogue among themselves for the sake of protecting nature, defending the poor, and building networks of respect and fraternity. Dialogue among the various sciences is likewise needed, since each can tend to become enclosed in its own language, while specialization leads to a certain isolation and the absolutization of its own field of knowledge. This prevents us from confronting environmental problems effectively. An open and respectful dialogue is also needed between the various ecological movements, among which ideological conflicts are not infrequently encountered. The gravity of the ecological crisis demands that we all look to the common good, embarking on a path of dialogue which demands patience, self-discipline and generosity, always keeping in mind that "realities are greater than ideas".[143]

CHAPTER SIX

ECOLOGICAL EDUCATION AND SPIRITUALITY

202. Many things have to change course, but it is we human beings above all who need to change. We lack an awareness of our common origin, of our mutual belonging, and of a future to be shared with everyone. This basic awareness would enable the development of new convictions, attitudes and forms of life. A great cultural, spiritual and educational challenge stands before us, and it will demand that we set out on the long path of renewal.

I. TOWARDS A NEW LIFESTYLE

203. Since the market tends to promote extreme consumerism in an effort to sell its products,

people can easily get caught up in a whirlwind of needless buying and spending. Compulsive consumerism is one example of how the techno-economic paradigm affects individuals. Romano Guardini had already foreseen this: “The gadgets and technics forced upon him by the patterns of machine production and of abstract planning mass man accepts quite simply; they are the forms of life itself. To either a greater or lesser degree mass man is convinced that his conformity is both reasonable and just”.[144] This paradigm leads people to believe that they are free as long as they have the supposed freedom to consume. But those really free are the minority who wield economic and financial power. Amid this confusion, postmodern humanity has not yet achieved a new self-awareness capable of offering guidance and direction, and this lack of identity is a source of anxiety. We have too many means and only a few insubstantial ends.

204. The current global situation engenders a feeling of instability and uncertainty, which in turn becomes “a seedbed for collective selfishness”.[145] When people become self-centred and self-enclosed, their greed increases. The emptier a person’s heart is, the more he or she needs things to buy, own and consume. It becomes almost impossible to accept the limits imposed by reality. In this horizon, a genuine sense of the common good also disappears. As these attitudes become more widespread, social norms are respected only to the extent that they do not clash with personal needs. So our concern cannot be limited merely to the threat of extreme weather events, but must also extend to the catastrophic consequences of social unrest. Obsession with a consumerist lifestyle, above all when few people are capable of maintaining it, can only lead to violence and mutual destruction.

205. Yet all is not lost. Human beings, while capable of the worst, are also capable of rising above themselves, choosing again what is good, and making a new start, despite their mental and social conditioning. We are able to take an honest look at ourselves, to acknowledge our deep dissatisfaction, and to embark on new paths to authentic freedom. No system can completely suppress our openness to what is good, true and beautiful, or our God-given ability to respond to his grace at work deep in our hearts. I appeal to everyone throughout the world not to forget this dignity which is ours. No one has the right to take it from us.

206. A change in lifestyle could bring healthy pressure to bear on those who wield political, economic and social power. This is what consumer movements accomplish by boycotting certain products. They prove successful in changing the way businesses operate, forcing them to consider their environmental footprint and their patterns of production. When social pressure affects their earnings, businesses clearly have to find ways to produce differently. This shows us the great need for a sense of social responsibility on the part of consumers. “Purchasing is always a moral – and not simply economic – act”.[146] Today, in a word, “the issue of environmental degradation challenges us to examine our lifestyle”.[147]

207. The Earth Charter asked us to leave behind a period of self-destruction and make a new start, but we have not as yet developed a universal awareness needed to achieve this. Here, I

would echo that courageous challenge: “As never before in history, common destiny beckons us to seek a new beginning… Let ours be a time remembered for the awakening of a new reverence for life, the firm resolve to achieve sustainability, the quickening of the struggle for justice and peace, and the joyful celebration of life”.[148]

208. We are always capable of going out of ourselves towards the other. Unless we do this, other creatures will not be recognized for their true worth; we are unconcerned about caring for things for the sake of others; we fail to set limits on ourselves in order to avoid the suffering of others or the deterioration of our surroundings. Disinterested concern for others, and the rejection of every form of self-centeredness and self-absorption, are essential if we truly wish to care for our brothers and sisters and for the natural environment. These attitudes also attune us to the moral imperative of assessing the impact of our every action and personal decision on the world around us. If we can overcome individualism, we will truly be able to develop a different lifestyle and bring about significant changes in society.

II. EDUCATING FOR THE COVENANT BETWEEN HUMANITY AND THE ENVIRONMENT

209. An awareness of the gravity of today’s cultural and ecological crisis must be translated into new habits. Many people know that our current progress and the mere amassing of things and pleasures are not enough to give meaning and joy to the human heart, yet they feel unable to give up what the market sets before them. In those countries which should be making the greatest changes in consumer habits, young people have a new ecological sensitivity and a generous spirit, and some of them are making admirable efforts to protect the environment. At the same time, they have grown up in a milieu of extreme consumerism and affluence which makes it difficult to develop other habits. We are faced with an educational challenge.

210. Environmental education has broadened its goals. Whereas in the beginning it was mainly centred on scientific information, consciousness-raising and the prevention of environmental risks, it tends now to include a critique of the “myths” of a modernity grounded in a utilitarian mindset (individualism, unlimited progress, competition, consumerism, the unregulated market). It seeks also to restore the various levels of ecological equilibrium, establishing harmony within ourselves, with others, with nature and other living creatures, and with God. Environmental education should facilitate making the leap towards the transcendent which gives ecological ethics its deepest meaning. It needs educators capable of developing an ethics of ecology, and helping people, through effective pedagogy, to grow in solidarity, responsibility and compassionate care.

211. Yet this education, aimed at creating an “ecological citizenship”, is at times limited to providing information, and fails to instil good habits. The existence of laws and regulations is insufficient in the long run to curb bad conduct, even when effective means of enforcement are present. If the laws are to bring about significant, long-lasting effects, the majority of the members of society must be adequately motivated to accept them, and personally transformed to respond.

Only by cultivating sound virtues will people be able to make a selfless ecological commitment. A person who could afford to spend and consume more but regularly uses less heating and wears warmer clothes, shows the kind of convictions and attitudes which help to protect the environment. There is a nobility in the duty to care for creation through little daily actions, and it is wonderful how education can bring about real changes in lifestyle. Education in environmental responsibility can encourage ways of acting which directly and significantly affect the world around us, such as avoiding the use of plastic and paper, reducing water consumption, separating refuse, cooking only what can reasonably be consumed, showing care for other living beings, using public transport or car-pooling, planting trees, turning off unnecessary lights, or any number of other practices. All of these reflect a generous and worthy creativity which brings out the best in human beings. Reusing something instead of immediately discarding it, when done for the right reasons, can be an act of love which expresses our own dignity.

212. We must not think that these efforts are not going to change the world. They benefit society, often unbeknown to us, for they call forth a goodness which, albeit unseen, inevitably tends to spread. Furthermore, such actions can restore our sense of self-esteem; they can enable us to live more fully and to feel that life on earth is worthwhile.

213. Ecological education can take place in a variety of settings: at school, in families, in the media, in catechesis and elsewhere. Good education plants seeds when we are young, and these continue to bear fruit throughout life. Here, though, I would stress the great importance of the family, which is “the place in which life – the gift of God – can be properly welcomed and protected against the many attacks to which it is exposed, and can develop in accordance with what constitutes authentic human growth. In the face of the so-called culture of death, the family is the heart of the culture of life”.[149] In the family we first learn how to show love and respect for life; we are taught the proper use of things, order and cleanliness, respect for the local ecosystem and care for all creatures. In the family we receive an integral education, which enables us to grow harmoniously in personal maturity. In the family we learn to ask without demanding, to say “thank you” as an expression of genuine gratitude for what we have been given, to control our aggressivity and greed, and to ask forgiveness when we have caused harm. These simple gestures of heartfelt courtesy help to create a culture of shared life and respect for our surroundings.

214. Political institutions and various other social groups are also entrusted with helping to raise people’s awareness. So too is the Church. All Christian communities have an important role to play in ecological education. It is my hope that our seminaries and houses of formation will provide an education in responsible simplicity of life, in grateful contemplation of God’s world, and in concern for the needs of the poor and the protection of the environment. Because the stakes are so high, we need institutions empowered to impose penalties for damage inflicted on the environment. But we also need the personal qualities of self-control and willingness to learn from one another.

215. In this regard, “the relationship between a good aesthetic education and the maintenance of a healthy environment cannot be overlooked”.[150] By learning to see and appreciate beauty, we learn to reject self-interested pragmatism. If someone has not learned to stop and admire something beautiful, we should not be surprised if he or she treats everything as an object to be used and abused without scruple. If we want to bring about deep change, we need to realize that certain mindsets really do influence our behaviour. Our efforts at education will be inadequate and ineffectual unless we strive to promote a new way of thinking about human beings, life, society and our relationship with nature. Otherwise, the paradigm of consumerism will continue to advance, with the help of the media and the highly effective workings of the market.

III. ECOLOGICAL CONVERSION

216. The rich heritage of Christian spirituality, the fruit of twenty centuries of personal and communal experience, has a precious contribution to make to the renewal of humanity. Here, I would like to offer Christians a few suggestions for an ecological spirituality grounded in the convictions of our faith, since the teachings of the Gospel have direct consequences for our way of thinking, feeling and living. More than in ideas or concepts as such, I am interested in how such a spirituality can motivate us to a more passionate concern for the protection of our world. A commitment this lofty cannot be sustained by doctrine alone, without a spirituality capable of inspiring us, without an “interior impulse which encourages, motivates, nourishes and gives meaning to our individual and communal activity”.[151] Admittedly, Christians have not always appropriated and developed the spiritual treasures bestowed by God upon the Church, where the life of the spirit is not dissociated from the body or from nature or from worldly realities, but lived in and with them, in communion with all that surrounds us.

217. “The external deserts in the world are growing, because the internal deserts have become so vast”.[152] For this reason, the ecological crisis is also a summons to profound interior conversion. It must be said that some committed and prayerful Christians, with the excuse of realism and pragmatism, tend to ridicule expressions of concern for the environment. Others are passive; they choose not to change their habits and thus become inconsistent. So what they all need is an “ecological conversion”, whereby the effects of their encounter with Jesus Christ become evident in their relationship with the world around them. Living our vocation to be protectors of God’s handiwork is essential to a life of virtue; it is not an optional or a secondary aspect of our Christian experience.

218. In calling to mind the figure of Saint Francis of Assisi, we come to realize that a healthy relationship with creation is one dimension of overall personal conversion, which entails the recognition of our errors, sins, faults and failures, and leads to heartfelt repentance and desire to change. The Australian bishops spoke of the importance of such conversion for achieving reconciliation with creation: “To achieve such reconciliation, we must examine our lives and acknowledge the ways in which we have harmed God’s creation through our actions and our

failure to act. We need to experience a conversion, or change of heart”.[153]

219. Nevertheless, self-improvement on the part of individuals will not by itself remedy the extremely complex situation facing our world today. Isolated individuals can lose their ability and freedom to escape the utilitarian mindset, and end up prey to an unethical consumerism bereft of social or ecological awareness. Social problems must be addressed by community networks and not simply by the sum of individual good deeds. This task “will make such tremendous demands of man that he could never achieve it by individual initiative or even by the united effort of men bred in an individualistic way. The work of dominating the world calls for a union of skills and a unity of achievement that can only grow from quite a different attitude”.[154] The ecological conversion needed to bring about lasting change is also a community conversion.

220. This conversion calls for a number of attitudes which together foster a spirit of generous care, full of tenderness. First, it entails gratitude and gratuitousness, a recognition that the world is God’s loving gift, and that we are called quietly to imitate his generosity in self-sacrifice and good works: “Do not let your left hand know what your right hand is doing… and your Father who sees in secret will reward you” (*Mt* 6:3-4). It also entails a loving awareness that we are not disconnected from the rest of creatures, but joined in a splendid universal communion. As believers, we do not look at the world from without but from within, conscious of the bonds with which the Father has linked us to all beings. By developing our individual, God-given capacities, an ecological conversion can inspire us to greater creativity and enthusiasm in resolving the world’s problems and in offering ourselves to God “as a living sacrifice, holy and acceptable” (*Rom* 12:1). We do not understand our superiority as a reason for personal glory or irresponsible dominion, but rather as a different capacity which, in its turn, entails a serious responsibility stemming from our faith.

221. Various convictions of our faith, developed at the beginning of this Encyclical can help us to enrich the meaning of this conversion. These include the awareness that each creature reflects something of God and has a message to convey to us, and the security that Christ has taken unto himself this material world and now, risen, is intimately present to each being, surrounding it with his affection and penetrating it with his light. Then too, there is the recognition that God created the world, writing into it an order and a dynamism that human beings have no right to ignore. We read in the Gospel that Jesus says of the birds of the air that “not one of them is forgotten before God” (*Lk* 12:6). How then can we possibly mistreat them or cause them harm? I ask all Christians to recognize and to live fully this dimension of their conversion. May the power and the light of the grace we have received also be evident in our relationship to other creatures and to the world around us. In this way, we will help nurture that sublime fraternity with all creation which Saint Francis of Assisi so radiantly embodied.

IV. JOY AND PEACE

222. Christian spirituality proposes an alternative understanding of the quality of life, and encourages a prophetic and contemplative lifestyle, one capable of deep enjoyment free of the obsession with consumption. We need to take up an ancient lesson, found in different religious traditions and also in the Bible. It is the conviction that “less is more”. A constant flood of new consumer goods can baffle the heart and prevent us from cherishing each thing and each moment. To be serenely present to each reality, however small it may be, opens us to much greater horizons of understanding and personal fulfilment. Christian spirituality proposes a growth marked by moderation and the capacity to be happy with little. It is a return to that simplicity which allows us to stop and appreciate the small things, to be grateful for the opportunities which life affords us, to be spiritually detached from what we possess, and not to succumb to sadness for what we lack. This implies avoiding the dynamic of dominion and the mere accumulation of pleasures.

223. Such sobriety, when lived freely and consciously, is liberating. It is not a lesser life or one lived with less intensity. On the contrary, it is a way of living life to the full. In reality, those who enjoy more and live better each moment are those who have given up dipping here and there, always on the look-out for what they do not have. They experience what it means to appreciate each person and each thing, learning familiarity with the simplest things and how to enjoy them. So they are able to shed unsatisfied needs, reducing their obsessiveness and weariness. Even living on little, they can live a lot, above all when they cultivate other pleasures and find satisfaction in fraternal encounters, in service, in developing their gifts, in music and art, in contact with nature, in prayer. Happiness means knowing how to limit some needs which only diminish us, and being open to the many different possibilities which life can offer.

224. Sobriety and humility were not favourably regarded in the last century. And yet, when there is a general breakdown in the exercise of a certain virtue in personal and social life, it ends up causing a number of imbalances, including environmental ones. That is why it is no longer enough to speak only of the integrity of ecosystems. We have to dare to speak of the integrity of human life, of the need to promote and unify all the great values. Once we lose our humility, and become enthralled with the possibility of limitless mastery over everything, we inevitably end up harming society and the environment. It is not easy to promote this kind of healthy humility or happy sobriety when we consider ourselves autonomous, when we exclude God from our lives or replace him with our own ego, and think that our subjective feelings can define what is right and what is wrong.

225. On the other hand, no one can cultivate a sober and satisfying life without being at peace with him or herself. An adequate understanding of spirituality consists in filling out what we mean by peace, which is much more than the absence of war. Inner peace is closely related to care for ecology and for the common good because, lived out authentically, it is reflected in a balanced lifestyle together with a capacity for wonder which takes us to a deeper understanding of life. Nature is filled with words of love, but how can we listen to them amid constant noise, interminable

and nerve-wracking distractions, or the cult of appearances? Many people today sense a profound imbalance which drives them to frenetic activity and makes them feel busy, in a constant hurry which in turn leads them to ride rough-shod over everything around them. This too affects how they treat the environment. An integral ecology includes taking time to recover a serene harmony with creation, reflecting on our lifestyle and our ideals, and contemplating the Creator who lives among us and surrounds us, whose presence "must not be contrived but found, uncovered".[155]

226. We are speaking of an attitude of the heart, one which approaches life with serene attentiveness, which is capable of being fully present to someone without thinking of what comes next, which accepts each moment as a gift from God to be lived to the full. Jesus taught us this attitude when he invited us to contemplate the lilies of the field and the birds of the air, or when seeing the rich young man and knowing his restlessness, "he looked at him with love" (*Mk* 10:21). He was completely present to everyone and to everything, and in this way he showed us the way to overcome that unhealthy anxiety which makes us superficial, aggressive and compulsive consumers.

227. One expression of this attitude is when we stop and give thanks to God before and after meals. I ask all believers to return to this beautiful and meaningful custom. That moment of blessing, however brief, reminds us of our dependence on God for life; it strengthens our feeling of gratitude for the gifts of creation; it acknowledges those who by their labours provide us with these goods; and it reaffirms our solidarity with those in greatest need.

V. CIVIC AND POLITICAL LOVE

228. Care for nature is part of a lifestyle which includes the capacity for living together and communion. Jesus reminded us that we have God as our common Father and that this makes us brothers and sisters. Fraternal love can only be gratuitous; it can never be a means of repaying others for what they have done or will do for us. That is why it is possible to love our enemies. This same gratuitousness inspires us to love and accept the wind, the sun and the clouds, even though we cannot control them. In this sense, we can speak of a "universal fraternity".

229. We must regain the conviction that we need one another, that we have a shared responsibility for others and the world, and that being good and decent are worth it. We have had enough of immorality and the mockery of ethics, goodness, faith and honesty. It is time to acknowledge that light-hearted superficiality has done us no good. When the foundations of social life are corroded, what ensues are battles over conflicting interests, new forms of violence and brutality, and obstacles to the growth of a genuine culture of care for the environment.

230. Saint Therese of Lisieux invites us to practise the little way of love, not to miss out on a kind word, a smile or any small gesture which sows peace and friendship. An integral ecology is also made up of simple daily gestures which break with the logic of violence, exploitation and

selfishness. In the end, a world of exacerbated consumption is at the same time a world which mistreats life in all its forms.

231. Love, overflowing with small gestures of mutual care, is also civic and political, and it makes itself felt in every action that seeks to build a better world. Love for society and commitment to the common good are outstanding expressions of a charity which affects not only relationships between individuals but also “macro-relationships, social, economic and political ones”.[156] That is why the Church set before the world the ideal of a “civilization of love”.[157] Social love is the key to authentic development: “In order to make society more human, more worthy of the human person, love in social life – political, economic and cultural – must be given renewed value, becoming the constant and highest norm for all activity”.[158] In this framework, along with the importance of little everyday gestures, social love moves us to devise larger strategies to halt environmental degradation and to encourage a “culture of care” which permeates all of society. When we feel that God is calling us to intervene with others in these social dynamics, we should realize that this too is part of our spirituality, which is an exercise of charity and, as such, matures and sanctifies us.

232. Not everyone is called to engage directly in political life. Society is also enriched by a countless array of organizations which work to promote the common good and to defend the environment, whether natural or urban. Some, for example, show concern for a public place (a building, a fountain, an abandoned monument, a landscape, a square), and strive to protect, restore, improve or beautify it as something belonging to everyone. Around these community actions, relationships develop or are recovered and a new social fabric emerges. Thus, a community can break out of the indifference induced by consumerism. These actions cultivate a shared identity, with a story which can be remembered and handed on. In this way, the world, and the quality of life of the poorest, are cared for, with a sense of solidarity which is at the same time aware that we live in a common home which God has entrusted to us. These community actions, when they express self-giving love, can also become intense spiritual experiences.

VI. SACRAMENTAL SIGNS AND THE CELEBRATION OF REST

233. The universe unfolds in God, who fills it completely. Hence, there is a mystical meaning to be found in a leaf, in a mountain trail, in a dewdrop, in a poor person’s face.[159] The ideal is not only to pass from the exterior to the interior to discover the action of God in the soul, but also to discover God in all things. Saint Bonaventure teaches us that “contemplation deepens the more we feel the working of God’s grace within our hearts, and the better we learn to encounter God in creatures outside ourselves”.[160]

234. Saint John of the Cross taught that all the goodness present in the realities and experiences of this world “is present in God eminently and infinitely, or more properly, in each of these sublime realities is God”.[161] This is not because the finite things of this world are really divine, but

because the mystic experiences the intimate connection between God and all beings, and thus feels that "all things are God".[162] Standing awestruck before a mountain, he or she cannot separate this experience from God, and perceives that the interior awe being lived has to be entrusted to the Lord: "Mountains have heights and they are plentiful, vast, beautiful, graceful, bright and fragrant. These mountains are what my Beloved is to me. Lonely valleys are quiet, pleasant, cool, shady and flowing with fresh water; in the variety of their groves and in the sweet song of the birds, they afford abundant recreation and delight to the senses, and in their solitude and silence, they refresh us and give rest. These valleys are what my Beloved is to me".[163]

235. The Sacraments are a privileged way in which nature is taken up by God to become a means of mediating supernatural life. Through our worship of God, we are invited to embrace the world on a different plane. Water, oil, fire and colours are taken up in all their symbolic power and incorporated in our act of praise. The hand that blesses is an instrument of God's love and a reflection of the closeness of Jesus Christ, who came to accompany us on the journey of life. Water poured over the body of a child in Baptism is a sign of new life. Encountering God does not mean fleeing from this world or turning our back on nature. This is especially clear in the spirituality of the Christian East. "Beauty, which in the East is one of the best loved names expressing the divine harmony and the model of humanity transfigured, appears everywhere: in the shape of a church, in the sounds, in the colours, in the lights, in the scents".[164] For Christians, all the creatures of the material universe find their true meaning in the incarnate Word, for the Son of God has incorporated in his person part of the material world, planting in it a seed of definitive transformation. "Christianity does not reject matter. Rather, bodiliness is considered in all its value in the liturgical act, whereby the human body is disclosed in its inner nature as a temple of the Holy Spirit and is united with the Lord Jesus, who himself took a body for the world's salvation".[165]

236. It is in the Eucharist that all that has been created finds its greatest exaltation. Grace, which tends to manifest itself tangibly, found unsurpassable expression when God himself became man and gave himself as food for his creatures. The Lord, in the culmination of the mystery of the Incarnation, chose to reach our intimate depths through a fragment of matter. He comes not from above, but from within, he comes that we might find him in this world of ours. In the Eucharist, fullness is already achieved; it is the living centre of the universe, the overflowing core of love and of inexhaustible life. Joined to the incarnate Son, present in the Eucharist, the whole cosmos gives thanks to God. Indeed the Eucharist is itself an act of cosmic love: "Yes, cosmic! Because even when it is celebrated on the humble altar of a country church, the Eucharist is always in some way celebrated on the altar of the world".[166] The Eucharist joins heaven and earth; it embraces and penetrates all creation. The world which came forth from God's hands returns to him in blessed and undivided adoration: in the bread of the Eucharist, "creation is projected towards divinization, towards the holy wedding feast, towards unification with the Creator himself".[167] Thus, the Eucharist is also a source of light and motivation for our concerns for the environment, directing us to be stewards of all creation.

237. On Sunday, our participation in the Eucharist has special importance. Sunday, like the Jewish Sabbath, is meant to be a day which heals our relationships with God, with ourselves, with others and with the world. Sunday is the day of the Resurrection, the "first day" of the new creation, whose first fruits are the Lord's risen humanity, the pledge of the final transfiguration of all created reality. It also proclaims "man's eternal rest in God".[168] In this way, Christian spirituality incorporates the value of relaxation and festivity. We tend to demean contemplative rest as something unproductive and unnecessary, but this is to do away with the very thing which is most important about work: its meaning. We are called to include in our work a dimension of receptivity and gratuity, which is quite different from mere inactivity. Rather, it is another way of working, which forms part of our very essence. It protects human action from becoming empty activism; it also prevents that unfettered greed and sense of isolation which make us seek personal gain to the detriment of all else. The law of weekly rest forbade work on the seventh day, "so that your ox and your donkey may have rest, and the son of your maidservant, and the stranger, may be refreshed" (*Ex* 23:12). Rest opens our eyes to the larger picture and gives us renewed sensitivity to the rights of others. And so the day of rest, centred on the Eucharist, sheds it light on the whole week, and motivates us to greater concern for nature and the poor.

VII. THE TRINITY AND THE RELATIONSHIP BETWEEN CREATURES

238. The Father is the ultimate source of everything, the loving and self-communicating foundation of all that exists. The Son, his reflection, through whom all things were created, united himself to this earth when he was formed in the womb of Mary. The Spirit, infinite bond of love, is intimately present at the very heart of the universe, inspiring and bringing new pathways. The world was created by the three Persons acting as a single divine principle, but each one of them performed this common work in accordance with his own personal property. Consequently, "when we contemplate with wonder the universe in all its grandeur and beauty, we must praise the whole Trinity".[169]

239. For Christians, believing in one God who is trinitarian communion suggests that the Trinity has left its mark on all creation. Saint Bonaventure went so far as to say that human beings, before sin, were able to see how each creature "testifies that God is three". The reflection of the Trinity was there to be recognized in nature "when that book was open to man and our eyes had not yet become darkened".[170] The Franciscan saint teaches us that *each creature bears in itself a specifically Trinitarian structure*, so real that it could be readily contemplated if only the human gaze were not so partial, dark and fragile. In this way, he points out to us the challenge of trying to read reality in a Trinitarian key.

240. The divine Persons are subsistent relations, and the world, created according to the divine model, is a web of relationships. Creatures tend towards God, and in turn it is proper to every living being to tend towards other things, so that throughout the universe we can find any number of constant and secretly interwoven relationships.[171] This leads us not only to marvel at the

manifold connections existing among creatures, but also to discover a key to our own fulfilment. The human person grows more, matures more and is sanctified more to the extent that he or she enters into relationships, going out from themselves to live in communion with God, with others and with all creatures. In this way, they make their own that trinitarian dynamism which God imprinted in them when they were created. Everything is interconnected, and this invites us to develop a spirituality of that global solidarity which flows from the mystery of the Trinity.

VIII. QUEEN OF ALL CREATION

241. Mary, the Mother who cared for Jesus, now cares with maternal affection and pain for this wounded world. Just as her pierced heart mourned the death of Jesus, so now she grieves for the sufferings of the crucified poor and for the creatures of this world laid waste by human power. Completely transfigured, she now lives with Jesus, and all creatures sing of her fairness. She is the Woman, “clothed in the sun, with the moon under her feet, and on her head a crown of twelve stars” (*Rev* 12:1). Carried up into heaven, she is the Mother and Queen of all creation. In her glorified body, together with the Risen Christ, part of creation has reached the fullness of its beauty. She treasures the entire life of Jesus in her heart (cf. *Lk* 2:19,51), and now understands the meaning of all things. Hence, we can ask her to enable us to look at this world with eyes of wisdom.

242. At her side in the Holy Family of Nazareth, stands the figure of Saint Joseph. Through his work and generous presence, he cared for and defended Mary and Jesus, delivering them from the violence of the unjust by bringing them to Egypt. The Gospel presents Joseph as a just man, hard-working and strong. But he also shows great tenderness, which is not a mark of the weak but of those who are genuinely strong, fully aware of reality and ready to love and serve in humility. That is why he was proclaimed custodian of the universal Church. He too can teach us how to show care; he can inspire us to work with generosity and tenderness in protecting this world which God has entrusted to us.

IX. BEYOND THE SUN

243. At the end, we will find ourselves face to face with the infinite beauty of God (cf. *1 Cor* 13:12), and be able to read with admiration and happiness the mystery of the universe, which with us will share in unending plenitude. Even now we are journeying towards the sabbath of eternity, the new Jerusalem, towards our common home in heaven. Jesus says: “I make all things new” (*Rev* 21:5). Eternal life will be a shared experience of awe, in which each creature, resplendently transfigured, will take its rightful place and have something to give those poor men and women who will have been liberated once and for all.

244. In the meantime, we come together to take charge of this home which has been entrusted to us, knowing that all the good which exists here will be taken up into the heavenly feast. In union

with all creatures, we journey through this land seeking God, for “if the world has a beginning and if it has been created, we must enquire who gave it this beginning, and who was its Creator”.[172] Let us sing as we go. May our struggles and our concern for this planet never take away the joy of our hope.

245. God, who calls us to generous commitment and to give him our all, offers us the light and the strength needed to continue on our way. In the heart of this world, the Lord of life, who loves us so much, is always present. He does not abandon us, he does not leave us alone, for he has united himself definitively to our earth, and his love constantly impels us to find new ways forward. *Praise be to him*!

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246. At the conclusion of this lengthy reflection which has been both joyful and troubling, I propose that we offer two prayers. The first we can share with all who believe in a God who is the all-powerful Creator, while in the other we Christians ask for inspiration to take up the commitment to creation set before us by the Gospel of Jesus.

A prayer for our earth

All-powerful God, you are present in the whole universe
and in the smallest of your creatures.
You embrace with your tenderness all that exists.
Pour out upon us the power of your love,
that we may protect life and beauty.
Fill us with peace, that we may live
as brothers and sisters, harming no one.
O God of the poor,
help us to rescue the abandoned and forgotten of this earth,
so precious in your eyes.
Bring healing to our lives,
that we may protect the world and not prey on it,
that we may sow beauty, not pollution and destruction.
Touch the hearts
of those who look only for gain
at the expense of the poor and the earth.
Teach us to discover the worth of each thing,
to be filled with awe and contemplation,
to recognize that we are profoundly united
with every creature
as we journey towards your infinite light.

We thank you for being with us each day.
Encourage us, we pray, in our struggle
for justice, love and peace.

A Christian prayer in union with creation

Father, we praise you with all your creatures.
They came forth from your all-powerful hand;
they are yours, filled with your presence and your tender love.
Praise be to you!

Son of God, Jesus,
through you all things were made.
You were formed in the womb of Mary our Mother,
you became part of this earth,
and you gazed upon this world with human eyes.
Today you are alive in every creature
in your risen glory.
Praise be to you!

Holy Spirit, by your light
you guide this world towards the Father’s love
and accompany creation as it groans in travail.
You also dwell in our hearts
and you inspire us to do what is good.
Praise be to you!

Triune Lord, wondrous community of infinite love,
teach us to contemplate you
in the beauty of the universe,
for all things speak of you.
Awaken our praise and thankfulness
for every being that you have made.
Give us the grace to feel profoundly joined
to everything that is.

God of love, show us our place in this world
as channels of your love
for all the creatures of this earth,
for not one of them is forgotten in your sight.
Enlighten those who possess power and money

that they may avoid the sin of indifference,
that they may love the common good, advance the weak,
and care for this world in which we live.
The poor and the earth are crying out.
O Lord, seize us with your power and light,
help us to protect all life,
to prepare for a better future,
for the coming of your Kingdom
of justice, peace, love and beauty.
Praise be to you!
Amen.

Given in Rome at Saint Peter's on 24 May, the Solemnity of Pentecost, in the year 2015, the third of my Pontificate.

Franciscus

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[1] *Canticle of the Creatures*, in *Francis of Assisi: Early Documents*, vol. 1, New York-London-Manila, 1999, 113-114.

[2] Apostolic Letter *Octogesima Adveniens* (14 May 1971), 21: AAS 63 (1971), 416-417.

[3] *Address to FAO on the 25th Anniversary of its Institution* (16 November 1970), 4: AAS 62 (1970), 833.

[4] Encyclical Letter *Redemptor Hominis* (4 March 1979), 15: AAS 71 (1979), 287.

[5] Cf. *Catechesis* (17 January 2001), 4: *Insegnamenti* 41/1 (2001), 179.

[6] Encyclical Letter *Centesimus Annus* (1 May 1991), 38: AAS 83 (1991), 841.

[7] Ibid., 58: AAS 83 (1991), p. 863.

[8] JOHN PAUL II, Encyclical Letter *Sollicitudo Rei Socialis* (30 December 1987), 34: AAS 80 (1988), 559.

[9] Cf. ID., Encyclical Letter *Centesimus Annus* (1 May 1991), 37: AAS 83 (1991), 840.

[10] *Address to the Diplomatic Corps Accredited to the Holy See* (8 January 2007): AAS 99

(2007), 73.

[11] Encyclical Letter *Caritas in Veritate* (29 June 2009), 51: AAS 101 (2009), 687.

[12] *Address to the Bundestag*, Berlin (22 September 2011): AAS 103 (2011), 664.

[13] *Address to the Clergy of the Diocese of Bolzano-Bressanone* (6 August 2008): AAS 100 (2008), 634.

[14] *Message for the Day of Prayer for the Protection of Creation* (1 September 2012).

[15] *Address in Santa Barbara, California* (8 November 1997); cf. JOHN CHRYSSAVGIS, *On Earth as in Heaven: Ecological Vision and Initiatives of Ecumenical Patriarch Bartholomew*, Bronx, New York, 2012.

[16] Ibid.

[17] *Lecture at the Monastery of Utstein, Norway (23 June 2003).*

[18] "Global Responsibility and Ecological Sustainability", Closing Remarks, Halki Summit I, Istanbul (20 June 2012).

[19] THOMAS OF CELANO, *The Life of Saint Francis*, I, 29, 81: in *Francis of Assisi: Early Documents*, vol. 1, New York-London-Manila, 1999, 251.

[20] *The Major Legend of Saint Francis*, VIII, 6, in *Francis of Assisi: Early Documents*, vol. 2, New York-London-Manila, 2000, 590.

[21] Cf. THOMAS OF CELANO, *The Remembrance of the Desire of a Soul*, II, 124, 165, in *Francis of Assisi: Early Documents*, vol. 2, New York-London-Manila, 2000, 354.

[22] SOUTHERN AFRICAN CATHOLIC BISHOPS' CONFERENCE, *Pastoral Statement on the Environmental Crisis* (5 September 1999).

[23] Cf. *Greeting to the Staff of FAO* (20 November 2014): AAS 106 (2014), 985.

[24] FIFTH GENERAL CONFERENCE OF THE LATIN AMERICAN AND CARIBBEAN BISHOPS, *Aparecida Document* (29 June 2007), 86.

[25] CATHOLIC BISHOPS' CONFERENCE OF THE PHILIPPINES, Pastoral Letter *What is Happening to our Beautiful Land?* (29 January 1988).

[26] BOLIVIAN BISHOPS’ CONFERENCE, Pastoral Letter on the Environment and Human Development in Bolivia *El universo, don de Dios para la vida* (23 March 2012), 17.

[27] Cf. GERMAN BISHOPS’ CONFERENCE, Commission for Social Issues, *Der Klimawandel: Brennpunkt globaler, intergenerationeller und ökologischer Gerechtigkeit* (September 2006), 28-30.

[28] PONTIFICAL COUNCIL FOR JUSTICE AND PEACE, *Compendium of the Social Doctrine of the Church*, 483.

[29] *Catechesis* (5 June 2013): *Insegnamenti* 1/1 (2013), 280.

[30] BISHOPS OF THE PATAGONIA-COMAHUE REGION (ARGENTINA), *Christmas Message* (December 2009), 2.

[31] UNITED STATES CONFERENCE OF CATHOLIC BISHOPS, *Global Climate Change: A Plea for Dialogue, Prudence and the Common Good* (15 June 2001).

[32] FIFTH GENERAL CONFERENCE OF THE LATIN AMERICAN AND CARIBBEAN BISHOPS, *Aparecida Document* (29 June 2007), 471.

[33] Apostolic Exhortation *Evangelii Gaudium* (24 November 2013), 56: AAS 105 (2013), 1043.

[34] JOHN PAUL II, *Message for the 1990 World Day of Peace*, 12: AAS 82 (1990), 154.

[35] ID., *Catechesis* (17 January 2001), 3: *Insegnamenti* 24/1 (2001), 178.

[36] JOHN PAUL II, *Message for the 1990 World Day of Peace*, 15: AAS 82 (1990), 156.

[37] *Catechism of the Catholic Church*, 357.

[38] *Angelus* in Osnabrück (Germany) with the disabled, 16 November 1980: *Insegnamenti* 3/2 (1980), 1232.

[39] BENEDICT XVI, *Homily for the Solemn Inauguration of the Petrine Ministry* (24 April 2005): AAS 97 (2005), 711.

[40] Cf. BONAVENTURE, *The Major Legend of Saint Francis*, VIII, 1, in *Francis of Assisi: Early Documents*, vol. 2, New York-London-Manila, 2000, 586.

[41] *Catechism of the Catholic Church*, 2416.

[42] GERMAN BISHOPS' CONFERENCE, *Zukunft der Schöpfung – Zukunft der Menschheit. Einklärung der Deutschen Bischofskonferenz zu Fragen der Umwelt und der Energieversorgung*, (1980), II, 2.

[43] *Catechism of the Catholic Church*, 339.

[44] *Hom. in Hexaemeron,* I, 2, 10: PG 29, 9.

[45] *The Divine Comedy, Paradiso*, Canto XXXIII, 145.

[46] BENEDICT XVI, *Catechesis* (9 November 2005), 3: *Insegnamenti* 1 (2005), 768.

[47] ID., Encyclical Letter *Caritas in Veritate* (29 June 2009), 51: AAS 101 (2009), 687.

[48] JOHN PAUL II, *Catechesis* (24 April 1991), 6: *Insegnamenti* 14 (1991), 856.

[49] The Catechism explains that God wished to create a world which is "journeying towards its ultimate perfection", and that this implies the presence of imperfection and physical evil; cf. *Catechism of the Catholic Church*, 310.

[50] Cf. SECOND VATICAN ECUMENICAL COUNCIL, Pastoral Constitution on the Church in the Modern World *Gaudium et Spes*, 36.

[51] THOMAS AQUINAS, *Summa Theologiae*, I, q. 104, art. 1 ad 4.

[52] ID., *In octo libros Physicorum Aristotelis expositio*, Lib. II, lectio 14.

[53] Against this horizon we can set the contribution of Fr Teilhard de Chardin; cf. PAUL VI, *Address in a Chemical and Pharmaceutical Plant* (24 February 1966): *Insegnamenti* 4 (1966), 992-993; JOHN PAUL II, *Letter to the Reverend George Coyne* (1 June 1988): *Insegnamenti* 11/2 (1988), 1715; BENEDICT XVI, *Homily for the Celebration of Vespers in Aosta* (24 July 2009): *Insegnamenti* 5/2 (2009), 60.

[54] JOHN PAUL II, *Catechesis* (30 January 2002),6: *Insegnamenti* 25/1 (2002), 140.

[55] CANADIAN CONFERENCE OF CATHOLIC BISHOPS, SOCIAL AFFAIRS COMMISSION, Pastoral Letter *You Love All that Exists… All Things are Yours, God, Lover of Life"* (4 October 2003), 1.

[56] CATHOLIC BISHOPS' CONFERENCE OF JAPAN, *Reverence for Life. A Message for the Twenty-First Century* (1 January 2000), 89.

[57] JOHN PAUL II, *Catechesis* (26 January 2000), 5: *Insegnamenti* 23/1 (2000), 123.

[58] ID., *Catechesis* (2 August 2000), 3: *Insegnamenti* 23/2 (2000), 112.

[59] PAUL RICOEUR, *Philosophie de la Volonté, t. II: Finitude et Culpabilité*, Paris, 2009, 216.

[60] *Summa Theologiae*, I, q. 47, art. 1.

[61] Ibid.

[62] Cf. ibid., art. 2, ad 1; art. 3.

[63] *Catechism of the Catholic Church*, 340.

[64] *Canticle of the Creatures*, in *Francis of Assisi: Early Documents*, New York-London-Manila, 1999, 113-114.

[65] Cf. NATIONAL CONFERENCE OF THE BISHOPS OF BRAZIL, *A Igreja e a Questão Ecológica,* 1992, 53-54.

[66] Ibid., 61.

[67] Apostolic Exhortation *Evangelii Gaudium* (24 November 2013), 215: AAS 105 (2013), 1109.

[68] Cf. BENEDICT XVI, Encyclical Letter *Caritas in Veritate* (29 June 2009), 14: AAS 101 (2009), 650.

[69] *Catechism of the Catholic Church*, 2418.

[70] CONFERENCE OF DOMINICAN BISHOPS, Pastoral Letter *Sobre la relación del hombre con la naturaleza* (21 January 1987).

[71] JOHN PAUL II, Encyclical Letter *Laborem Exercens* (14 September 1981), 19: AAS 73 (1981), 626.

[72] Encyclical Letter *Centesimus Annus* (1 May 1991), 31: AAS 83 (1991), 831.

[73] Encyclical Letter *Sollicitudo Rei Socialis* (30 December 1987), 33: AAS 80 (1988), 557.

[74] *Address to Indigenous and Rural People,* Cuilapán, Mexico (29 January 1979), 6: AAS 71 (1979), 209.

[75] *Homily at Mass for Farmers,* Recife, Brazil (7 July 1980): AAS 72 (1980): AAS 72 (1980), 926.

[76] Cf. *Message for the 1990 World Day of Peace*, 8: AAS 82 (1990), 152.

[77] PARAGUAYAN BISHOPS' CONFERENCE, Pastoral Letter *El campesino paraguayo y la tierra* (12 June 1983), 2, 4, d.

[78] NEW ZEALAND CATHOLIC BISHOPS CONFERENCE, *Statement on Environmental Issues* (1 September 2006).

[79] Encyclical Letter *Laborem Exercens* (14 September 1981), 27: AAS 73 (1981), 645.

[80] Hence Saint Justin could speak of "seeds of the Word" in the world; cf. *II Apologia* 8, 1-2; 13, 3-6: PG 6, 457-458, 467.

[81] JOHN PAUL II, *Address to Scientists and Representatives of the United Nations University*, Hiroshima (25 February 1981), 3: AAS 73 (1981), 422.

[82] BENEDICT XVI, Encyclical Letter *Caritas in Veritate* (29 June 2009), 69: AAS 101 (2009), 702.

[83] ROMANO GUARDINI, *Das Ende der Neuzeit*, 9th ed., Würzburg, 1965, 87 (English: *The End of the Modern World*, Wilmington, 1998, 82).

[84] Ibid.

[85] Ibid., 87-88 (*The End of the Modern World,* 83).

[86] PONTIFICAL COUNCIL FOR JUSTICE AND PEACE, *Compendium of the Social Doctrine of the Church*, 462.

[87] ROMANO GUARDINI, *Das Ende der Neuzeit*, 63-64 (*The End of the Modern World*, 56).

[88] Ibid., 64 (*The End of the Modern World*, 56).

[89] Cf. BENEDICT XVI, Encyclical Letter *Caritas in Veritate* (29 June 2009), 35: AAS 101 (2009), 671.

[90] Ibid., 22: p. 657.

[91] Apostolic Exhortation *Evangelii Gaudium* (24 November 2013), 231: AAS 105 (2013), 1114.

[92] ROMANO GUARDINI, *Das Ende der Neuzeit*, 63 (*The End of the Modern World*, 55).

[93] JOHN PAUL II, Encyclical Letter *Centesimus Annus* (1 May 1991), 38: AAS 83 (1991), 841.

[94] Cf. *Love for Creation. An Asian Response to the Ecological Crisis*, Declaration of the Colloquium sponsored by the Federation of Asian Bishops' Conferences (Tagatay, 31 January-5 February 1993), 3.3.2.

[95] JOHN PAUL II, Encyclical Letter *Centesimus Annus* (1 May 1991), 37: AAS 83 (1991), 840.

[96] BENEDICT XVI, *Message for the 2010 World Day of Peace*, 2: AAS 102 (2010), 41.

[97] ID., Encyclical Letter *Caritas in Veritate* (29 June 2009), 28: AAS 101 (2009), 663.

[98] Cf. VINCENT OF LERINS, *Commonitorium Primum*, ch. 23: PL 50, 688: "Ut annis scilicet consolidetur, dilatetur tempore, sublimetur aetate".

[99] No. 80: AAS 105 (2013), 1053.

[100] SECOND VATICAN ECUMENICAL COUNCIL, Pastoral Constitution on the Church in the Modern World *Gaudium et Spes*, 63.

[101] Cf. JOHN PAUL II, Encyclical Letter *Centesimus Annus* (1 May 1991), 37: AAS 83 (1991), 840.

[102] PAUL VI, Encyclical Letter *Populorum Progressio* (26 March 1967), 34: AAS 59 (1967), 274.

[103] BENEDICT XVI, Encyclical Letter *Caritas in Veritate* (29 June 2009), 32: AAS 101 (2009), 666.

[104] Ibid.

[105] Ibid.

[106] *Catechism of the Catholic Church*, 2417.

[107] Ibid., 2418.

[108] Ibid., 2415.

[109] *Message for the 1990 World Day of Peace*, 6: AAS 82 (1990), 150.

[110] *Address to the Pontifical Academy of Sciences* (3 October 1981), 3: *Insegnamenti* 4/2 (1981), 333.

[111] *Message for the 1990 World Day of Peace*, 7: AAS 82 (1990), 151.

[112] JOHN PAUL II, *Address to the 35th General Assembly of the World Medical Association* (29 October 1983), 6: AAS 76 (1984), 394.

[113] EPISCOPAL COMMISSION FOR PASTORAL CONCERNS IN ARGENTINA, *Una tierra para todos* (June 2005), 19.

[114] *Rio Declaration on Environment and Development* (14 June 1992), Principle 4.

[115] Apostolic Exhortation *Evangelii Gaudium* (24 November 2013), 237: AAS 105 (2013), 1116.

[116] BENEDICT XVI, Encyclical Letter *Caritas in Veritate* (29 June 2009), 51: AAS 101 (2009), 687.

[117] Some authors have emphasized the values frequently found, for example, in the *villas*, *chabolas* or *favelas* of Latin America: cf. JUAN CARLOS SCANNONE, S.J., “La irrupción del pobre y la lógica de la gratuidad”, in JUAN CARLOS SCANNONE and MARCELO PERINE (eds.), *Irrupción del pobre y quehacer filosófico. Hacia una nueva racionalidad,* Buenos Aires, 1993, 225-230.

[118] PONTIFICAL COUNCIL FOR JUSTICE AND PEACE, *Compendium of the Social Doctrine of the Church*, 482.

[119] Apostolic Exhortation *Evangelii Gaudium* (24 November 2013), 210: AAS 105 (2013), 1107.

[120] *Address to the German Bundestag*, Berlin (22 September 2011): AAS 103 (2011), 668.

[121] *Catechesis* (15 April 2015): *L’Osservatore Romano*, 16 April 2015, p. 8.

[122] SECOND VATICAN ECUMENICAL COUNCIL, Pastoral Constitution on the Church in the Modern World *Gaudium et Spes*, 26.

[123] Cf. Nos. 186-201: AAS 105 (2013), 1098-1105.

[124] PORTUGUESE BISHOPS’ CONFERENCE, Pastoral Letter *Responsabilidade Solidária pelo Bem Comum* (15 September 2003), 20.

[125] BENEDICT XVI, *Message for the 2010 World Day of Peace*, 8: AAS 102 (2010), 45.

[126] *Rio Declaration on Environment and Development* (14 June 1992), Principle 1.

[127] BOLIVIAN BISHOPS' CONFERENCE, Pastoral Letter on the Environment and Human Development in Bolivia *El universo, don de Dios para la vida* (March 2012), 86.

[128] PONTIFICAL COUNCIL FOR JUSTICE AND PEACE, *Energy, Justice and Peace,* IV, 1, Vatican City (2014), 53.

[129] BENEDICT XVI, Encyclical Letter *Caritas in Veritate* (29 June 2009), 67: AAS 101 (2009).

[130] Apostolic Exhortation *Evangelii Gaudium* (24 November 2013), 222: AAS 105 (2013), 1111.

[131] PONTIFICAL COUNCIL FOR JUSTICE AND PEACE, *Compendium of the Social Doctrine of the Church*, 469.

[132] *Rio Declaration on the Environment and Development* (14 June 1992), Principle 15.

[133] Cf. MEXICAN BISHOPS' CONFERENCE, EPISCOPAL COMMISSION FOR PASTORAL AND SOCIAL CONCERNS, *Jesucristo, vida y esperanza de los indígenas e campesinos* (14 January 2008).

[134] PONTIFICAL COUNCIL FOR JUSTICE AND PEACE, *Compendium of the Social Doctrine of the Church*, 470.

[135] *Message for the 2010 World Day of Peace*, 9: AAS 102 (2010), 46.

[136] Ibid.

[137] Ibid., 5: p. 43.

[138] BENEDICT XVI, Encyclical Letter *Caritas in Veritate* (29 June 2009), 50: AAS 101 (2009), 686.

[139] Apostolic Exhortation *Evangelii Gaudium* (24 November 2013), 209: AAS 105 (2013), 1107.

[140] Ibid., 228: AAS 105 (2013), 1113.

[141] Cf. Encyclical Letter *Lumen Fidei* (29 June 2013), 34: AAS 105 (2013), 577: "Nor is the light of faith, joined to the truth of love, extraneous to the material world, for love is always lived out in body and spirit; the light of faith is an incarnate light radiating from the luminous life of Jesus. It also illumines the material world, trusts its inherent order, and knows that it calls us to an ever widening path of harmony and understanding. The gaze of science thus benefits from faith: faith

encourages the scientist to remain constantly open to reality in all its inexhaustible richness. Faith awakens the critical sense by preventing research from being satisfied with its own formulae and helps it to realize that nature is always greater. By stimulating wonder before the profound mystery of creation, faith broadens the horizons of reason to shed greater light on the world which discloses itself to scientific investigation".

[142] Apostolic Exhortation *Evangelii Gaudium* (24 November 2013), 256: AAS 105 (2013), 1123.

[143] Ibid., 231: p. 1114.

[144] ROMANO GUARDINI, *Das Ende der Neuzeit*, 9th edition, Würzburg, 1965, 66-67 (English: *The End of the Modern World*, Wilmington, 1998, 60).

[145] JOHN PAUL II, *Message for the 1990 World Day of Peace,* 1: AAS 82 (1990), 147.

[146] BENEDICT XVI, Encyclical Letter *Caritas in Veritate* (29 June 2009), 66*:* AAS 101 (2009), 699.

[147] ID., *Message for the 2010 World Day of Peace*, 11*:* AAS 102 (2010), 48.

[148] *Earth Charter*, The Hague (29 June 2000).

[149] JOHN PAUL II, Encyclical Letter *Centesimus Annus* (1 May 1991), 39: AAS 83 (1991), 842.

[150] ID., *Message for the 1990 World Day of Peace*, 14: AAS 82 (1990), 155.

[151] Apostolic Exhortation *Evangelii Gaudium* (24 Nov 2013), 261: AAS 105 (2013), 1124.

[152] BENEDICT XVI, *Homily for the Solemn Inauguration of the Petrine Ministry* (24 April 2005): AAS 97 (2005), 710.

[153] AUSTRALIAN CATHOLIC BISHOPS' CONFERENCE, *A New Earth – The Environmental Challenge* (2002).

[154] ROMANO GUARDINI, *Das Ende der Neuzeit*, 72 (*The End of the Modern World*¸ 65-66).

[155] Apostolic Exhortation *Evangelii Gaudium* (24 November 2013), 71: AAS 105 (2013), 1050.

[156] BENEDICT XVI, Encyclical Letter *Caritas in Veritate* (29 June 2009) 2: AAS 101 (2009), 642.

[157] PAUL VI, *Message for the 1977 World Day of Peace*: AAS 68 (1976), 709.

[158] PONTIFICAL COUNCIL FOR JUSTICE AND PEACE, *Compendium of the Social Doctrine of the Church*, 582.

[159] The spiritual writer Ali al-Khawas stresses from his own experience the need not to put too much distance between the creatures of the world and the interior experience of God. As he puts it: “Prejudice should not have us criticize those who seek ecstasy in music or poetry. There is a subtle mystery in each of the movements and sounds of this world. The initiate will capture what is being said when the wind blows, the trees sway, water flows, flies buzz, doors creak, birds sing, or in the sound of strings or flutes, the sighs of the sick, the groans of the afflicted...” (EVA DE VITRAY-MEYEROVITCH [ed.], *Anthologie du soufisme,* Paris 1978, 200).

[160] *In II Sent.*, 23, 2, 3.

[161] *Cántico Espiritual*, XIV, 5.

[162] Ibid.

[163] Ibid., XIV, 6-7.

[164] JOHN PAUL II, Apostolic Letter *Orientale Lumen* (2 May 1995), 11: AAS 87 (1995), 757.

[165] Ibid.

[166] ID., Encyclical Letter *Ecclesia de Eucharistia* (17 April 2003), 8: AAS 95 (2003), 438.

[167] BENEDICT XVI, *Homily for the Mass of Corpus Domini* (15 June 2006): AAS 98 (2006), 513.

[168] *Catechism of the Catholic Church*, 2175.

[169] JOHN PAUL II, *Catechesis* (2 August 2000), 4: *Insegnamenti* 23/2 (2000), 112.

[170] *Quaest. Disp. de Myst. Trinitatis*, 1, 2 concl.

[171] Cf. THOMAS AQUINAS, *Summa Theologiae,* I, q. 11, art. 3; q. 21, art. 1, ad 3; q. 47, art. 3.

[172] BASIL THE GREAT, *Hom. in Hexaemeron*, I, 2, 6: PG 29, 8.