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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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.*

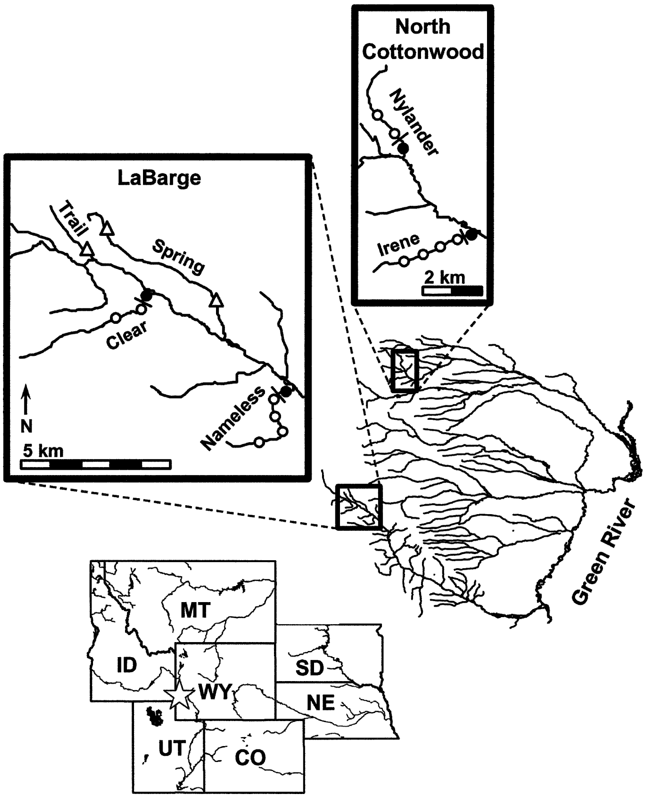

Figure 1. Study sites on headwater streams in the Green River watershed of western Wyoming. Sites were located both upstream (open circles) and downstream (closed circles) of fish migration barriers on Clear and Nameless creeks in the LaBarge Creek watershed and Nylander and Irene creeks in the North 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-

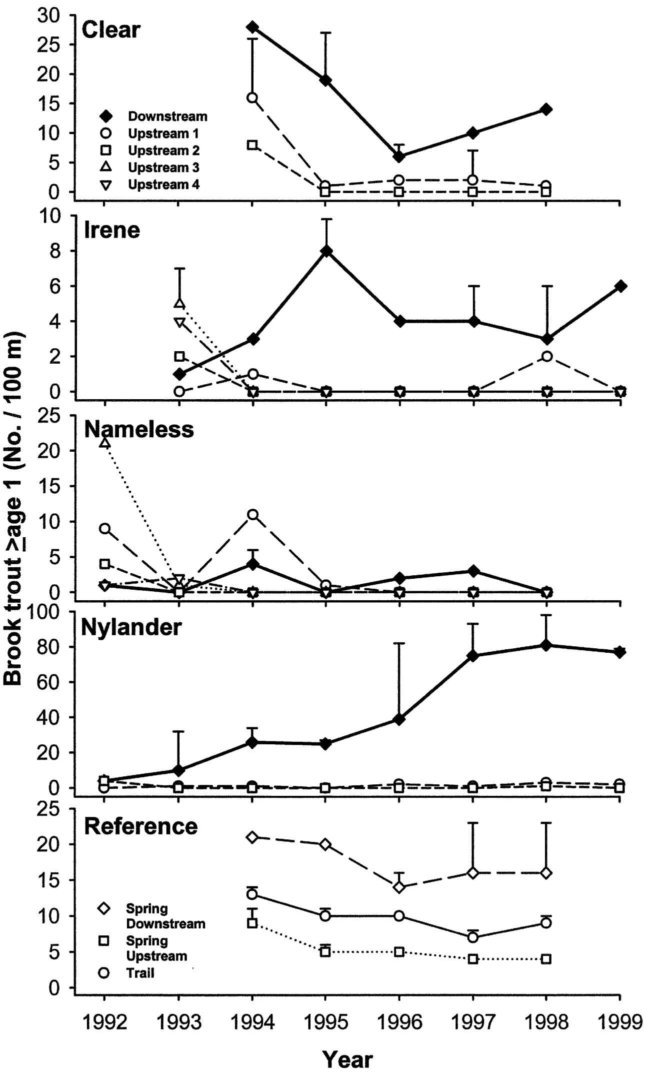

Figure 2. Population estimates (+95% C.I.) for brook trout aged 1 year and older (≥age 1) in sites upstream and downstream of barriers in treatment streams and in sites in reference streams in 1992–1999. The y-axis scaling is different among streams.

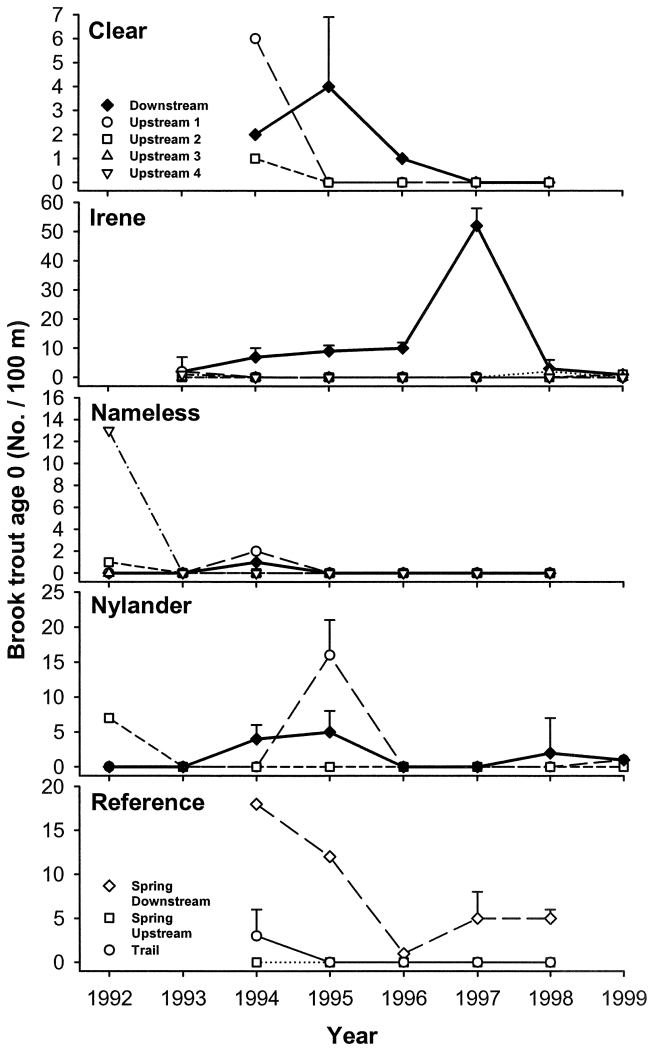

Figure 3. Population estimates (+95% C.I.) for young-of-year brook trout (age 0) in sites upstream and downstream of barriers in treatment streams and in sites in reference streams in 1992 through 1999. The y-axis scaling is different among streams.

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.

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-

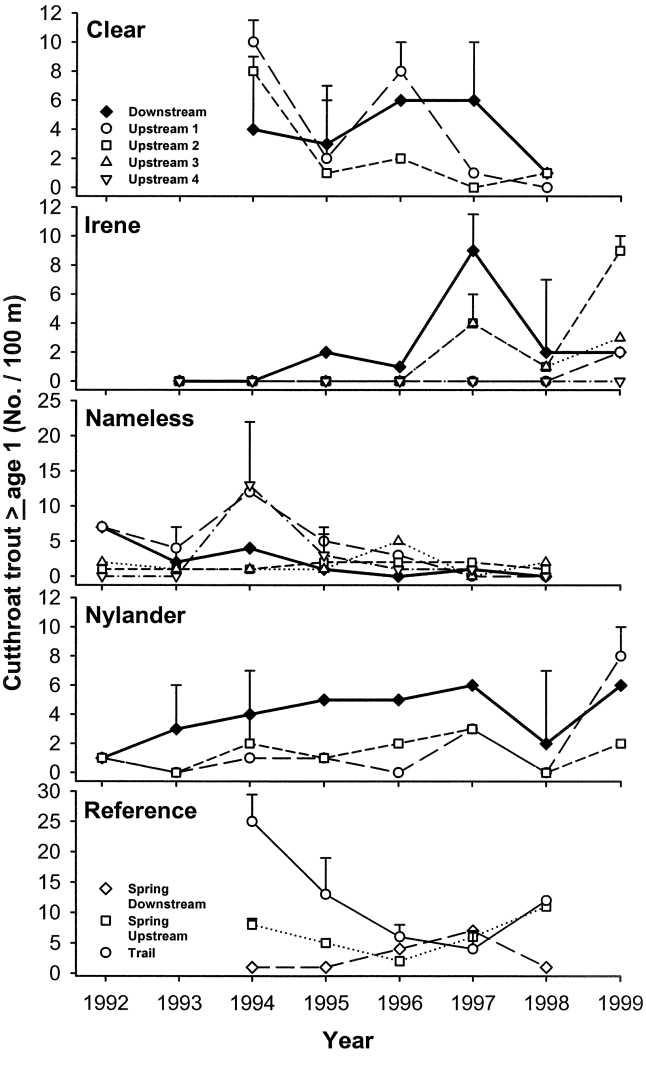

Figure 4. Population estimates (+ 95% C.I.) for wild cutthroat trout ≥ age 1 in sites upstream and downstream of barriers in treatment streams and in sites in reference streams in 1992–1999. The y-axis scaling is different among streams.

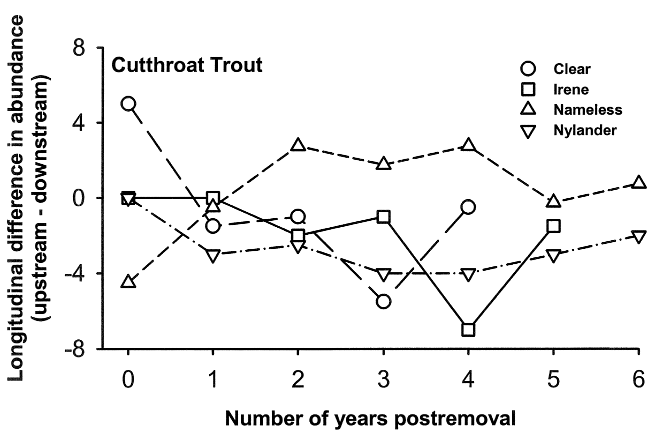

Figure 5. Longitudinal differences in abundance of wild cutthroat trout ≥ age 1 before and after removal of non-native trout, calculated by subtracting the population estimate (trout/100 m) in the downstream site from the mean population estimate of the upstream sites in each stream for each year.

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 La-Barge 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.

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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.

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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.

Saving the World's Terrestrial Megafauna

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From the late Pleistocene to the Holocene and now the so-called Anthropocene, humans have been driving an ongoing series of species declines and extinctions (Dirzo et al. 2014). Large-bodied mammals are typically at a higher risk of extinction than smaller ones (Cardillo et al. 2005). However, in some circumstances, terrestrial megafauna populations have been able to recover some of their lost numbers because of strong conservation and political commitment, as well as human cultural changes (Chapron et al. 2014). Indeed, many would be in considerably worse predicaments in the absence of conservation action (Hoffmann et al. 2015). Nevertheless, most mammalian megafauna face dramatic range contractions and population declines. In fact, 59% of the world's largest carnivores (more than or equal to 15 kilograms, $n = 27$) and 60% of the world's largest herbivores (more than or equal to 100 kilograms, $n = 74$) are classified as threatened with extinction on the International Union for the Conservation of Nature (IUCN) Red List (supplemental tables S1 and S2). This situation is particularly dire in sub-Saharan Africa and Southeast Asia, home to the greatest diversity of extant megafauna (figure 1). Species at risk of extinction include some of the world's most iconic animals—such as gorillas, rhinos, and big cats (figure 2 top row)—and, unfortunately, they are vanishing just as science is discovering their essential ecological roles (Estes et al. 2011). Here, our objectives are to raise awareness of how these megafauna are imperiled (species in tables S1 and S2) and to stimulate broad interest in developing specific recommendations and concerted action to conserve them.

Megafauna provide a range of distinct ecosystem services through top-down biotic and knock-on abiotic processes (Estes et al. 2011). Many megafauna function as keystone species and ecological engineers, generating strong cascading effects in the ecosystems in which they occur. These species also provide important economic and social services. For example, ecotourism is the fastest growing subsector of tourism in developing countries (UNEP 2013), and megafauna are a major draw for these tourists. Besides contributing considerable revenue to conservation, wildlife-based tourism can contribute significantly to education, economies, job creation, and human livelihoods.

Many of the surviving mammalian megafauna remain beset by long-standing and generally escalating threats of habitat loss, persecution, and exploitation (Ripple et al. 2014, 2015). Large mammals are extremely vulnerable to these threats because of their large area requirements, low densities (particularly for carnivores), and relatively "slow" life-history traits (Wallach et al. 2015). Various anthropogenic forces such as deforestation, agricultural expansion, increasing livestock numbers, and other forms of human encroachment have severely degraded critical habitat for megafauna by increased fragmentation or reduced resource availability. Although some species show resilience by adapting to new scenarios under certain conditions (Chapron et al. 2014), livestock production, human population growth, and cumulative land-use impacts can trigger new conflicts or exacerbate existing ones, leading to additional declines. According to the Food and Agriculture Organization, as of 2014, there were an estimated 3.9 billion ruminant livestock on Earth compared with approximately 8.5 million individuals of 51 of the 74 species of wild megaherbivores for which population estimates are available within their native ranges (table S2), a magnitude difference of approximately 400 times.

The current depletion of megafauna is also due to overhunting and persecution: shooting, snaring, and poisoning by humans ranging from individuals to governments, as well as by organized criminals and terrorists (Darimont et al. 2015). Megafauna are killed for meat and body parts for traditional medicine and ornaments or because of actual or perceived threats to humans, their crops, or livestock. Meat and body parts are sold locally, sold to urban markets, or traded regionally and internationally. Striking instances include the slaughter of thousands of megafauna, such as African elephants (*Loxodonta africana*) for their ivory, rhinoceroses for their horns, and tigers (*Panthera tigris*) for their body parts. In addition, many lesser-known megafauna species (figure 2, bottom row) are now

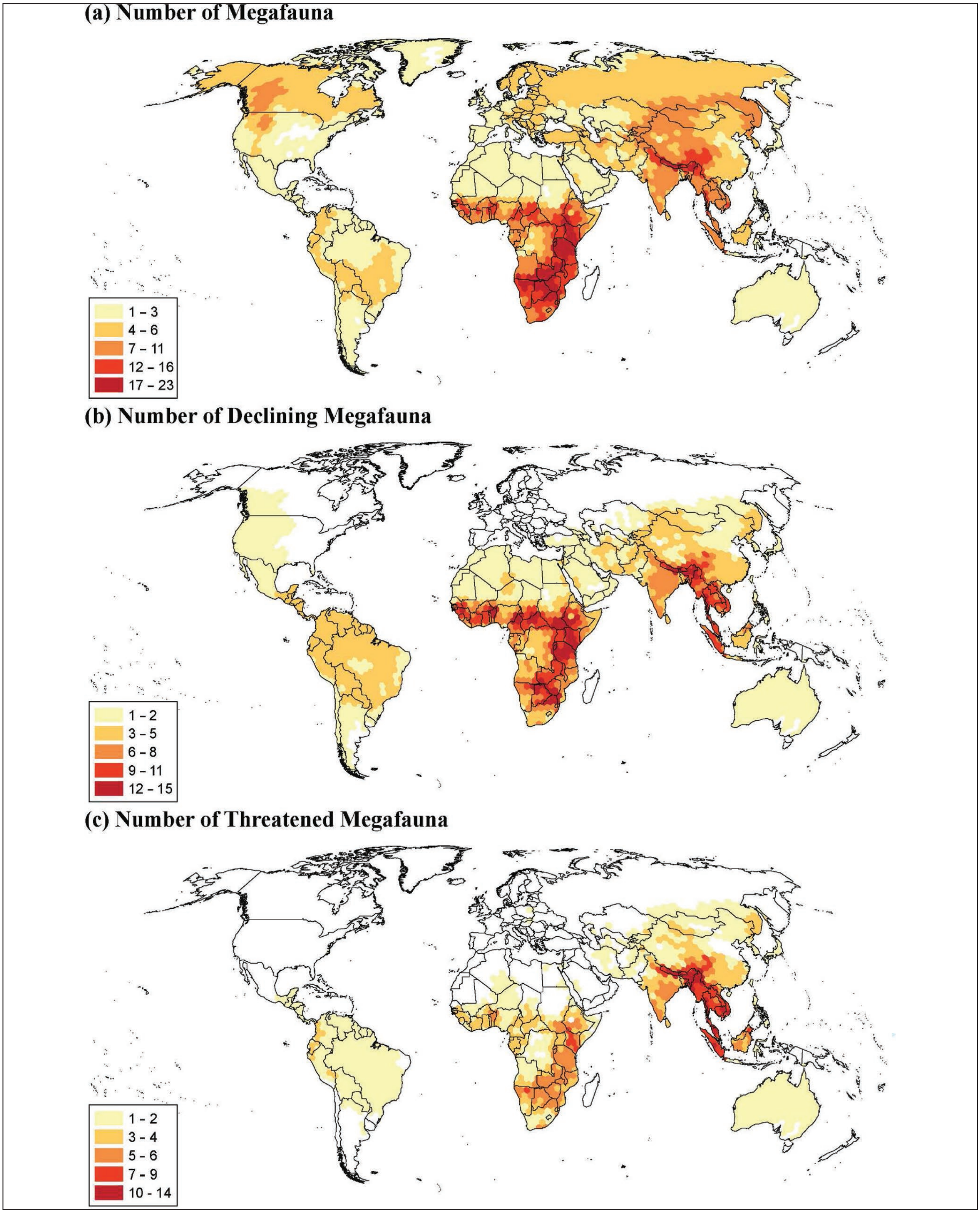

Figure 1. A richness map of (a) the number of megafaunal species, (b) the number of declining megafauna species, and (c) the number of threatened megafaunal species in their native ranges. Megafauna *are defined as terrestrial large carnivores (more than 15 kilograms) and large herbivores (more than 100 kilograms).* Threatened *includes all species categorized as Vulnerable, Endangered, or Critically Endangered on the IUCN Red List (see supplemental tables).*

Figure 2. Photographic examples of threatened megafauna. Top row left to right: photos of well-known species, including the Western gorilla (*Gorilla gorilla*) (CR), black rhino (*Diceros bicornis*) (CR), and Bengal tiger, (*Panthera tigris tigris*) (EN). Bottom row left to right: photos of lesser-known species, including the African wild ass (*Equus africanus*) (CR), Visayan warty pig (*Sus cebifrons*) (CR), and banteng (*Bos javanicus*) (EN). Photo credits: Julio Yeste, Four Oaks, Dave M. Hunt, Mikhail Blajenov, KMW Photography, and Kajornyot.

imperiled (tables S1 and S2). Most of the world's megaherbivores remain poorly studied, and this knowledge gap makes conserving them even more difficult (Ripple et al. 2015).

Under a business-as-usual scenario, conservation scientists will soon be busy writing obituaries for species and subspecies of megafauna as they vanish from the planet. In fact, this process is already underway: eulogies have been written for Africa's western black rhinoceros (*Diceros bicornis longipes*) and the Vietnamese subspecies of the Javan rhinoceros (*Rhinoceros sondaicus annamiticus*, IUCN 2015). Epitaphs will probably soon be needed for the kouprey (*Bos sauveli*), last seen in 1988; and the northern white rhinoceros (*Ceratotherium simum cottoni*), which now numbers three individuals (IUCN 2015). The Sumatran rhino (*Dicerorhinus sumatrensis*) is already extinct in the wild in Malaysia and is very close to extinction in Indonesia, with the population collapsing during the last 30 years from over 800 to fewer than 100 (table S2). The Javan rhino (*Rhinoceros sondaicus*) is down to a single population of approximately 58 in a single reserve (table S2). The Critically Endangered Bactrian camel (*Camelus ferus*) and African wild ass (*Equus africanus*) are not far behind. Even in protected areas, megafauna are increasingly under assault. For example, in West and Central Africa, several large carnivores (including lions, *Panthera leo*; African wild dogs, *Lycaon pictus*; and cheetahs, *Acinonyx jubatus*) have experienced recent severe range contractions and have declined markedly in many protected areas (IUCN 2015).

Although many of the general causes and mechanisms of declines are well identified and recognized, this understanding has not translated into adequate conservation action. Some of the existing mammal-prioritization schemes could be incorporated into a comprehensive global strategy for conserving the largest mammals (Rondinini et al. 2011). Increasing prioritization and political will to conserve megafauna—and actions to restore or reintroduce them in areas where they have declined or been extirpated (such as plans to reintroduce scimitar-horned oryx into Chad and to rehabilitate the entire Gorongosa ecosystem in Mozambique)—are urgently needed. We suggest that the problem has two

Box 1. A declaration to save the world's terrestrial megafauna.

We conservation scientists

1. Acknowledge that most of the terrestrial megafauna species are threatened with extinction and have declining populations. Some megafauna species that are not globally threatened nonetheless face local extinctions or have Critically Endangered subspecies.
2. Appreciate that "business as usual" will result in the loss of many of the Earth's most iconic species.
3. Understand that megafauna have ecological roles that directly and indirectly affect ecosystem processes and other species throughout the food web; failure to reverse megafaunal declines will disrupt species interactions, with negative consequences for ecosystem function; biological diversity; and the ecological, economic, and social services that these species provide.
4. Realize that megafauna are epitomized as a symbol of the wilderness, exemplifying the public's engagement in nature, and that this is a driving force behind efforts to maintain the ecosystem services they can provide.
5. Recognize the importance of integrating and better aligning human development and biodiversity conservation needs through the engagement and support of local communities in developing countries.
6. Propose that funding agencies and scientists increase conservation research efforts in developing countries, where most threatened megafauna occur. Specifically, there is a need to increase the amount of research directed at finding solutions for the conservation of megafauna, especially for lesser-known species.
7. Request the help of individuals, governments, corporations, and nongovernmental organizations to stop practices that are harmful to these species and to actively engage in helping to reverse declines in megafauna.
8. Strive for increased awareness among the global public of the current megafauna crisis using traditional media as well as social media and other networking approaches.
9. Seek a new and comprehensive global commitment and framework for conserving megafauna. The international community should take necessary action to prevent mass extinction of the world's megafauna and other species.
10. Urge the development of new funding mechanisms to transfer the current benefits accrued through the existence values of megafauna into tangible payments to support research, conservation actions, and local people who bear the cost of living with wildlife in the places where highly valued megafauna must be preserved.
11. Advocate for interdisciplinary scientific interchange between nations to improve the social and ecological understanding of the drivers of the decline of megafauna and to increase the capacity for megafauna science and conservation.
12. Recommend the reintroduction and rehabilitation, following accepted IUCN guidelines, of degraded megafauna populations whenever possible, the ecological and economic importance of which is evidenced by a growing number of success stories, from Yellowstone's wolves (*Canis lupus*) and the Père David's deer (*Elaphurus davidianus*) in China to the various megafauna species of Gorongosa National Park in Mozambique.
13. Affirm an abiding moral obligation to protect the Earth's megafauna.

parts: (1) a need to further and more effectively implement, expand, and refine current interventions at relevant scales and (2) a need for large-scale policy shifts and global increases in funding for conservation to alter the framework and ways in which people interact with wildlife.

In order to save declining species, there is a need to increase global conservation funding by at least an order of magnitude (McCarthy et al. 2012). Without such a transformation, there is a risk that many of the world's most iconic species may not survive to the twenty-second century. We must not go quietly into this impoverished future. Rather, we believe it is our collective responsibility as scientists who study megafauna to act to prevent their decline. We therefore present a call to the broader international community to join together in conserving the remaining terrestrial megafauna (see declaration in box 1).

From declaration to action

Social and political commitment to provide sufficient protection across the vast landscapes needed for the conservation of the world's megafauna is increasingly required. International frameworks and conventions such as the Convention on Biological Diversity (CBD), the Convention on the Conservation of Migratory Species of Wild Animals (CMS), and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) have had some success in safeguarding species. However, the decisions of these conventions are not always binding, and they will require substantially increased political will and financial support if they are to be effective in the critical task of securing the survival of the world's megafauna. Some regional instruments such as the CMS Gorilla Agreement and the Global Tiger Initiative incorporate environmental or biodiversity commitments and are playing a growing role in protecting biodiversity. International agreements are often well placed for enforcing regional frameworks for megafauna; examples include the

African Elephant Action Plan and the regional conservation strategy for cheetahs and African wild dogs. However, the implementation of such initiatives requires financial resources and capacity that are seldom available at those locations where the highest diversity of megafauna remains (figure 1). Therefore, the onus is on developed countries, which have long ago lost most of their megafauna, to not only embark on conservation and restoration programs on their own lands but also support conservation initiatives in those nations where diverse megafauna still persist. For conservation efforts to be successful, actions should be taken at all levels by authorities who have the public interest in mind and who work to secure the continued existence of these species.

Successfully conserving megafauna requires bold social, political, and financial commitments from nations around the world. Through understanding the value and importance of local human needs and by combining international financial support with a coordinated multilateral approach to conservation, it may be possible to rescue megafauna from the brink of extinction. As biologists, ecologists, and conservation scientists, we are mindful that none of our arguments are new and that our prescriptions are far easier to write out than to accomplish. However, our objective in presenting them together here is to demonstrate a consensus of opinion amongst the global community of scientists who study and conserve these animals, thereby emphasizing to the wider world the gravity of the problem. Our hope is that this declaration, with the proposed actions and list of signatories, will attract the public and media attention that this issue requires to galvanize opinion, catalyze action, and establish new funding mechanisms. Comprehensive actions to save these iconic wildlife species will help to curb an extinction process that appears to have begun with our ancestors in the late Pleistocene.

In the supplemental material for this article, this entire paper is available in six other languages: Spanish, Chinese, French, Portuguese, Malay (Bahasa Malaysia), and Thai.

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Supplemental material
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References cited
Cardillo RN, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme DL, Purvis A. 2005. Multiple causes of high extinction risk in large mammal species. Science 309: 1239–1241.

Chapron G, et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346: 1518–1519.

Darimont CT, Fox CH, Bryan HM, and Reimchen TE. 2015. The unique ecology of human predators. Science 349: 858–860.

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. 2014. Defaunation in the Anthropocene. Science 345: 401–406.

Estes JA, et al. 2011. Trophic downgrading of planet Earth. Science 333: 301–306.

Hoffmann M, Duckworth JW, Holmes K, Mallon DP, Rodrigues ASL, Stuart SN. 2015. The difference conservation makes to extinction risk of the world's ungulates. Conservation Biology 29: 1303–1313.

[IUCN] International Union for Conservation of Nature. 2015. The IUCN Red List of Threatened Species. IUCN. (17 March 2016; *www.iucnRedList.org*)

McCarthy DP, et al. 2012. Financial costs of meeting global biodiversity conservation targets: Current spending and unmet needs. Science 338: 946–949.

Ripple WJ, et al. 2014. Status and ecological effects of the world's largest carnivores. Science 343 (art. 1241484).

Ripple WJ, et al. 2015. Collapse of the world's largest herbivores. Science Advances 1 (art. e1400103).

Rondinini C, et al. 2011. Reconciling global mammal prioritization schemes into a strategy. Philosophical Transactions of the Royal Society B 366: 2722–2728.

UNEP [United Nations Environment Programme]. 2013. Green Economy and Trade: Trends, Challenges, and Opportunities. UNEP. (17 March 2016; *http://web.unep.org/greeneconomy/sites/unep.org.greeneconomy/files/field/image/fullreport.pdf*).

Wallach AD, Izhaki I, Toms JD, Ripple WJ, Shanas U. 2015. What is an apex predator? Oikos 124: 1453–1461.

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Conserving Megafauna or Sacrificing Biodiversity?

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In their recent contribution, Ripple and colleagues (doi:10.1093/biosci/biw092) highlight the issue of large (more than 15 kilograms) terrestrial mammal (i.e., *megafauna*) declines, with the intent to "attract the public and media attention that this issue requires to galvanize opinion, catalyze action, and establish new funding mechanisms." At the heart of this argument are the twin assertions that, compared with other taxa, terrestrial megafauna are (a) more imperiled and (b) more ecologically impactful. We agree that many species of large mammals are declining, that such declines could potentially alter ecosystems, and that new ways of thinking about this problem are needed to prevent extinctions. However, the formulation of their "declaration" suggests five questions that potentially undermine broader efforts to conserve biodiversity. We hope that our Viewpoint will help promote a net conservation gain for nature—megafauna and other forms of biodiversity—in a world of limited financial resources, public attention, and political will.

1. **Will funding megafauna conservation help fund other species?** Declaration points 3 and 4 of Ripple and colleagues' box 1 suggest that megafauna exemplify the public's engagement in nature and that they are symbols of wilderness. We agree with Ripple and colleagues that megafauna are often more easily recognized than many other species are and that this could potentially be helpful in rallying public attention toward broader conservation objectives. This strategy has long been the position of many conservation nongovernmental organizations (Clucas et al. 2008). However, conservation campaigns promoting "flagship" species tend to direct the majority of funds exclusively toward the flagship species (Smith R et al. 2012). In many cases, these flagship species are megafauna (Clucas et al. 2008), which suggests that the strategies used to promote the conservation of megafauna are, as practiced, inadequate for the conservation of other species.
2. **Do megafauna need more attention?** We agree with Ripple and colleagues that more research on some species of megafauna could provide insights that are useful for conservation. However, the knowledge gaps in megafauna ecology are relatively thin cracks compared with the chasms of knowledge that exist for the vast majority of species—many of which we have yet to identify, let alone understand their natural history, biology, or conservation status (Wilson EO 1987, Costello et al. 2013, Donaldson et al. 2016). Indeed, studies have documented systematic biases toward large mammals in social media (Roberge 2014), in popular media (Clucas et al. 2008, Sergio et al. 2008), and in conservation research (Clark and May 2002) and fundraising (Smith R et al. 2012). This bias means that most animals and plants at risk of extinction receive far less funding than larger, warm-blooded vertebrates do, even if those larger species are less imperiled (Brodie 2009, Donaldson et al. 2016). We extend declaration point 8 of Ripple and colleagues to include raising funds for and awareness of other taxa whose status is at risk.
3. **Do megafauna play a distinct role in the ecosystem?** The argument that megafauna have a distinct role in the ecosystem and that their impacts cascade to affect other organisms or abiotic processes (declaration point 3) glosses over at least four important issues. First, although it is true that megafauna can precipitate trophic cascades in some systems, not all ecological communities possess the conditions necessary for such cascades to occur (Heupel et al. 2014, Ford and Goheen 2015, Ford et al. 2015). In order for megafauna species (or any other consumer) to trigger trophic cascades, there must be a series of strong and sequential pairwise interactions whereby consumers limit resources (Shurin et al. 2002, Schmitz 2010). It is not known how commonly this structure occurs in ecological communities comprising megafauna (Ford and Goheen 2015). Second, bottom-up control of ecological communities can also be strong (Schmitz 2010) such that arguments for conserving species that trigger knock-on effects could just as readily be directed toward primary producers. Efforts to conserve species in lower trophic levels could then facilitate megafauna conservation. Third, if the justification for increased conservation of megafauna is their potential role as ecosystem engineers, then it follows that other ecological engineers should receive increased support for conservation. Megafauna do not exclusively engineer ecosystems—consider the engineering roles of rodents (Wright et al. 2002, Davidson et al. 2012), fish (Moore 2006), and invertebrates (Hastings et al. 2007). Fourth, there remain questions about functional redundancy among megafauna and smaller species (Keesing 2000, Rosenfeld 2002, Maclean et al. 2011, Pringle et al. 2014, Veblen et al. 2016). High redundancy would

suggest that the loss of individual species (or even guilds) may not have cascading effects or that the ecological role of some species—including megafauna—may not be distinct. Together, these four points suggests that megafauna are either as ecologically distinct as any other taxonomic group or that the evidence for megafauna distinction is highly uncertain. In either case, ecological distinction *per se* is not a compelling argument to support the primacy of megafauna conservation.

4. **Is a declaration to conserve megafauna counterproductive?** The answer to this question depends on the extent to which the "new funding mechanisms" and attention sought for megafauna are additive or compensatory. We argue that resources and attention are extendable but ultimately finite. Therefore, Ripple and colleagues' suggestion to increase funding for megafauna would likely detract from resources potentially available for other species. In some jurisdictions, dedicated funds for megafauna conservation (e.g., for harvestable populations) are the result of policies targeting the enhancement of certain species for the benefit of user groups (e.g., recreational hunting opportunities). Such policies can be altered to include or exclude nonmegafauna taxa, but these policies typically are not designed to make the resource pie bigger. Consequently, increasing the attention and resources for megafauna could imperil the conservation of other species by drawing an even larger share of limited resources. Conversely, if substantially greater resources do become available for conservation, one could readily argue that they should be disproportionately allocated to smaller animal, plants, and microbes, if only to partially level the playing field.
5. **Are megafauna more imperiled than other species?** One explanation for the observed declines in many megafaunal populations is the attention directed toward them—the declines are noticed precisely because people are paying attention. For taxa with a lower research profile, there often are not enough data available to document species occurrence, let alone population trends (Costello et al. 2013, Donaldson et al. 2016). Indeed, in spite of taxonomic bias in the assessment process (Donaldson et al. 2016), the International Union for Conservation of Nature reports that none of the 15 species (not subspecies) known to have gone extinct in the wild between 1984 and 2004 are megafauna (Baillie et al. 2004).We agree with Ripple and colleagues that megafauna are declining in many areas, but declines are not exclusive to megafauna, nor are they necessarily steeper. Moreover, the declines in abundance or diversity of other taxa are staggering and include insectivorous passerines (Parody et al. 2001), native pollinators (Potts et al. 2010), medicinal plants (Shanley and Luz 2003), amphibians (Stuart et al. 2004), bats (Blehert et al. 2009), coral (De'ath et al. 2012), phytoplankton (Boyce et al. 2010), and marine (Worm et al. 2009) and freshwater fish (Bruton 1995). The impact of these declines threatens livelihoods and human well-being (Salafsky and Wollenberg 2000) in a way that the loss of many megafauna, although tragic, simply may not have. To further illustrate our point, we note that Ripple and colleagues suggest that we are just learning about the ecological role of megafauna. However, we have comparatively little knowledge about the natural history, ecology, or conservation status of human-gut microbiota—species that literally shape our internal and external ecosystems—in an era of widespread antibiotic use (Blaser and Falkow 2009). Finally, smaller species are also subject to illegal trade, perhaps more so than megafauna (Smith KF et al. 2009). For these reasons, it is difficult to argue for the prioritization of megafauna conservation in a world of competing social, physical, and environmental needs.

Moving forward: What is the best way to promote an agenda of conservation for megafauna and other species? We reiterate our agreement that the conservation of megafauna is important, that many species are facing decline, and that new ways of thinking about the problem are needed to offset these declines. In this way, Ripple and colleagues' declaration is commendable for its spirit, its intention, and its calls to change "business-as-usual" practices—we agree wholeheartedly. However, for many in the conservation community, "business as usual" is, in fact, the overrepresentation of megafauna in research, funding, and media attention. Unfortunately, Ripple and colleagues' declaration risks further increasing this disparity. One could see a similar declaration (needlessly) developed for virtually every taxonomic group (e.g., freshwater fish, insects, amphibians, or plants). All but a few words in Ripple and colleagues' declaration would need to be replaced for it to be relevant to these other taxonomic groups. Indeed, were their declaration positioned more broadly (for conservation of biodiversity rather than a specific taxonomic group), it might have greater influence across diverse taxa and among a broader audience of conservationists.

We briefly highlight three emerging approaches to conservation that could provide a more objective and comprehensive approach to allocation and prioritization than what was suggested by Ripple and colleagues. First, a common-threats approach (Donaldson et al. 2016) may help unify and direct funding toward the sources of decline for both megafauna and other species. For example, habitat loss is a significant threat to many species in the tropics (Brooks et al. 2002), and efforts to prevent the conversion of native rainforest into agriculture could produce broad, community-wide conservation gains (Brodie and Giordano 2013). Such an approach, as Ripple and colleagues advocate (declaration points 5 and 10), would need to address the impacts of conservation on the livelihoods and cultures of local people. Second, accounting and optimization approaches provide a transparent means of quantifying the effectiveness of conservation spending (Wilson KA et al. 2006, Joseph et al. 2009). This approach allows society to compare the unit cost of increasing the population growth rate for different species of conservation concern, thereby grounding management decisions in objective criteria. Indeed, Czech and colleagues (1998) suggest that, relative to birds and mammals, plants and amphibians may offer a more productive investment in conservation funding. Third, shifting the focus from taxa *per se* to the conservation or restoration of landscape-scale systems and processes could be another means of addressing the declines of both megafauna and other species. For example, the "umbrella-species" utility of megafauna (Fleishman et al. 2001)—often used as an indicator of ecological condition or conservation planning—could be shifted toward a focus on umbrella *processes*. In this way, the presence of renewal processes such as fires (Bowman and Legge 2016) and floods (Hauer et al. 2016) would potentially confer persistence for a host of species, including megafauna (Sensenig et al. 2010, Palmer and Ruhl 2015).

We believe that an inclusive approach to conservation is needed. Such an approach would coordinate resources, research efforts, policy changes, and the mitigation of common threats for a host of ecological process and taxa. We embrace the spirit of Ripple and colleagues' declaration, but we believe that the conservation benefits arising from its adoption will have a much greater impact if they are not targeted at the taxonomic group that is arguably the most well-studied and well-funded one on Earth.

References cited

Baillie J, Hilton-Taylor C, Stuart SN. 2004. International Union for Conservation of Nature (IUCN) Red List of Threatened Species: A Global Species Assessment. IUCN.

Blaser MJ, Falkow S. 2009. What are the consequences of the disappearing human microbiota? Nature Reviews Microbiology 7: 887–894.

Blehert DS, et al. 2009. Bat white-nose syndrome: An emerging fungal pathogen? Science 323: 227–227.

Bowman DM, Legge S. 2016. Pyrodiversity—Why managing fire in food webs is relevant to restoration ecology. Restoration Ecology 24: 848–853. doi:10.1111/rec.12401

Boyce DG, Lewis MR, Worm B. 2010. Global phytoplankton decline over the past century. Nature 466: 591–596.

Brodie JF. 2009. Is research effort allocated efficiently for conservation? Felidae as a global case study. Biodiversity and Conservation 18: 2927–2939.

Brodie JF, Giordano A. 2013. Lack of trophic release with large mammal predators and prey in Borneo. Biological Conservation 163: 58–67.

Brooks TM, et al. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16: 909–923.

Bruton MN. 1995. Have fishes had their chips? The dilemma of threatened fishes. Environmental Biology of Fishes 43: 1–27.

Clark JA, May RM. 2002. Taxonomic bias in conservation research. Science 297: 191–192.

Clucas B, McHugh K, Caro T. 2008. Flagship species on covers of US conservation and nature magazines. Biodiversity and Conservation 17: 1517–1528.

Costello MJ, May RM, Stork NE. 2013. Can we name Earth's species before they go extinct? Science 339: 413–416.

Czech B, Kausman PR, Borkhataria R. 1998. Social construction, political power, and the allocation of benefits to endangered species. Conservation Biology 12: 1103–1112.

Davidson AD, Detling JK, Brown JH. 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. Frontiers in Ecology and the Environment 10: 477–486.

De'ath G, Fabricius KE, Sweatman H, Puotinen M. 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proceedings of the National Academy of Sciences 109: 17995–17999.

Donaldson MR, Burnett NJ, Braun DC, Suski CD, Hinch SG, Cooke SJ, Kerr JT. 2016. Taxonomic bias and international biodiversity conservation research. FACETS 1 (art. 105).

Fleishman E, Blair RB, Murphy DD. 2001. Empirical validation of a method for umbrella species selection. Ecological Applications 11: 1489–1501.

Ford AT, Goheen JR. 2015. Trophic cascades by large carnivores: A case for strong inference and mechanism. Trends in Ecology and Evolution 30: 725–735.

Ford AT, Goheen JR, Augustine DJ, Kinnaird MF, O'Brien TG, Palmer TM, Pringle RM, Woodroffe R. 2015. Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade. Ecology 96: 2705–2714.

Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG. 2007. Ecosystem engineering in space and time. Ecology Letters 10: 153–164.

Hauer R, Locke H, Dreitz VJ, Hebblewhite M, Lowe WH, Muhlfeld CC, Nelson CR, Proctor MF, Rood SB. 2016. Gravel-bed river floodplains are the ecological nexus of glaciated mountain landscapes. Science Advances 2 (art. e1600026).

Heupel MR, Knip DM, Simpfendorfer CA, Dulvy NK. 2014. Sizing up the ecological role of sharks as predators. Marine Ecology Progress Series 495: 291–298.

Joseph LN, Maloney RF, Possingham HP. 2009. Optimal allocation of resources among threatened species: A project prioritization protocol. Conservation Biology 23: 328–338.

Keesing F. 2000. Cryptic consumers and the ecology of an African savanna. BioScience 50: 205–215.

Maclean JE, Goheen JR, Doak DF, Palmer TM, Young TP. 2011. Cryptic herbivores mediate the strength and form of ungulate impacts on a long-lived savanna tree. Ecology 92: 1626–1636.

Moore JW. 2006. Animal ecosystem engineers in streams. BioScience 56: 237–246.

Palmer MA, Ruhl J. 2015. Aligning restoration science and the law to sustain ecological infrastructure for the future. Frontiers in Ecology and the Environment 13: 512–519.

Parody JM, Cuthbert FJ, Decker EH. 2001. The effect of 50 years of landscape change on species richness and community composition. Global Ecology and Biogeography 10: 305–313.

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010. Global pollinator declines: Trends, impacts and drivers. Trends in Ecology and Evolution 25: 345–353.

Pringle RM, Goheen JR, Palmer TM, Charles GK, DeFranco E, Hohbein R, Ford AT, Tarnita CE. 2014. Low functional redundancy among mammalian browsers in regulating an encroaching shrub (*Solanum campylacanthum*) in African savannah. Proceedings of the Royal Society B 281 (art. 20140390).

Roberge JM. 2014. Using data from online social networks in conservation science: Which species engage people the most on Twitter? Biodiversity and Conservation 23: 715–726.

Rosenfeld JS. 2002. Functional redundancy in ecology and conservation. Oikos 98: 156–162.

Salafsky N, Wollenberg E. 2000. Linking livelihoods and conservation: A conceptual framework and scale for assessing the integration of human needs and biodiversity. World Development 28: 1421–1438.

Schmitz O. 2010. Resolving Ecosystem Complexity. Princeton University Press.

Sensenig RL, Demment MW, Laca EA. 2010. Allometric scaling predicts preferences for burned patches in a guild of East African grazers. Ecology 91: 2898–2907.

Sergio F, Caro T, Brown D, Clucas B, Hunter J, Ketchum J, McHugh K, Hiraldo F. 2008. Top predators as conservation tools: Ecological rationale, assumptions, and efficacy. Annual Review of Ecology Evolution and Systematics 39: 1–19.

Shanley P, Luz L. 2003. The impacts of forest degradation on medicinal plant use and implications for health care in eastern Amazonia. BioScience 53: 573–584.

Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B, Cooper SD, Halpern BS. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5: 785–791.

Smith KF, Behrens MD, Schloegel LM, Marano N, Burgiel S, Daszak P. 2009. Reducing the risks of the wildlife trade. Science 324: 594–595.

Smith R, Veríssimo D, Isaac N, Jones K. 2012. Identifying Cinderella species: Uncovering mammals with conservation flagship appeal. Conservation Letters 5: 205–212.

Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues AS, Fischman DL, Waller RW. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783–1786.

Veblen KE, Porensky LM, Riginos C, Young TP. 2016. Are cattle surrogate wildlife? Savanna plant community composition explained by total herbivory more than herbivore type. Ecological Applications 26: 1610–1623. doi:10.1890/15-1367.1

Wilson EO. 1987. The little things that run the world (the importance and conservation of invertebrates). Conservation Biology 1: 344–346.

Wilson KA, McBride MF, Bode M, Possingham HP. 2006. Prioritizing global conservation efforts. Nature 440: 337–340.

Worm B, et al. 2009. Rebuilding global fisheries. Science 325: 578–585.

Wright JP, Jones CG, Flecker AS. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132: 96–101.

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Conserving the World's Megafauna and Biodiversity: The Fierce Urgency of Now

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In our recent perspective article, we noted that most (approximately 60 percent) terrestrial large carnivore and large herbivore species are now threatened with extinction, and we offered a 13-point declaration designed to promote and guide actions to save these iconic mammalian megafauna (Ripple et al. 2016). Some may worry that a focus on saving megafauna might undermine efforts to conserve biodiversity more broadly. We believe that all dimensions of biodiversity are important and that efforts to conserve megafauna are not in themselves sufficient to halt the dispiriting trends of species and population losses in recent decades. From 1970 to 2012, a recent global analysis showed a 58 percent overall decline in vertebrate population abundance (WWF 2016). Bold and varied approaches are necessary to conserve what remains of Earth's biodiversity, and our declaration in no way disputes the value of specific conservation initiatives targeting other taxa. Indeed, the evidence is clear that without massively scaling up conservation efforts for all species, we will fail to achieve internationally agreed-upon targets for biodiversity (Tittensor et al. 2014).

However, megafauna remain strong candidates—and we believe the strongest candidates—to serve as "umbrellas" for the conservation of many species and ecosystems (Caro 2010). This is because megafauna typically have large habitat requirements relative to those of other species; therefore, conserving megafauna necessitates conserving large tracts of landscapes and the diversity of species and ecosystem processes they contain (Kerley et al. 2003b). As such, efforts to protect the world's rapidly dwindling megafauna populations should be viewed as complementary to, not in conflict with, the conservation of other species across the taxonomic and body-size spectra.

Biodiversity is not evenly distributed on planet Earth, and some countries house far greater concentrations of biodiversity than others. Indeed, most of the world's terrestrial species diversity can be found in the top 17 most biodiverse countries (Mittermeier et al. 1997). These 17 countries support populations of at least two-thirds of all nonfish vertebrate species and three-quarters of all higher plant species (Mittermeier et al. 1997). A surprising number of threatened megafauna species are also found within these biodiversity-rich countries (figure 1), underscoring the fundamental compatibility of targeted efforts to conserve ecosystems containing both megafauna and biodiversity as a whole. Accordingly, significant co-benefits should arise from future conservation efforts in countries that are rich in both threatened megafauna and overall biodiversity in areas where the distribution of megafauna overlaps significantly with the distribution of many other species.

Abundant evidence shows that many megafauna populations are strong interactors whose loss causes direct and indirect effects on other species and ecosystem functions (Beschta and Ripple 2009, Estes et al. 2011, Dirzo et al. 2014, Ripple et al. 2014, 2015). In many instances, megafaunal extinction will cause disproportionate ecological disruption relative to the loss of other smaller animals. This is due not only to the large body size of megafauna but also to the limited functional redundancy both within megafaunal guilds (e.g., Pringle et al. 2014) and between megafauna and other animals. For example, jaguars (*Panthera onca*) are the primary nonhuman predators of adult tapirs (*Tapirus* spp.) in Latin America, only lions (*Panthera leo*) routinely kill African buffalo (*Syncerus caffer*) and giraffe (*Giraffa camelopardalis*) across Africa, and gray wolves (*Canis lupus*) and bears (*Ursus* spp.) alone are responsible for the vast majority of predation on large herbivores in most Holarctic regions. The accumulated (and in our view unequivocal) evidence that megafauna frequently fulfill unique and far-reaching functional roles does not imply that other species should be ignored or that taxon-centric programs should supersede systems-based approaches; it simply underscores the crucial importance of

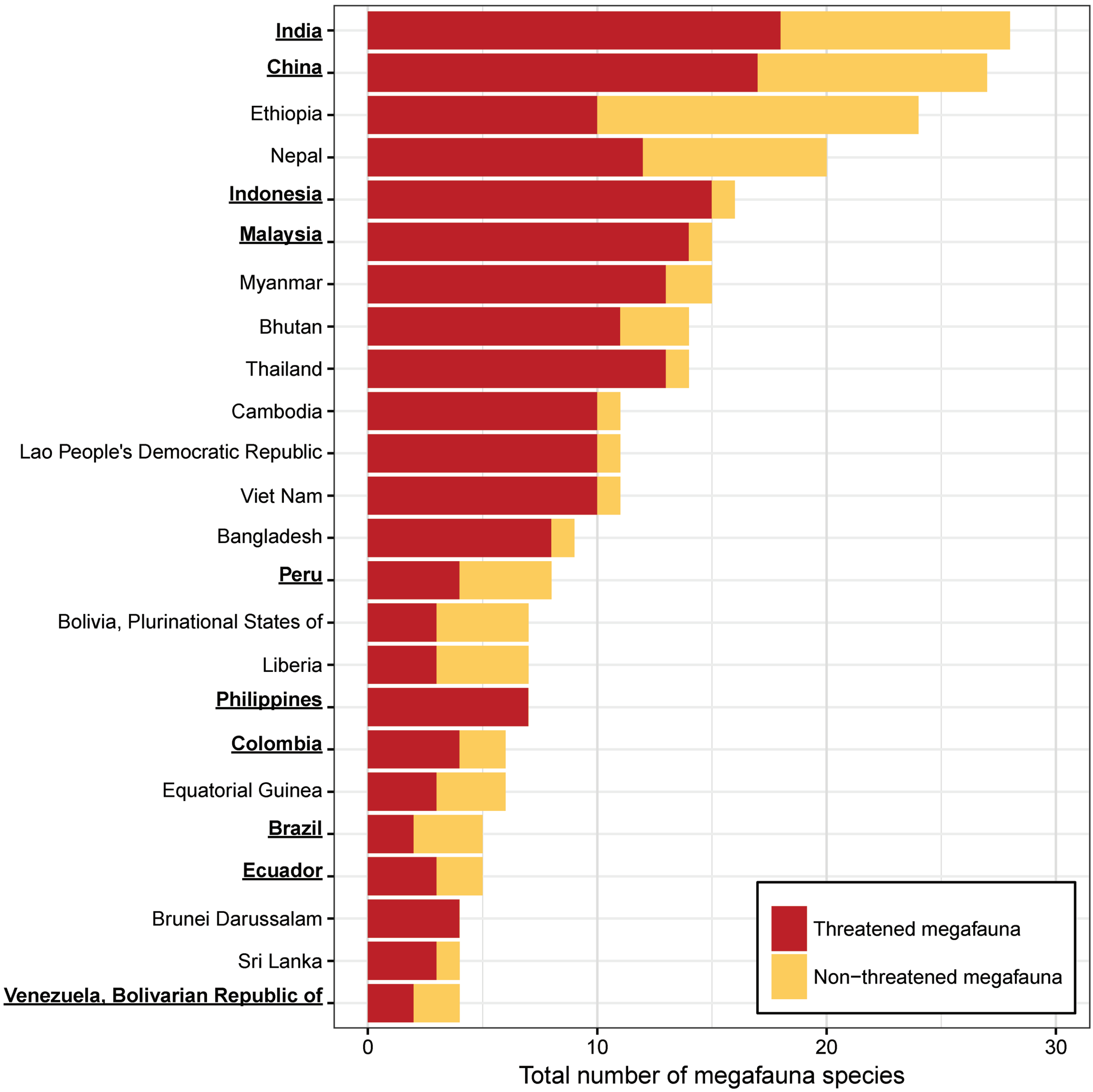

Figure 1. The number of mammalian terrestrial megafauna species found in countries with at least four megafauna species overall and at least 40 percent of their megafauna threatened; the countries underlined with bold labels are biodiversity-rich countries (Mittermeier et al. 1997). Each species was treated as present in a country if it was listed as native to that country on its IUCN Red List species fact sheet page (IUCN 2015). Threatened megafauna are those with IUCN Red List status vulnerable, endangered, *or* critically endangered. *Of the 17 biodiversity-rich countries, more than half (10) appear in this figure. Many of the other countries listed in the figure also have relatively high levels of biodiversity because they are located at low latitudes where productivity and biodiversity are high. The megafauna in this figure are terrestrial carnivores greater than or equal to 15 kilograms in size and herbivores greater than or equal to 100 kilograms in size, as defined in Ripple and colleagues (2014, 2015).*

not allowing relict megafaunal populations to vanish.

Without passing judgment on the appropriateness of conservation triage—a complicated topic beyond the scope of this article—we appreciate that funding for conservation is finite and that great care is needed when considering resource allocation. But it would be a mistake to assume that conservation funding has already peaked and that therefore allocation decisions are a zero-sum game. Our call to develop new funding mechanisms is rooted in the evidence that large animals evoke strong emotional responses in many people, providing powerful routes to develop new conservation funders and leaders (Batt 2009, Clayton and Myers 2009). We are not the first to call for additional conservation resources to achieve conservation gains. Even with increased investment, however, careful prioritization will still be necessary to inform decisions about which areas to protect and which actions to undertake for particular species (e.g., McCarthy et al. 2012). Although trade-offs are inevitable, we welcome all ethical efforts to grow the resource base for biodiversity conservation at large so that such trade-offs may be fewer and less painful. Although funding for conservation is often not easily substitutable among causes or from one conservation target to another, evidence suggests that much of the current public support for conservation might diminish if megafauna species were made less of a focus (Kerley et al. 2003a). One way to increase conservation gains is to focus on megafauna species with special public appeal, using them to create support and funding that could also help less charismatic species (Macdonald et al. 2015).

For these reasons, we believe that megafauna, with their unique socioeconomic and cultural values and their ability to harness public and political support, have the power to lift many conservation boats (Macdonald et al. 2015). For example, in Africa, several countries have set aside vast tracts of land for conservation and have a firm political commitment to preserving those lands. This is due in part to appreciation of the megafauna they contain, as well as to notions of the importance of preserving natural heritage for future generations (e.g. see the Ugandan Constitution; *www.ulii.org/node/23824*). In other cases, political assistance for conservation is mostly the product of popular support. Because of their charisma, megafauna have more potential than most taxa to engender that kind of support. If we cannot muster the political will to save even the widely appreciated megafauna, then our prospects seem grim.

Our declaration was necessary because despite being among the most cherished species by the public, many megafauna populations and species are steadily sliding toward extinction. We have yet to implement mechanisms that will save these species, so our declaration highlights the urgent need to raise additional support and identify alternative approaches—especially those that integrate support to and from local communities and that consider the rights of future generations and broader society. Our rallying call is certainly not "megafauna to the exclusion of all else" but could perhaps better be framed with reference to Dr. Martin Luther King Jr.'s famous lines: "We are now faced with the fact that tomorrow is today. We are confronted with the fierce urgency of now. In this unfolding conundrum of life and history, there *is* such a thing as being too late. This is no time for apathy or complacency. This is a time for vigorous and positive action."

Megafauna need immediate attention, and, yes, other species do as well. As concerned conservation scientists, we invite everyone to join the effort to confront the fierce necessity of "how?" in the fierce urgency of now.

References cited

Batt S. 2009. Human attitudes towards animals in relation to species similarity to humans: A multivariate approach. Bioscience Horizons 2: 180–190.

Beschta RL, Ripple WJ. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142: 2401–2414.

Caro T. 2010. Conservation by Proxy: Indicator, Umbrella, Keystone, Flagship, and Other Surrogate Species. Island Press.

Clayton S, Myers G. 2009. Conservation Psychology. Understanding and Promoting Human Care for Nature. Wiley-Blackwell.

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. 2014. Defaunation in the Anthropocene. Science 345: 401–406.

Estes JA, et al. 2011. Trophic downgrading of planet Earth. Science 333: 301–306.

[IUCN] International Union for Conservation of Nature. 2015. IUCN Red List of Threatened Species. Version 2015.2. IUCN.

Kerley GIH, Geach BGS, Vial C. 2003a. Jumbos or bust: Do tourists' perceptions lead to an under-appreciation of biodiversity? South African Journal of Wildlife Research 33: 13–21.

Kerley GI, Pressey RL, Cowling RM, Boshoff AF, Sims-Castley R. 2003b. Options for the conservation of large and medium-sized mammals in the Cape Floristic Region hotspot, South Africa. Biological Conservation 112: 169–190.

Macdonald EA, Burnham D, Hinks AE, Dickman AJ, Malhi Y, Macdonald DW. 2015. Conservation inequality and the charismatic cat: *Felis felicis*. Global Ecology and Conservation 3: 851–866.

McCarthy DP, et al. 2012. Financial costs of meeting global biodiversity conservation targets: Current spending and unmet needs. Science 338: 946–949.

Mittermeier RA, Gil PR, Mittermeier CG. 1997. Megadiversity: Earth's Biologically Wealthiest Nations. Agrupacion Sierra Madre.

Pringle RM, Goheen JR, Palmer TM, Charles GK, DeFranco E, Hohbein R, Ford AT, Tarnita CE. 2014. Low functional redundancy among mammalian browsers in regulating an encroaching shrub (*Solanum campylacanthum*) in African savannah. Proceedings of the Royal Society B 281 (art. 20140390).

Ripple WJ, et al. 2014. Status and ecological effects of the world's largest carnivores. Science 343 (art. 1241484).

Ripple WJ, et al. 2015. Collapse of the world's largest herbivores. Science Advances 1: e1400103–e1400103.

Ripple WJ, et al. 2016. Saving the world's terrestrial megafauna. BioScience 66: 807–812.

Tittensor DP, et al. 2014. A mid-term analysis of progress toward international biodiversity targets. Science 346: 241–244.

[WWF] World Wide Fund for Nature. 2016. Living Planet Report 2016: Risk and Resilience in a New Era. WWF. (10 November 2016; *http://awsassets.panda.org/downloads/lpr_living_planet_report_2016.pdf*)

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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

JIM AND JAMIE DUTCHER/NATIONAL GEOGRAPHIC CREATIVE

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.

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.)

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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 stream-side 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

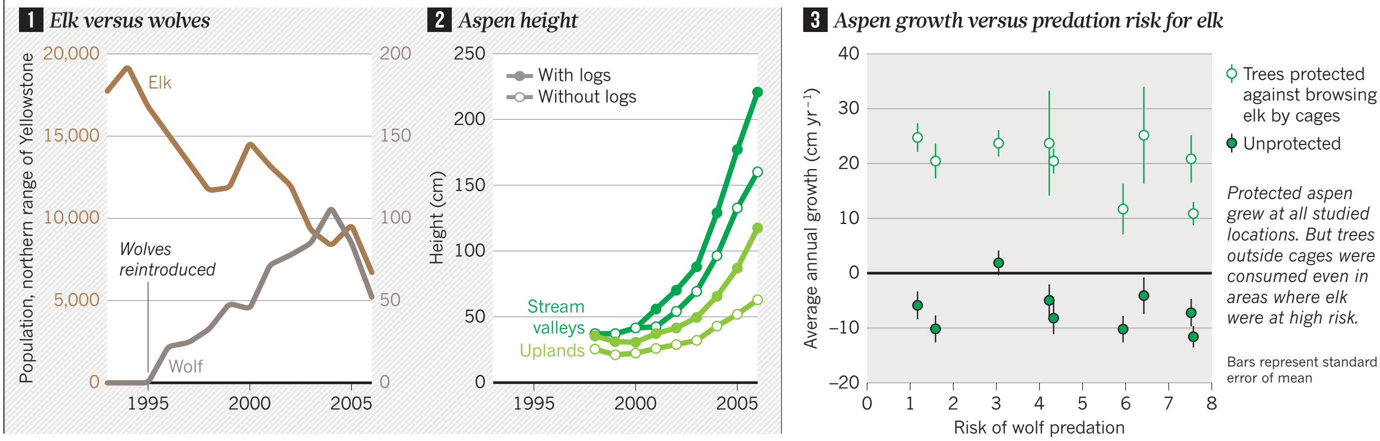
But some ecologists had their doubts. The first major study[7] critical of the wolf effect appeared in 2010, led by Matthew Kauffman of the Wyoming Cooperative Fish and Wildlife Research Unit in Laramie. When researchers drilled boreholes into more than 200 trees in Yellowstone and analysed growth patterns, 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**).



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).

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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.

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

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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

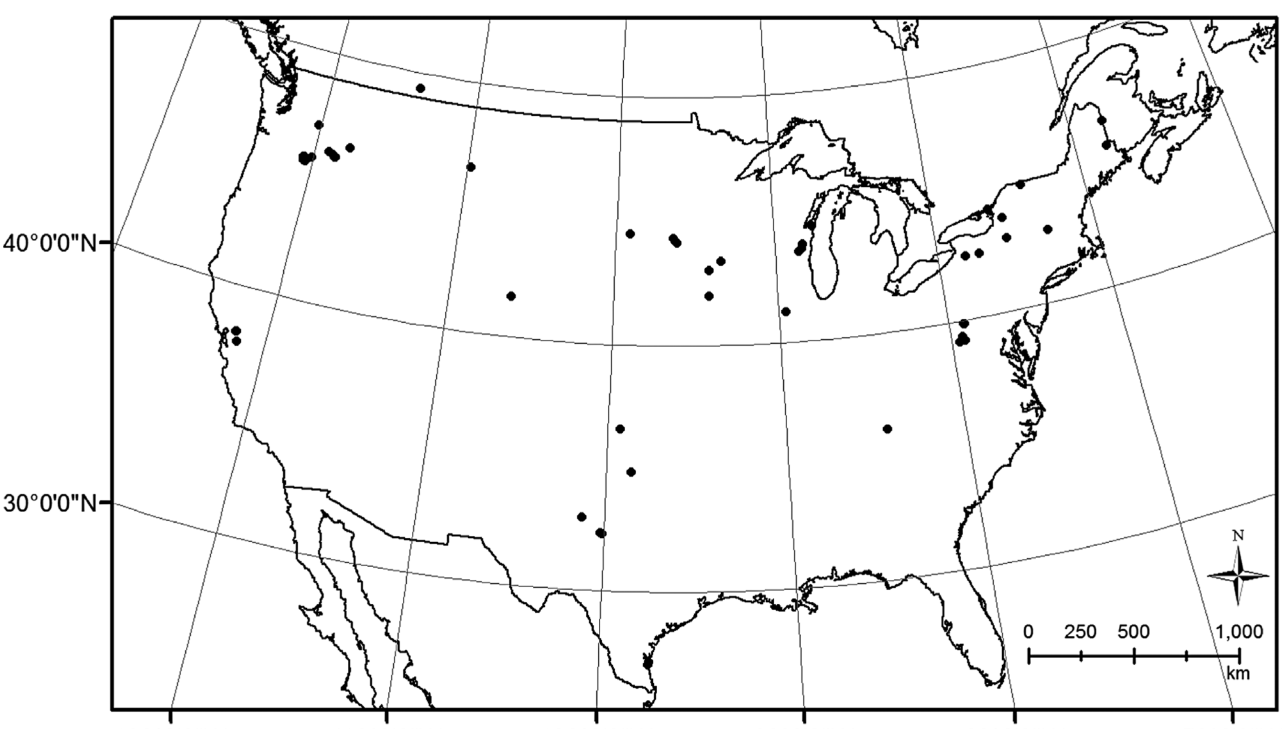

Figure 1. Locations of wind energy facilities used to estimate the relationship between mortality monitoring effort and the number of bird species observed.

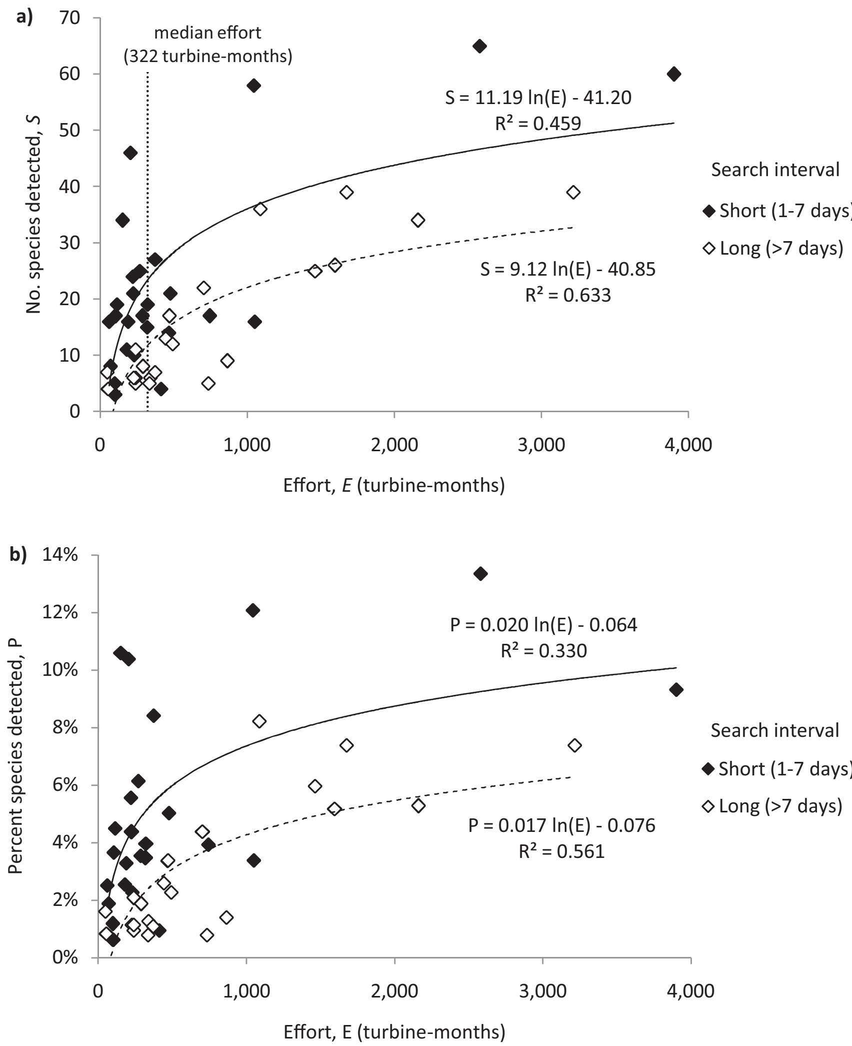

Figure 2. Number of species (a) and (b) percent of birds occurring in the state detected during fatality monitoring at 50 North American wind facilities sampled between 1995 and 2011 based on sampling interval and the sampling effort (number of turbines multiplied by the duration of study in months). 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

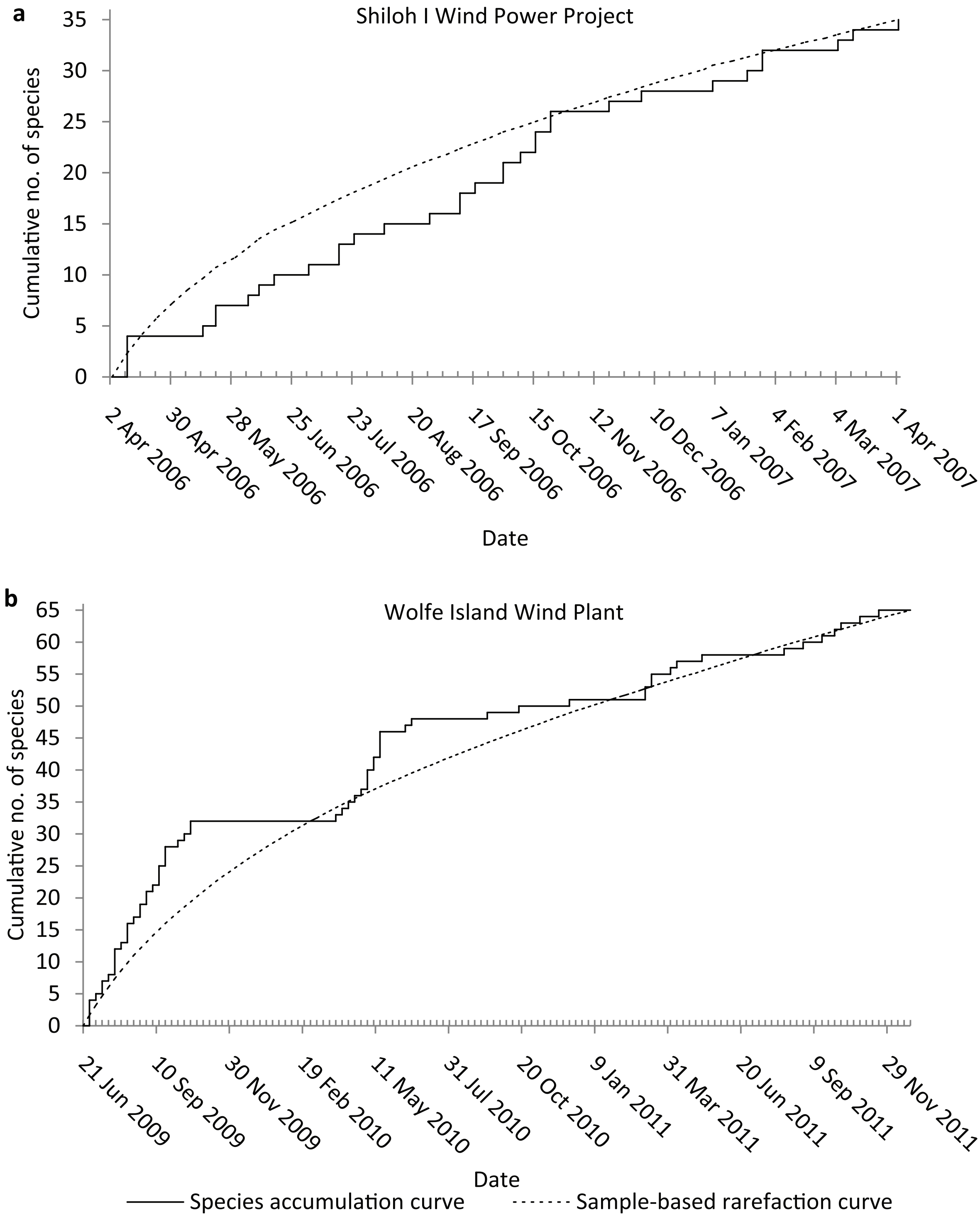

Figure 3. Species accumulation (solid) and sample-based rarefaction (dashed) curves for (a) a 52-week study at 50 turbines at Shiloh I Wind Power Project in Rio Vista, California, and (b) a 131-week study at 86 turbines at Wolfe Island Wind Plant in Frontenac Islands, Ontario.

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

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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.

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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 $\pm$ SE = 35.4 $\pm$ 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 $\geq$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

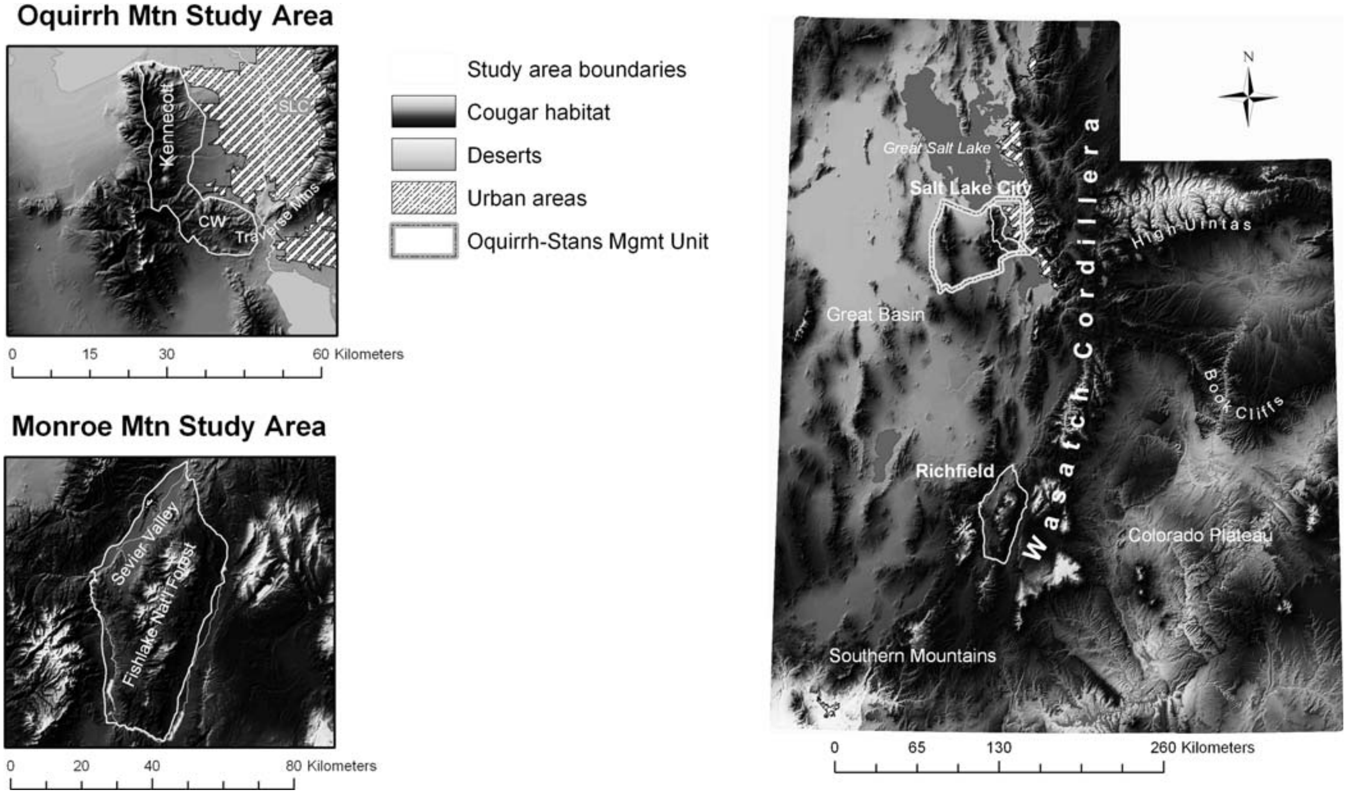

Figure 1. Study-area locations and cougar habitat across Utah, USA, 1996–2004.

(*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 back-calculated 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%

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

(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.

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 $\pm$ 0.3 (2002–2004). Oquirrh density showed minimal variation over the study interval averaging 2.8 $\pm$ 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 $\pm$ 0.2 years (F = 3.7 $\pm$ 0.4; M = 3.1 $\pm$ 0.3). Adult cougars from the Oquirrh population ($n = 33$) averaged 4.6 $\pm$ 0.3 years (F = 5.9 $\pm$ 0.5; M = 3.4 $\pm$ 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

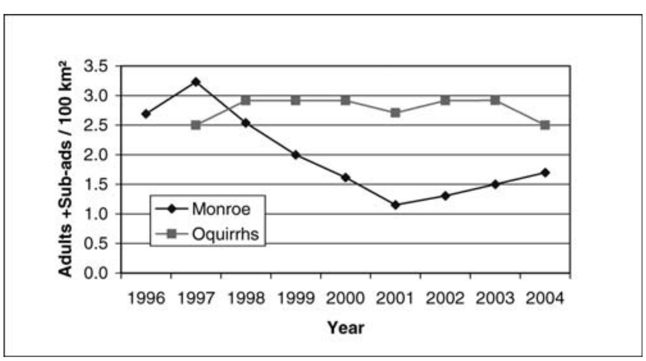

Figure 2. Annual nonjuvenile cougar density as determined from capture, tracking, and harvest, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

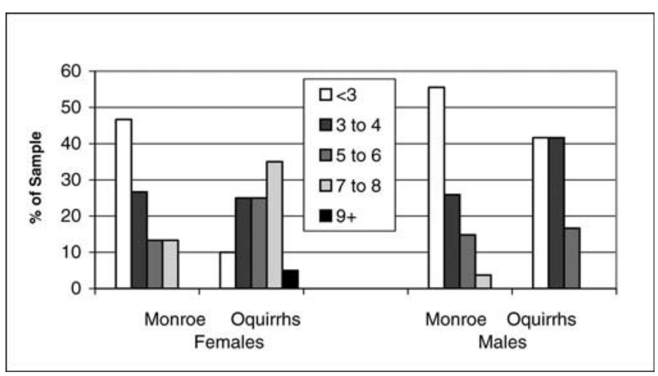

Figure 3. Age distribution of radiocollared cougars by sex, Monroe ($n = 57$) and Oquirrh ($n = 30$) Mountain study sites, Utah, USA, 1996–2004.

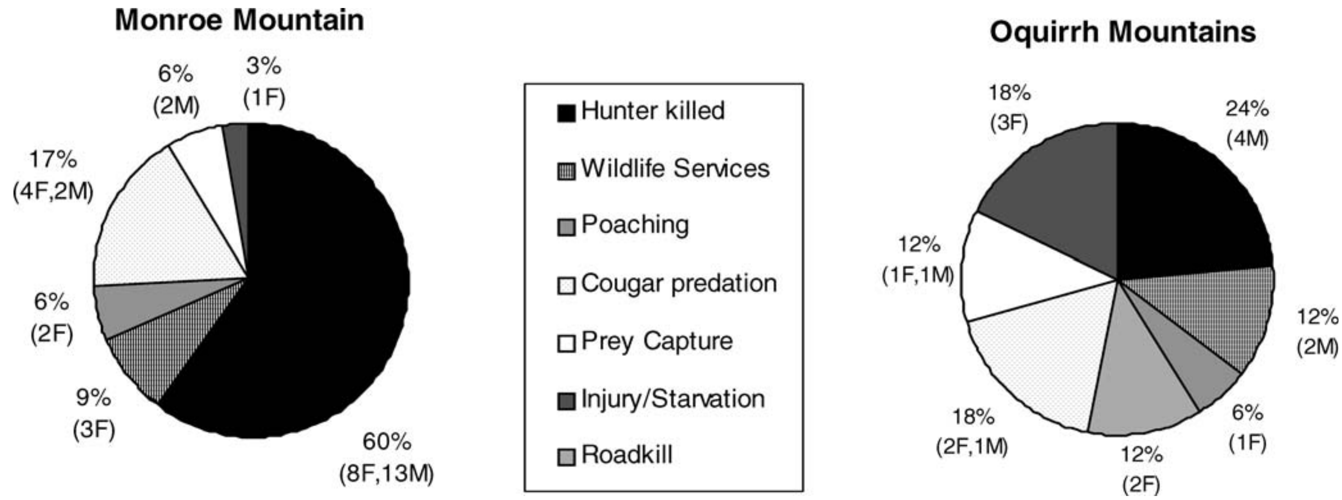

Figure 4. Cause-specific mortality among radiocollared cougars from the Monroe ($n = 35$) and Oquirrh Mountain ($n = 17$), study sites, Utah, USA, 1996–2004.

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

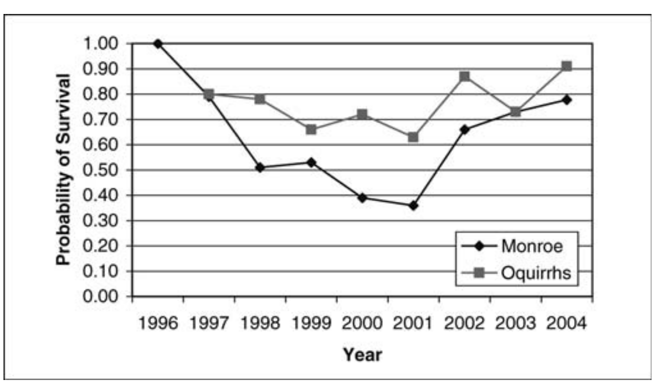

Figure 5. Estimated annual survival rates for radiocollared cougars, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

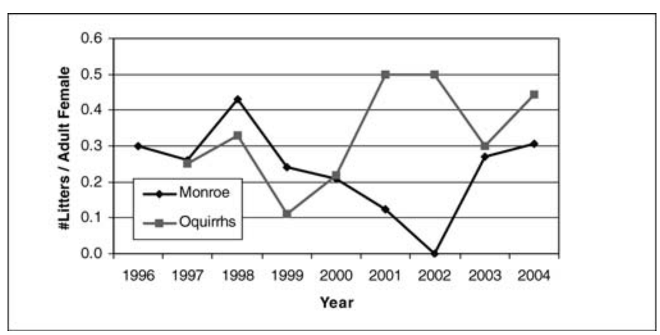

Figure 6. Annual fecundity rates for adult cougars on the Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

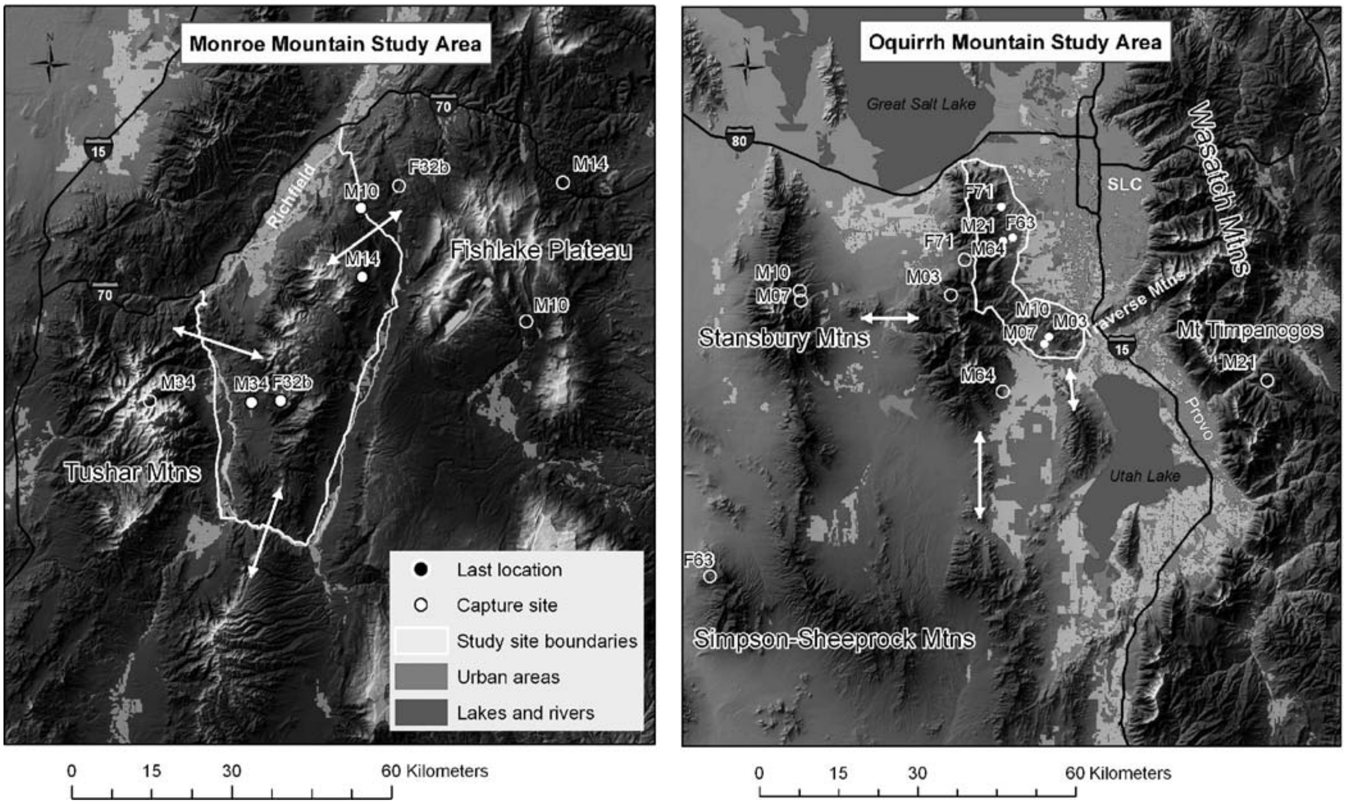

Figure 7. Dispersal patterns and landscape connectivity, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004. Arrows represent points of habitat connectivity.

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 $\geq$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.

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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.

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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.

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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

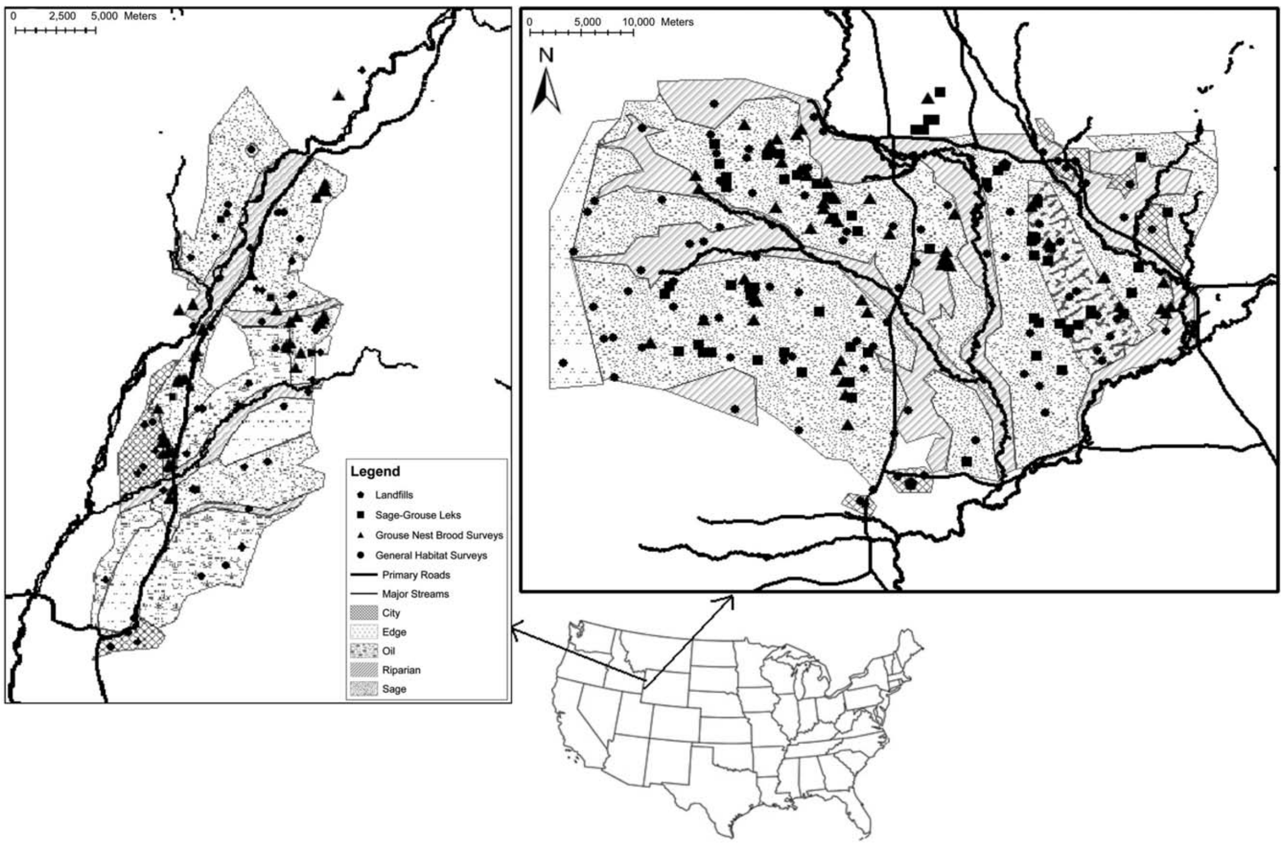

FIGURE 1. Locations of study areas in Wyoming, with magnified views of Pinedale (upper right) and Jackson study area (left) showing locations of raven survey points, sage-grouse leks, main roads, major streams, and land cover (sagebrush, riparian woodland, oil field, edge, city, hayfield). Filled pentagons 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%; $t_{72} = -5.5$, $P < 0.001$).

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

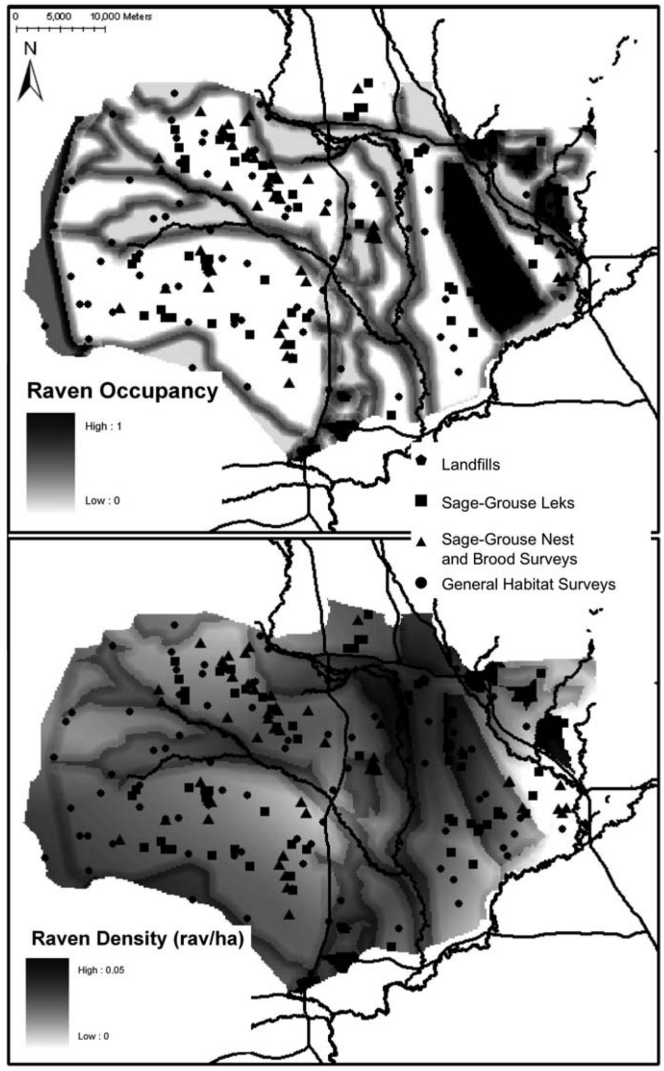

FIGURE 2. Major cities and landmarks, sage-grouse leks, expected raven occurrence (top), and expected raven density (ravens ha^{-1}) (bottom) in the Pinedale study area as predicted by our model. Filled pentagons represent landfills, filled squares represent sage-grouse leks, filled triangles represent 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).

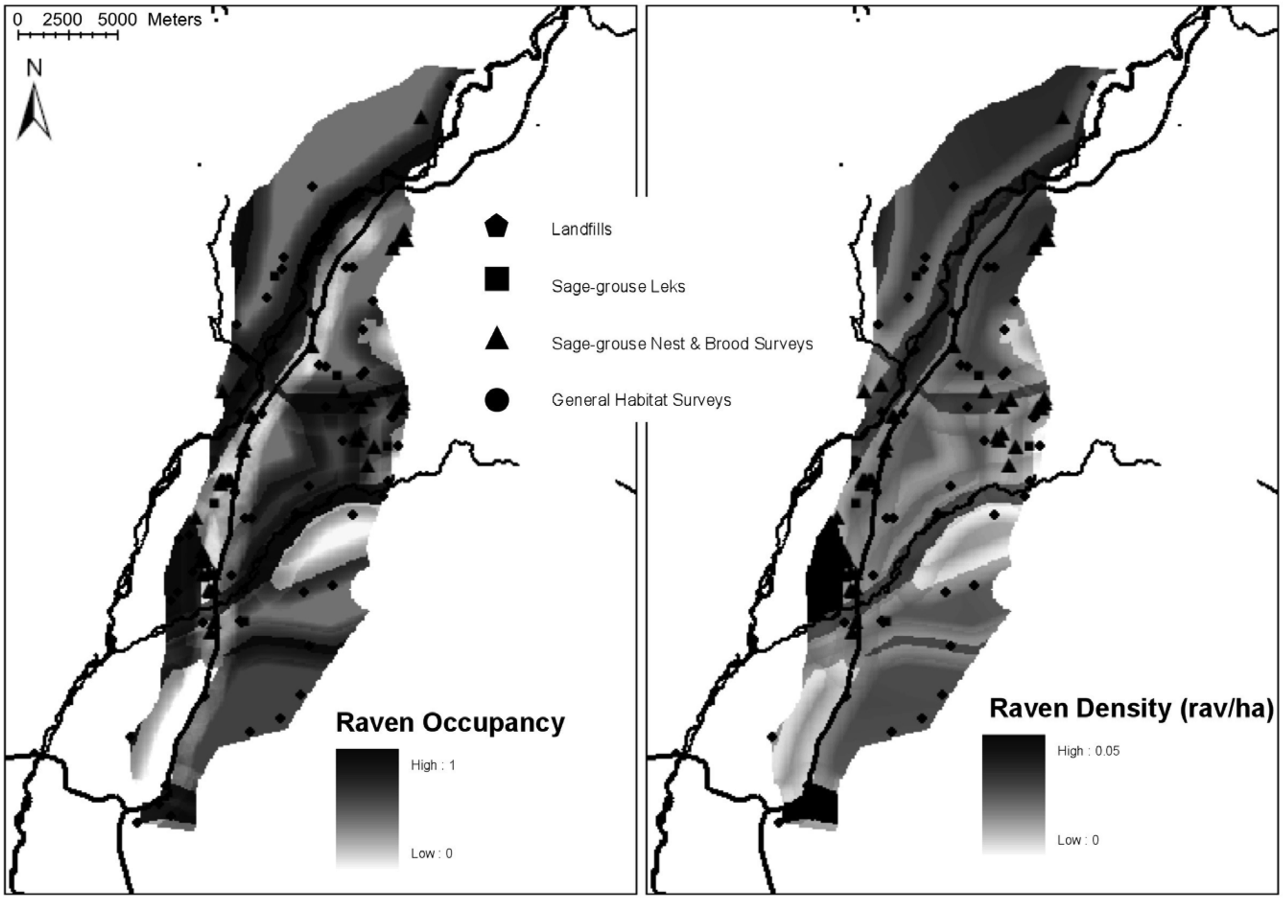

FIGURE 3. Major cities and landmarks, sage-grouse leks, expected raven occurrence (left), and expected raven density (ravens ha^{-1}; right) across the Jackson study area as predicted by our models (unstandardized coefficients in Table 3). Filled pentagons represent landfills, filled squares represent 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 ± 0.002 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 = 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.

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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 pot-holes 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 America, 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)

WHAT WE KNOW:

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University of Georgia

The overwhelming evidence of human-caused climate change documents both current impacts with significant costs and extraordinary future risks to society and natural systems. The scientific community has convened conferences, published reports, spoken out at forums and proclaimed, through statements by virtually every national scientific academy and relevant major scientific organization — including the American Association for the Advancement of Science (AAAS) — that climate change puts the well-being of people of all nations at risk.

Surveys show that many Americans think climate change is still a topic of significant scientific disagreement.[i] Thus, it is important and increasingly urgent for the public to know there is now a high degree of agreement among climate scientists that human-caused climate change is real. Moreover, while the public is becoming aware that climate change is increasing the likelihood of certain local disasters, many people do not yet understand that there is a small, but real chance of abrupt, unpredictable and potentially irreversible changes with highly damaging impacts on people in the United States and around the world.

It is not the purpose of this paper to explain why this disconnect between scientific knowledge and public perception has occurred. Nor are we seeking to provide yet another extensive review of the scientific evidence for climate change. Instead, we present key messages for every American about climate change:

1. Climate scientists agree: climate change is happening here and now. Based on well-established evidence, about 97% of climate scientists have concluded that human-caused climate change is happening. This agreement is documented not just by a single study, but by a converging stream of evidence over the past two decades from surveys of scientists, content analyses of peer-reviewed studies, and public statements issued by virtually every membership organization of experts in this field. Average global temperature has increased by about 1.4° F over the last 100 years. Sea level is rising, and some types of extreme events – such as heat waves and heavy precipitation events – are happening more frequently. Recent scientific findings indicate that climate change is likely responsible for the increase in the intensity of many of these events in recent years.

2. We are at risk of pushing our climate system toward abrupt, unpredictable, and potentially irreversible changes with highly damaging impacts. Earth's climate is on a path to warm beyond the range of what has been experienced over the past millions of years.[ii] The range of uncertainty for the warming along the current emissions path is wide enough to encompass massively disruptive consequences to societies and ecosystems: as global temperatures rise, there is a real risk, however small, that one or more critical parts of the Earth's climate system will experience abrupt, unpredictable and potentially irreversible changes. Disturbingly, scientists do not know how much warming is required to trigger such changes to the climate system.

3. The sooner we act, the lower the risk and cost. And there is much we can do. Waiting to take action will inevitably increase costs, escalate risk, and foreclose options to address the risk. The

CO_2 we produce accumulates in Earth's atmosphere for decades, centuries, and longer. It is not like pollution from smog or wastes in our lakes and rivers, where levels respond quickly to the effects of targeted policies. The effects of CO_2 emissions cannot be reversed from one generation to the next until there is a large- scale, cost-effective way to scrub carbon dioxide from the atmosphere. Moreover, as emissions continue and warming increases, the risk increases.

By making informed choices now, we can reduce risks for future generations and ourselves, and help communities adapt to climate change. People have responded successfully to other major environmental challenges such as acid rain and the ozone hole with benefits greater than costs, and scientists working with economists believe there are ways to manage the risks of climate change while balancing current and future economic prosperity.

As scientists, it is not our role to tell people what they should do or must believe about the rising threat of climate change. But we consider it to be our responsibility as professionals to ensure, to the best of our ability, that people understand what we know: human-caused climate change is happening, we face risks of abrupt, unpredictable and potentially irreversible changes, and responding now will lower the risk and cost of taking action.

I. CLIMATE REALITY

A. Climate scientists agree: Humans are driving climate change

Many Americans believe scientists disagree. Based on well-established evid ence, about 97% of climate scientists have concluded that humans are changing th e climate.

In 2013, only 42% of American adults understood that "most scientists think global warming is happening" and 33% said, "… there is a lot of disagreement among scientists about whether or not global warming is happening." Twenty percent said they "don't know enough to say."[iv]

Even Americans who have come to recognize that climate change is occurring know there are limits to their ability to make this judgment from their own experiences. It might appear as if it's raining more or less often, that it's hotter than usual, or there are more storms than there once were. But is this true climate change, or just natural variation? Does a particularly cold or snowy winter, such as the one the eastern United States experienced in 2013 and 14, or variations in rate of in global surface temperature change, call global warming into question? If the climate is changing, are human activities or natural factors responsible?

Americans look to experts for guidance. If people believe the experts are in doubt about whether global warming is happening, it is no surprise that they will have less confidence in their own beliefs.

Perceived expert disagreement has other consequences for the American people. Research shows that Americans who think the scientific experts disagree about human-caused climate change are less likely to believe that it might have serious consequences. Failure to appreciate the scientific consensus reduces support for a broad societal response to the challenges and risks that climate change presents.[v]

So let us be clear: Based on well-established evidence, about 97% of climate scientists conclude humans are changing the climate.

This widespread agreement is documented not by a single study but by a converging stream of evidence over the past two decades from polls of scientists,[iii,iv] content analyses of peer-reviewed literature[v,vi] and from public statements issued by virtually every expert scientific membership organization on this topic.[vii] The evidence is overwhelming: levels of greenhouse gases in the atmosphere are rising. Temperatures are going up. Springs are arriving earlier. Ice sheets are melting. Sea level is rising. The patterns of rainfall and drought are changing. Heat waves are getting worse as is extreme precipitation. The oceans are acidifying.

The science linking human activities to climate change is analogous to the science linking smoking to lung and cardiovascular diseases. Physicians, cardiovascular scientists, public health experts and others all agree smoking causes cancer. And this consensus among the health community has convinced most Americans that the health risks from smoking are real. A similar consensus now exists among climate scientists, a consensus that maintains climate change is happening, and human activity is the cause. The National Academy of Sciences, for example, says that “the Earth system is warming and that much of this warming is very likely due to human activities.”[viii]

B. Climate change is happening now. And it's going to get worse.

Climate change is already happening. More heat waves, greater sea level rise, and other changes with consequences for human health, natural ecosystems, and agriculture are already occurring in the United States and worldwide. These problems are very likely to become worse over the next 10-20 years and beyond.

No matter where they live, Americans are experiencing the effects of climate change. Of course, extreme weather events of varied intensity have always occurred. Family photo albums, community lore and history books recount the big storms, droughts and floods that communities have borne. Against this backdrop of natural variation, however, something different is happening. Greenhouse gases from manmade sources such as smokestacks and tailpipes have altered our climate system. Greenhouse gases have supercharged the climate just as steroids supercharged hitting in Major League Baseball. Over the course of a baseball season in the steroid era, we witnessed more – and longer – homers, even though we cannot attribute any specific homer to steroids. Similarly, even though we cannot attribute any particular weather event to climate change, some types of extreme events such as heat waves are now more frequent.

Extreme weather is not just an abstract concept. It is a reality that affects people across the country. In 2013, two out of three Americans said weather in the U.S. has been worse over the past several years, up 12 percentage points since spring 2012. Many (51%) say weather in their local area has been worse over the past several years. Not surprisingly, then, the gap between what we know as scientists (that global warming impacts are here and now) and what Americans perceive is narrowing: about six in 10 Americans already say, "global warming is affecting weather in the U.S."[ix]

The core science of global warming

After remaining relatively stable at around 280 parts-per-million (ppm) for millennia, carbon dioxide (CO_2) began to rise in the 19th century as people burned fossil fuels in ever-increasing amounts. This upward trend continues today with concentrations breaking the 400 ppm mark just last year. The rate of increase during the last 100 to 150 years has been much more rapid than in other periods of the Earth's history. The warming effect of CO_2 and other heat-trapping gases is well-established and can be demonstrated with simple science experiments and satellite observations. Without the natural "greenhouse" effect from gases in our atmosphere, Earth would be a frozen planet.

In addition to greenhouse gases, there are many other forces that can cause changes in the Earth's climate – including the creation and destruction of the Earth's crust, the planet's wobbly path around (and tilt toward) the sun, variation in the sun's energy output, volcanic eruptions, shifting ocean currents, and natural changes in CO_2 and other greenhouse gases. These factors have driven the planet through eras of blazing heat and mile-thick ice sheets. But decades of human-generated greenhouse gases are now the major force driving the direction of climate change, currently overwhelming the effects of these other factors. Many studies show that the combined effects of natural drivers of climate cannot explain the temperature increase observed over the past half century.

Since the late 19th century, Earth's global average temperature has risen by about 1.4° F. Although this may appear to be a small change, the Earth's temperature has remained nearly as stable as that of the human body over the course of Western civilization. Just as a 1.4° F fever would be seen as significant in a child's body, a similar change in our Earth's temperature is also a concern for human society.

The difference was about 9° F between the last Ice Age, when half of North America was covered in a mile-thick ice sheet, and today. However, whereas that warming occurred over thousands of years, today's atmosphere has already warmed by 1.4° F in just over 100 years. The projected rate of temperature change for this century is greater than that of any extended global warming period over the past 65 million years. The Intergovernmental Panel on Climate Change states that continuing on a path of rapid increase in atmospheric CO_2 could cause another 4 to 8° F warming before the year 2100.[x]

Here's a brief summary of some the impacts of climate change that are already occurring and will increase over the coming years:

Sea Ice

Arctic sea ice has been shrinking dramatically, and the rate of loss is accelerating.[xi] In September 2012, Arctic summer sea ice fell to a new record low at half the historical average - a loss in area nearly twice the size of Alaska.[xii]

Ice Sheets and Glaciers

The melting of the Greenland and Antarctica ice sheets has also accelerated notably.[xiii] Glaciers continue to melt rapidly, contributing to sea-level rise and also affecting water supplies for as many as a billion people around the world.[xiv]

Ocean Acidification

The oceans are absorbing much of the CO_2 that smokestacks and tailpipes emit into the atmosphere. As a result, the oceans are rapidly acidifying, with early impacts on shelled organisms such as oysters already documented. The current acidification rate is likely the fastest in 300 million years.[xv]

Ecological Impacts

As the world has gotten hotter, many of the world's plants and animals, on land and in the oceans, have begun moving toward the poles. Where possible, some terrestrial species are moving up mountainsides, and marine species are moving to deeper depths and higher latitudes. These changes are happening on every continent and in every ocean[xvi,xvii,xviii]. In some places seasonal behaviors are taking place two or three weeks earlier than they did just a few decades ago.[xix] The organisms that cannot adapt to the new climate conditions — because they cannot move fast enough or run out of room — will be worse off.

Extinctions are likely to increase, as climate change combines with other human-related environmental pressures. Moreover, the impacts of climate change on ecosystem processes such as decomposition, plant production and nutrient cycling – processes that determine how much fossil fuel-derived CO_2 the land and ocean will continue to sequester in coming decades – remain largely unknown.

Sea Level Rise

Sea level rise has also accelerated, making storm surges higher and pushing salt water into the aquifers that coastal communities depend on for fresh water, and increasing the extent of coastal flooding. Over the last two decades, sea levels have risen almost twice as fast as the average during the 20th century.[xx] Salt-water intrusion can be witnessed in southern Florida, where sea level rise is contributing to salt water infiltration of coastal wells.[xxi]

Floods, Heat Waves and Drought

Global warming has changed the pattern of precipitation worldwide.[xxii] Flooding in the northern half of the eastern U.S., Great Plains and over much of the Midwest has been increasing, especially over the last several decades. These regional flooding trends in the northeast and upper Midwest are linked to increases in extreme precipitation and are consistent with the global trends driven by climate change.[xxiii] At the same time, areas such as the U.S. Southwest are witnessing more droughts, and these too are consistent with global climate change patterns projected by climate models as a consequence of rising CO_2 levels.[xxiv]

Since 1950, heat waves worldwide have become longer and more frequent.[xxv] One study indicates that the global area hit by extremely hot summertime temperatures has increased 50-fold,[xxvi] and the fingerprint of global warming has been firmly identified in these trends.[xxvii] In the U.S., new record high temperatures now regularly outnumber new record lows by a ratio of 2:1.[xxviii]

Wildfires

Climate change has amplified the threat of wildfires in many places. In the western U.S., both the area burned by wildfires as well as the length of the fire season have increased substantially in recent decades. Earlier spring snowmelt and higher spring and summer temperatures contribute to this change.[xxix] Climate change has increased the threat of "mega-fires" – large fires that burn proportionately greater areas.[xxx] Warming has also led to wildfires present in some regions where they have been absent in recent history.[xxxi]

Effects on Health and Well-being

Climate disruption is already affecting human health and well-being in many ways, and health threats are expected to intensify.[xxxii] Some of the well-understood impacts include the direct effects of heat and the effects of other weather conditions such as droughts, floods, and severe storms. Heat waves cause deaths and illness, with urban dwellers, the elderly, the poor, and certain other especially vulnerable groups.[xxxiii] While heat-related deaths and illnesses have diminished in recent decades, thanks to better forecasting, early warning systems, and/or increased air conditioning, factors such as the aging of the population are expected to increase vulnerability.[xxxiv] Storms and floods can injure and kill victims in the short term while lingering consequences may range from mold growth in flooded buildings (aggravating asthma) to contaminated drinking water supplies to post-traumatic stress and other mental health disorders.[xxxv,xxxvi] Some air pollutants increase with climate change, with the potential to aggravate heart and respiratory diseases. Some plant products such as ragweed pollen reach higher concentrations for longer stretches each year, affecting people with allergies. [xxxvii,xxxviii, xxxix,xl]

Scientists have extensively studied the impact of climate change on the risk of infectious diseases.[xli] Climate change affects the life cycle and distribution of disease-carrying "vectors"—

mosquitoes, ticks, and rodents, which transmit such diseases as West Nile virus, equine encephalitis, Lyme disease, Rocky Mountain Spotted Fever and Hantavirus.[xlii] There is uncertainty about how climate change will affect infectious disease risk, since many factors other than climate affect the spread of disease. The role of climate change on the ranges of vector-borne diseases in the U.S., such as Lyme disease, West Nile virus and dengue is an active area of research.[xliii]

Climate Change and National Security

Recent reports from U.S. Department of Defense (DOD) and National Academy of Science studies have called attention to the implications of current and probable future climate change for U.S. national security.[xliv] They identify obvious coastal concerns relating to sea level rise, and others linked to storms, freshwater availability, and agricultural productivity around the globe. For example: "Climate change could have significant geopolitical impacts around the world, contributing to poverty, environmental degradation, and the further weakening of fragile governments. Climate change will contribute to food and water scarcity, will increase the spread of disease, and may spur or exacerbate mass migration."[xlv] In the context of other global dynamics that give rise to political instability, and societal tensions, changes in climate are considered as potential threat multipliers or instability accelerants according to the CNA Military Advisory Board — a panel of our nation's highest-ranking retired military leaders.[xlvi] Further, national security assets are often global first respondents to humanitarian needs associated with natural disasters including typhoons, hurricanes, and flooding.

Climate change can influence resource competition and place new burdens on economies, societies, and governance institutions. The reports call attention to the fact that these burdens can trigger violence. There is a growing recognition that the displacement of large numbers of people due to water scarcity and agricultural failure, as in the recent history of Syria, can exacerbate tensions that can lead to civil unrest. Senior officers and officials in the U.S. DOD are now regularly speaking publically about how an unabated rise in greenhouse gas emissions could add additional burdens to the infrastructure and mission capacity of our military forces.[xlvii]

II. CLIMATE RISKS

*Given the high stakes, it is valuable to understand not just what **is most likely to** happen, but what **might possibly** happen to our climate. There is a possibility that temperatures will rise much higher and impacts will be much worse than expected. Moreover, as global temperature rises, the risk increases that one or more important parts of the Earth's climate system will experience changes that may be ab* *rupt, unpredictable, and potentially irreversible, causing large damages and high c osts.*[xlviii]

We manage risk every day, often without thinking about it. We buckle our seat belts, latch our kids into car seats and buy insurance for a host of unlikely, but serious possibilities such as losing our homes or belongings to theft, fire or flood. We don't think these things will happen, but we cannot be sure they won't. Uncertainty means risk. Much of our day-to-day risk management is to lessen the danger directly. For example, we purchase cars with the latest safety devices and use these. But another form of risk management is to spread the risk, as with insurance. This helps with recovery if the unthinkable happens.

When we take the long view on climate change, we face these same uncertainties and risks. Climate projections for the year 2100 (when many children born this year will still be living) give a range of plausible temperatures. We are uncertain whether we will experience the high or low end of the range, but the risks of bad outcomes increase greatly at the high end of warming scenarios. By analogy, we are acting like people who take risks with their health (e.g., with behaviors like smoking, poor food choices) but still hoping to live long lives free of serious illness.

To make decisions about managing a risk, we consider the likelihood that a particular event will happen, the consequences if it did, and the cost of effective actions to prevent it. These are the same steps that go into making decisions about climate change. The process starts with an understanding of the risks. What is the likelihood that extreme climate changes will occur, and if they do, what consequences will we face? How much will it cost to prevent the risk?

A. High-risk scenarios: the high-side projections

Where there is a range of uncertainty, the high-side projections represent tail risk, a common concept in the world of finance. As most people understand, no investment is a sure thing. There is a range of possibilities about how that investment will fare. You could lose all you invested or make many times what you paid, but the most likely result is closer to the middle of these extremes. Although the chance of a very bad outcome — or tail risk — is small, it cannot be ignored. That is why advisors often recommend not investing any more than you can afford to lose.

With our future health and well-being at stake, it is common sense to consider the tail risks of climate change as a part of future plans. Consider the example of a seaside community in Florida. There are three futures to consider. Even under the most optimistic scenario (very aggressive greenhouse gas reductions and minimal melting), sea level is projected to rise about one foot this century.[xlix] The middle-of-the-road projection for the current pathway is about two feet. This is a fairly likely possibility. The Intergovernmental Panel on Climate Change estimates the probability of a sea level rise of 2 to 3 feet to be more than about 60%.[l] But the tail risk projection as forecast by the U.S. National Climate Assessment sees the community contending with a sea level rise of close to seven feet.[li]

Below are some of the high-side projections and tail risks we incur by following the current path for CO_2 and other greenhouse gas emissions. Most of these projections derive from computer simulations of Earth and its climate system. These models apply the best understanding science has to offer about how our climate works and how it will change in the future. There are many such models and all of them have been validated, to varying degrees, by their ability to replicate past climate changes.

Global Temperature

According to the IPCC, given the current pathway for carbon emissions the high-end of the "likely" range for the expected increase in global temperature is about 8° F by the end of the century.[lii] This is similar to the roughly 9° F warming that ended the last ice age. It is important to remember that temperature change due to CO_2 emissions is essentially irreversible for several hundred years since this CO_2 is removed from the atmosphere only very slowly by natural processes.[liii]

Floods, Heat Waves, and Drought

Globally, if human society follows the high-end scenario, extreme heat events that currently occur only once every 20 years are projected to occur annually.[liv] Global warming will also leads to shifting precipitation patterns and concentration of precipitation into heavier downpours — critical risk factors for flooding and drought.

Sea Level

Sea level rise projections over the next century vary considerably, with the high-end scenarios yielding a rise of up to 6 or 7 feet by 2100. [lv,lvi] About 7 to 8 million people in the U.S. live within 6 feet of the local high tide line, and storm surge can extend flooding far beyond the high tide line, as witnessed in Superstorm Sandy.[lvii] Coastal flooding events that currently occur once every 100 years will occur much more frequently, possibly as often as yearly for many locations, rendering many cities and communities uninhabitable as is.[lviii]

Current greenhouse gas emissions would have considerable impact on sea level rise beyond the year 2100. In addition to driving sea level rise in the 21st century, current emissions might lead to dramatically higher sea level rise in the distant future, possibly beyond 16 feet, which is higher than the elevation of many major cities around the world. There is a slight risk that such large rise could occur faster than expected (see below).[lix]

B. Abrupt climate change

Most projections of climate change presume that future changes — greenhouse gas emissions, temperature increases and effects such as sea level rise — will happen incrementally. A given amount of emission will lead to a given amount of temperature increase that will lead to a given amount of smooth incremental sea level rise. However, the geological record for the climate reflects instances where a relatively small change in one element of climate led to abrupt changes in the system as a whole. In other words, pushing global temperatures past certain thresholds could trigger abrupt, unpredictable and potentially irreversible changes that have massively disruptive and large-scale impacts. At that point, even if we do not add any additional CO_2 to the atmosphere, potentially unstoppable processes are set in motion. We can think of this as sudden climate brake and steering failure where the problem and its consequences are no longer something we can control. In climate terms, abrupt change means change occurring over periods as short as decades or even years.[lx]

The risk of abrupt climate change is particularly challenging because, while plausible, we have few historical measurements to guide our judgment of likelihood. The financial meltdown of 2008 was a good example of this kind of risk. We had no history of intertwined real estate and financial markets to draw on, and few experts recognized the risk indicators that led to enormous and rapid economic consequences. It is no surprise that we use a metaphor like bursting bubbles for such highly damaging financial events. We do not recognize we are in one; things seem stable, until suddenly they are not.

If human emissions cause temperatures to increase toward the high end of our projections, we increase the risk that we will push parts of our climate system past certain thresholds that lead to abrupt, unpredictable and potentially irreversible changes to our planet and impacts for Americans and people worldwide.

Some of the planetary climate-related systems — both physical and biological —that could trigger such abrupt changes for the planet, if pushed past their limits, include: large-scale ice sheet collapse, collapse of part of the Gulf Stream, dieback of the Amazon rainforest, and coral reef die-off. Disturbingly, there is low confidence in the estimates of the temperature thresholds that would trigger such changes. While some scenarios – such as the disruption of the Gulf Stream/Atlantic Meridional Overturning Circulation (AMOC) and rapid methane release from the sea floor – based on the latest research are considered very unlikely, this does not mean their likelihood has gone to zero.[lxi] Given the complexity of these systems and uncertainties in how they will respond to high-end warming, there may be surprises that we are not yet aware of. As per the National Academy of Sciences Report on Abrupt Impacts of Climate Change: "…'dragons' in the climate system still may exist."[lxii]

Some potential climate change scenarios include:

Ecosystem Collapse

Climate change threatens the collapse of some ecosystems and amplifies extinction pressures on species, which have already elevated extinction rates well above natural background rates.[lxiii,lxiv,lxv] The rate of climate change now may be as fast as any extended warming period over the past 65 million years, and it is projected to accelerate in the coming decades.[lxvi] When rapid climate change is added to other sources of extinction pressure such as ocean acidification, land use, invasive species, and/or exploitation, the resulting rates of extinction are likely to place our era among a handful of severe biodiversity crises in the Earth's geological record.

Arctic Sea Ice Collapse

Warmer Arctic temperatures have caused Arctic summer sea ice to shrink rapidly over the past decade, with potentially large consequences including shifts in climate and weather around the northern hemisphere. Projections suggest that late summer sea ice may disappear entirely in the coming decades.[lxvii] The loss of Arctic sea ice has serious consequences for the Earth's climate system. Arctic sea ice covers an important portion of the planet's surface and reflects sunlight back into space that would otherwise warm the ocean. The loss of Arctic sea ice creates a feedback loop, as lost ice leads to additional ocean warming. The ice loss has major effects on the Arctic, and may have effects on weather patterns extending into the lower latitudes.[lxviiilxix]

Large-Scale Ice Sheet Collapse

Large-scale melting of both the Greenland and Antarctic Ice Sheets include large-scale losses of ice, potentially leading to tens of feet of sea level rise. While most of these losses are projected as being unlikely to occur before 2100, we may pass the point where these losses will be set in motion in the coming decades, with at least a slight chance that we have already done so.[lxx]

In Antarctica, marine ice/ice sheet instability threatens abrupt and large losses from both the West Antarctic Ice Sheet (WAIS) and portions of the East Antarctic Ice Sheet. Any significant ice loss likely would be irreversible for thousands of years. Simulations of warming and ice loss during earlier warm periods of the last 5 million years indicate these areas can contribute 23 feet of sea level rise.[lxxi]

Some studies indicate that abrupt and irreversible ice loss from WAIS is possible, yet uncertainty regarding the threshold is such that it is not possible to say what temperature rise is necessary to trigger collapse.[lxxii,lxxiii] An abrupt change in the WAIS this century is deemed plausible, with an unknown but probably low probability.[lxxiv] Recently an acceleration of ice loss from the WAIS has been observed, and it is not possible to dismiss or confirm that these changes are associated with destabilization of the WAIS.[lxxv]

Destabilizing of Sea Floor Methane

Frozen methane in the shallow shelves of the Arctic Ocean represents an unlikely but potentially strong feedback loop in a warming climate. Methane is a short-lived but potent greenhouse gas. While the release of these deposits due to global warming is likely to be slow and mitigated by dissolution into the sea, these deposits are large and vulnerable to warming expected on the higher emission pathway.[lxxvi] The release of Arctic methane hydrates to the atmosphere would further increase, and perhaps substantially, the rate of global warming.[lxxvii]

Permafrost Melt

The release of CO_2 and methane from thawing Arctic permafrost represents another critical feedback loop triggered by global warming.

The amount of carbon stored in the permafrost is the largest reservoir of readily accessible organic carbon on land.[lxxviii] However, the positive feedback warming due to the loss of carbon from frozen soils is generally missing from the major climate change models.[lxxix] Not surprisingly, methane and carbon dioxide emissions from thawing permafrost are thus regarded as a key uncertainty in climate change projections.

Disturbingly, there is low confidence in the estimates of expected emissions from thawing permafrost.[lxxx] While an abrupt release on the timescale of a few decades is judged unlikely, this conclusion is based on immature science and sparse monitoring capabilities.[lxxxi] The high end of the best estimate range for the total carbon released from thawed permafrost by 2100 is 250 GtC on the higher pathway. Other individual estimates are far higher.[lxxxii]

III. CLIMATE RESPONSE

A. The sooner we act, the lower the risk and cost.

The longer we wait to respond, the more the risks of climate change will increase. Conversely, the sooner we take action, the more options we will have to reduce risk and limit the human and economic cost of climate change.

What steps society takes to meet the challenge of climate change — the questions of when, how and to what extent we respond — is a matter on which all Americans must decide. We urge that these decisions be guided by two inescapable facts: first, the effects of <u>any</u> additional CO_2 emissions will last for centuries; second, there is a risk of abrupt, unpredictable and potentially irreversible changes in the Earth's climate system with massively disruptive impacts.

Emissions of greenhouse gases today commit the planet to unavoidable warming and other impacts in the future. As we continue to increase greenhouse gas emissions, we accelerate and compound the effects and risks of climate change into the future. Conversely, the sooner we make a concerted effort to curtail the burning of fossil fuels as our primary energy source and releasing the CO2 to the air, the lower our risk and cost will be.

B. There is much we can do.

We’ve successfully faced environmental challenges before. There’s much we can do to respond to the challenge and risks of climate change, particularly by tapping America’s strength in innovation.

The United States is one of the most resourceful and innovative societies in the world. We are a nation of problem solvers. When scientists identified the grave environmental threats posed by the acid rain and the ozone hole, they worked together with other stakeholders — consumers, industry and government — to develop solutions that would successfully reduce the threat while minimizing short- and long-term economic impacts. As we hope this paper has made clear, however, successfully responding to climate change will test our resolve and ingenuity in ways unlike any other environmental challenge we have faced.

Many of our major cities — New York, Seattle, Boston and Chicago are just a few — have assessed the scientific evidence, and decided to reduce greenhouse gas emissions and prepare for the impacts of climate change.

We believe that our responsibility as scientists is to ensure, to the best of our ability, that people fully understand the climate realities and risks we face. Prior experience shows that we and future generations will be better off when science effectively informs decision-making and action. Armed with scientific understanding about the gravity of certain environmental problems, our nation has successfully used innovative approaches to address these challenges.

In summary, responding effectively to the challenge of climate change requires a full understanding that there is now a high degree of agreement among climate scientists about the fact that climate change is happening now, because of human activities, and that the risks –including the possibility for abrupt and disruptive changes — will increase the longer greenhouse gas emissions continue.

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[i] Leiserowitz et al. (2013). “Climate change in the American mind: Americans’ global warming beliefs. Yale Project on Climate Change Communication and the George Mason University Center for Climate Change Communication. http://environment.yale.edu/climate-communication/files/Climate-Beliefs-April-2013.pdf

[ii] National Research Council (2013). *Abrupt Impacts of Climate Change: Anticipating Surprises,* Washington, DC: The National Academies Press.

[iii] Doran, P. and M. Zimmerman (2009). Examining the scientific consensus on climate change. *Eos, Transactions, American Geophysical Union, 90* (3), 22-23. http://onlinelibrary.wiley.com/doi/10.1029/2009EO030002/abstract

[iv] Cook et al. (2013). Quantifying the consensus on anthropogenic global warming in the scientific literature. *Environmental Research Letters,* 8 024024. doi:10.1088/1748-9326/8/2/024024

[v] Oreskes, N. (2004). The scientific consensus on climate change. *Science, 306.* http://cmbc.ucsd.edu/Research/Climate_Change/Oreskes%202004%20Climate%20change.pdf

[vi] Cook et al. (2013).

[vii] National Aeronautics and Space Administration. Consensus. http://climate.nasa.gov/scientific-consensus

[viii] National Research Council. (2010). *Advancing the Science of Climate Change*. Washington, DC: The National Academies Press.

[ix] Leiserowitz et al. (2013) Extreme weather and climate change in the American mind, April 2013. Yale Project on Climate Change Communication and the George Mason University Center for Climate Change Communication. http://www.climatechangecommunication.org/report/climate-change-american-mind-series-spring-2013

[x] IPCC (2013). Summary for Policymakers. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press. Table SPM.2, Page 25.

[xi] IPCC (2013). AR5 WGI SPM.

[xii] National Snow and Ice Data Center, (2012). Arctic sea ice extent settles at record seasonal minimum. *Arctic Sea Ice News and Analysis, September 19, 2012*. http://nsidc.org/arcticseaicenews/2012/09/arctic-sea-ice-extent-settles-at-record-seasonal-minimum/

[xiii] IPCC (2013). AR5 WGI SPM

[xiv] IPCC (2013). AR5 WGI SPM

[xv] Hönisch et al. (2012). The geological record of ocean acidification. *Science*, *335* (6072), 1058-63. doi: 10.1126/science.1208277

[xvi] Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics, 37,* 637669.

[xvii] Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007). Shifting plant phenology in response to global change. *Trends in Ecology and Evolution, 22,* 357365.

[xviii] Parmesan, C. and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature, 421,* 37-42.

[xix] Linderholm, Hans W. (2006). Review: Growing season changes in the last century. *Agricultural and Forest Meteorology, 137*.
http://research.eeescience.utoledo.edu/lees/papers_PDF/Linderholm_2006_AFM.pdf

[xx] IPCC (2013). AR5 WGI SPM

[xxi] Langevin, C. D. and Zygnerski, M. (2013). Effect of sea-level rise on salt water intrusion near a coastal well field in southeastern Florida. *Ground Water, 51*, 781–803.
doi: 10.1111/j.1745-6584.2012.01008.x

[xxii] Trenberth, K. E. (2011). Changes in precipitation with climate change. *Climate Research, 47,* 123-138.

[xxiii] Melillo et al. (2013). *Third National Climate Assessment Draft Report*. Washington, DC: United States Global Change Research Program.

[xxiv] Melillo et al. (2013).

[xxv] Trenberth, K.E., P.D. Jones, P. Ambenje, R. Bojariu, D. Easterling, A. Klein Tank, D. Parker, F. Rahimzadeh, J.A. Renwick, M. Rusticucci, B. Soden and P. Zhai. (2007). Chapter 3, Observations: Surface and Atmospheric Climate Change. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

[xxvi] Hansen, James, Makiko Sato and Reto Ruedy. (2012). Perception of climate change. August 6, 2012. *Proceedings of the National Academy of Sciences,* 10.1073/pnas.1205276109
http://www.pnas.org/content/early/2012/07/30/1205276109.abstract

[xxvii] Gutowski, W.J., G.C. Hegerl, G.J. Holland, T.R. Knutson, L.O. Mearns, R.J. Stouffer, P.J. Webster, M.F. Wehner, F.W. Zwiers. (2008). Causes of Observed Changes in Extremes and Projections of Future Changes in *Weather and Climate Extremes in a Changing Climate. Regions of Focus: North America, Hawaii, Caribbean, and U.S. Pacific Islands.* T.R. Karl, G.A. Meehl, C.D. Miller, S.J. Hassol, A.M. Waple, and W.L. Murray (eds.). A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research, Washington, DC.

[xxviii] Meehl, G. A., C. Tebaldi, G. Walton, D. Easterling, and L. McDaniel. (2009). Relative increase of record high maximum temperatures compared to record low minimum temperatures in the U.S. *Geophysical Research Letters, 36,* L23701.
doi:10.1029/2009GL040736.

[xxix] Karl, T.R., G.A. Meehl, and T.C. Peterson. (2009). *Global Climate Change Impacts in the United States.* Cambridge, UK: Cambridge University Press.

[xxx] Melillo et al. (2013).

[xxxi] Melillo et al. (2013).

[xxxii] McMichael T., Montgomery H., Costello A. (2012). Health risks, present and future, from global climate change. BMJ 2012; 344:e1359. doi: 10.1136/bmj.e1359

[xxxiii] Luber, G. and McGeehin, M. (2008). Climate change and extreme heat. *American Journal of Preventive Medicine, 35* (5), 429-435.

[xxxiv] Kalkstein, L.S., S. Greene, D.M. Mills, and J. Samenow. (2011). An evaluation of the progress in 30 reducing heat-related human mortality in major US cities. *Natural Hazards, 56,* 113-129.

[xxxv] Lane, K., Charles-Guzman, K., Wheeler, K., et al. (2013). Health effects of coastal storms and flooding in urban areas: A review and vulnerability assessment. *Journal of Environmental and Public Health, 2013,* (2013), Article ID 913064. http://dx.doi.org/10.1155/2013/913064

[xxxvi] Landesman, L.Y. (2005). *Public Health Management of Disasters.* Second Edition. Washington, DC: American Public Health Association.

[xxxvii] Kinney, P.L. (2008). Climate change, air quality, and human health. *American Journal of Preventive Medicine, 35,* 459-467.

[xxxviii] Tagaris, E., K. Manomaiphiboon, K.J. Liao, L.R. Leung, J.H. Woo, S. He, P. Amar, and A.G. Russell. (2007). Impacts of global climate change and emissions on regional ozone and fine particulate matter concentrations over the United States. *Journal of Geophysical Research, 2112,* (33), D14312.

[xxxix] Ziska, L., K. Knowlton, C. Rogers, D. Dalan, N. Tierney, M.A. Elder, W. Filley, J. Shropshire, 16 L.B. Ford, and C. Hedberg. (2011). Recent warming by latitude associated with increased length 17 of ragweed pollen season in central North America. *Proceedings of the National Academy of 18 Sciences, 108,* 4248-4251.

[xl] Ariano, R., G.W. Canonica, and G. Passalacqua. (2010). Possible role of climate changes in 23 variations in pollen seasons and allergic sensitizations during 27 years. *Annals of Allergy, 24 Asthma & Immunology, 104,* 215-222.

[xli] Altizer S, Ostfeld RS, Johnson PT, Kutz S, Harvell CD. (2013). Climate change and infectious diseases: From evidence to a predictive framework. *Science, 341* (6145), 514-9.

[xlii] Karl, T.R., G.A. Meehl, and T.C. Peterson. (2009). *Global Climate Change Impacts in the United States.* Cambridge, UK: Cambridge University Press.

[xliii] Karl, T.R. et al. (2009).

[xliv] United States Department of Defense (2011). *2014 Quadrennial Defense Review.* Washington, DC. http://www.defense.gov/pubs/2014_Quadrennial_Defense_Review.pdf

[xlv] National Research Council (2011). National Security Implications of Climate Change for U.S. Naval Forces. Washington, DC: The National Academies Press.

[xlvi] Goodman, S., Sullivan, G. (2013). Climate change as a “threat multiplier.” *Politico.* http://www.politico.com/story/2013/02/climate-change-is-threat-multiplier-87338.html

[xlvii] Castellaw, Lt. Gen. J., Titley, R. Adm. D. (2014). The U.S. military leads on climate change. *The Hill.* http://thehill.com/blogs/congress-blog/energy-environment/200412-the-us-military-leads-on-climate-change

[xlviii] National Research Council (2013). *Abrupt Impacts of Climate Change….*

[xlix] IPCC (2013). AR5 WGI SPM

[l] IPCC (2013). AR5 WGI SPM

[li] Melillo et al. (2013).

[lii] IPCC (2012). IPCC Guidance Note for Lead Authors of the IPCC Fifth Assessment Report on Consistent Treatment of Uncertainties. "Likely" defined by the IPCC as a probability of 66% -100%.

[liii] IPCC (2013). Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press.

[liv] IPCC (2012). Managing the Risk of Extreme Events and Disasters to Advance Climate Change Adaptation: Special Report of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press.

[lv] Melillo et al. (2013).

[lvi] Melillo et al. (2013).

[lvii]Strauss, B.H. et al. (2012). Tidally adjusted estimates of topographic vulnerability to sea level rise and flooding for the contiguous United States. *Environmental Research Letters, 7,* 014033. doi:10.1088/1748-9326/7/1/014033

[lviii] IPCC (2013) WGI Technical Summary.

[lix] Strauss, B. (2013). Rapid accumulation of committed sea-level rise from global warming. *Proceedings of the National Academy of Sciences*. http://assets.climatecentral.org/pdfs/Strauss-PNAS-2013-v2.pdf

[lx] National Research Council (2013). *Abrupt Impacts of Climate Change….*

[lxi] National Research Council (2013). *Abrupt Impacts of Climate Change….*

[lxii] National Research Council (2013). *Abrupt Impacts of Climate Change….*

[lxiii] National Research Council (2013). *Abrupt Impacts of Climate Change….*

[lxiv] National Research Council (2013). *Abrupt Impacts of Climate Change….*

[lxv] Peterson, T.C., D.M. Anderson, S.J. Cohen, M. Cortez-Vázquez, R.J. Murnane, C. Parmesan, D. Phillips, R.S. Pulwarty, J.M.R. Stone. (2008). Why Weather and Climate Extremes Matter in *Weather and Climate Extremes in a Changing Climate. Regions of Focus: North America, Hawaii, Caribbean, and U.S.*

Pacific Islands. T.R. Karl, G.A. Meehl, C.D. Miller, S.J. Hassol, A.M. Waple, and W.L. Murray (eds.). A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research, Washington, DC.

[lxvi] National Research Council (2013). *Abrupt Impacts of Climate Change….*

[lxvii] National Research Council (2013). *Abrupt Impacts of Climate Change….*

[lxviii] Francis, J. A. and S. J. Vavrus (2012) Evidence Linking Arctic Amplification to Extreme Weather in Mid-Latitudes, *Geophysical Research Letters, 39,* L06801. doi:10.1029/2012GL051000

[lxix] Tang, Q., X. Zhang, X. Yang, and J. A. Francis (2013). Cold winter extremes in northern continents linked to Arctic sea ice loss. *Environmental Research Letters, 8,* 014036.

[lxx] IPCC AR5 WGI Technical Summary.

[lxxi] IPCC AR5 WGI Technical Summary.

[lxxii] IPCC AR5 WGI Technical Summary.

[lxxiii] National Research Council (2013). *Abrupt Impacts of Climate Change….*

[lxxiv] National Research Council (2013). *Abrupt Impacts of Climate Change….*

[lxxv] IPCC AR5 WGI Technical Summary.

[lxxvi] IPCC AR5 WGI Technical Summary.

[lxxvii] IPCC AR5 WGI Technical Summary.

[lxxviii] IPCC AR5 WGI Technical Summary.

[lxxix] IPCC AR5 WGI Technical Summary.

[lxxx] IPCC AR5 WGI Technical Summary.

[lxxxi] National Research Council (2013). *Abrupt Impacts of Climate Change….*

[lxxxii] IPCC AR5 WGI Technical Summary.

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Research Article

Energy Development Affects Populations of Sagebrush Songbirds in Wyoming

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ABSTRACT Oil and natural gas development in the Intermountain West region of North America has expanded over the last 2 decades, primarily within sagebrush dominated landscapes. Although the effects of energy development on high-profile game species such as the greater sage-grouse (*Centrocercus urophasianus*) have been documented, studies examining responses of non-game birds are lacking. Simultaneously, many songbirds that breed within sagebrush steppe habitats have shown range-wide population declines that are likely due to widespread habitat loss and alteration. We evaluated songbird abundance and species richness across gradients of oil and natural gas development intensity, as indexed by well density, at 3 energy fields (2 natural gas and 1 oil) in the Upper Green River Basin, Wyoming, USA during 2008–2009. While simultaneously accounting for important habitat attributes, increased well density was associated with significant decreases in Brewer's sparrow (*Spizella breweri*) and sage sparrow (*Amphispiza belli*) abundance, particularly in the Jonah natural gas field. Vesper sparrows (*Pooecetes gramineus*) were also negatively influenced by increased well density. Horned larks (*Eremophila alpestris*) increased with well density in the Pinedale Anticline natural gas field, and sage thrashers (*Oreoscoptes montanus*) showed no response to energy development. Species richness was not significantly affected by well density. Results suggest that regional declines of some songbird species, especially sagebrush-obligates, may be exacerbated by increased energy development. Understanding the specific mechanisms underlying responses to energy development is an important next step and will aid land managers in the development of effective mitigation and management strategies for the maintenance of stable bird communities in sagebrush habitat.

KEY WORDS avian abundance, Brewer's sparrow, natural gas, oil, sage sparrow, sage thrasher, shrubsteppe, species richness.

Habitat loss, fragmentation, and alteration due to anthropogenic activities are major factors contributing to wildlife population declines and biodiversity loss across a variety of ecosystems (Saunders et al. 1991, Wilcove et al. 1998). Rapid loss, fragmentation, and severe degradation of sagebrush (*Artemesia tridentata*) communities (Knick and Rotenberry 2000) have been primarily due to human activities including agricultural conversion (Braun et al. 1976, Vander Haegen et al. 2000) and livestock overgrazing (Beck and Mitchell 2000), invasive species such as cheatgrass (*Bromus tectorum*; Monsen and Shaw 2000, Rich et al. 2005), and altered fire regimes (Connelly and Braun 1997). Simultaneously, many wildlife species dependent on sagebrush have declined or been locally extirpated due to loss of historical habitat, behavioral avoidance of disturbance, increased predation risk, and decreased annual survival, reproductive success, and recruitment (Braun et al. 2002, Knick et al. 2003, Holloran 2005, Vander Haegen 2007).

Concurrent with increased anthropogenic land use in North American sagebrush habitats, shrubland and grassland bird populations have declined faster than other avian species groups (Paige and Ritter 1999, Knick et al. 2003). In particular, the Brewer's sparrow (*Spizella breweri*), sage sparrow (*Amphispiza belli*), and sage thrasher (*Oreoscoptes montanus*), 3 migratory passerine species considered sagebrush-obligates during the breeding season (Braun et al. 1976), have shown average annual declines in nationwide abundance between 1980 and 2007 of 1.5%, 0.2%, and 1.1%, respectively (Sauer et al. 2008). Indeed, species dependent on a single habitat type are usually more sensitive to anthropogenic habitat modifications than are generalists (Saab and Rich 1997). Although efforts to understand habitat relationships of non-game sagebrush birds have increased recently, we still know little about the impacts of specific types of habitat change on individual habitat use, reproductive success, and annual survival or how anthropogenic changes may interact with critical habitat components to influence populations.

Oil and natural gas development has expanded across the Intermountain West over the last 2 decades, primarily within sagebrush dominated landscapes (Knick et al. 2003). In Wyoming, for example, as of 2008 there were >2 million ha

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of producing oil and gas leases and >5.5 million ha authorized for production (U.S. Department of the Interior [USDI] 2009; Fig. 1). Energy development infrastructure such as drill pads, waste pits, access roads, and pipelines convert and fragment sagebrush habitats, often negatively impacting wildlife populations (Weller et al. 2002, Walker et al. 2007, Doherty et al. 2008, Sawyer et al. 2009, Holloran et al. 2010).

Research focusing on effects of energy development on sagebrush birds has centered on the greater sage-grouse (*Centrocercus urophasianus*; Walker et al. 2007, Doherty et al. 2008, Holloran et al. 2010). Adverse effects of energy development on this high-profile game species are well-documented and include decreased recruitment to or abandonment of leks, avoidance of nesting near infrastructure, decreased nest and chick survival, and increased adult mortality due to increasing disease prevalence, vehicle collisions, and raptor predation (Naugle et al. 2011). Yet

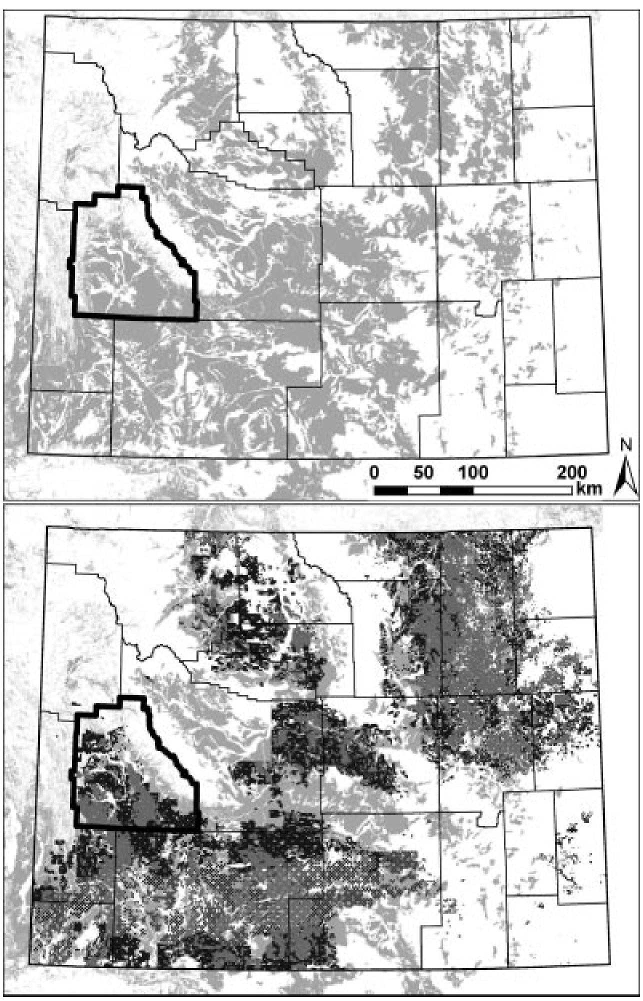

Figure 1. We examined sagebrush songbird population responses to energy development in Sublette County (outlined in bold), Wyoming, USA, 2008–2009. Top: Sagebrush habitats (light gray shading) are predominant throughout Wyoming (U.S. Geological Survey 2001). Bottom: Producing (medium gray) and authorized (dark gray) oil and natural gas leases (as of 2008; Wyoming Geographic Information Science Center 2009) show extensive overlap with sagebrush habitats across the state.

studies examining responses of the rest of the sagebrush bird community to oil and natural gas development are lacking (Ingelfinger and Anderson 2004). Understanding how songbird populations may be impacted by anthropogenic disturbance, and how disturbance impacts may interact with critical habitat features, is an important step in developing effective recommendations for management strategies geared towards maintenance of stable sagebrush bird communities.

Our objective was to assess the relationship between energy development intensity in sagebrush habitat and songbird populations and avian community composition. Specifically, we evaluated the relative abundance and species richness of songbirds across gradients of oil and natural gas well density and habitat variation.

STUDY AREA

We conducted our study within sagebrush habitat coinciding with energy development in the Upper Green River Basin (42°60′N, 109°75′W) of southwestern Wyoming, USA (Fig. 1). Specifically, our 3 study areas were the northern portion of the Pinedale Anticline Project Area (PAPA) natural gas field, the Jonah natural gas field, and the northern portion of the Big Piney-LaBarge (LaBarge) oil field (Fig. 2). Located south of Pinedale, Wyoming, PAPA, and Jonah ranked among the most highly concentrated and productive natural gas fields in North America (USDI 2006, 2008). The LaBarge area was an aggregation of oil fields south of Big Piney, Wyoming. The Upper Green River Basin landscape was dominated by big sagebrush (*Artemisia tridentata* spp.) with a primarily native understory of grasses and forbs (Lyon and Anderson 2003). Yearly precipitation averaged 27.5 cm (Western Regional Climate Center 2010).

METHODS

Site Selection

To ensure sampling spanned a gradient of energy development intensity, we stratified each study area into 4 levels of development based on existing variation in well density: none (0 wells/km^2), light (1–6 wells), moderate (7–15 wells), and heavy (>15 wells) development. Using aerial imagery and geographic well locations (Wyoming Geographic Information Science Center, Laramie, WY), we mapped well density in each energy field (Fig. 2) using ArcGIS 9.2 software, and randomly selected potential sampling sites within those strata.

Songbird habitats in sagebrush steppe have been characterized by measures of patch size, spatial homogeneity, and shrub attributes (Rotenberry and Wiens 1980; Wiens and Rotenberry 1981; Petersen and Best 1985*a*,*b*; Knopf et al. 1990). Therefore, we ground-truthed potential sampling sites to ensure they consisted of ≥20% shrub cover (Wiens and Rotenberry 1981, Chalfoun and Martin 2007), average shrub height ≥35 cm (Rich 1980; Petersen and Best 1985*a*,*b*), and average shrub crown vigor ≥50%

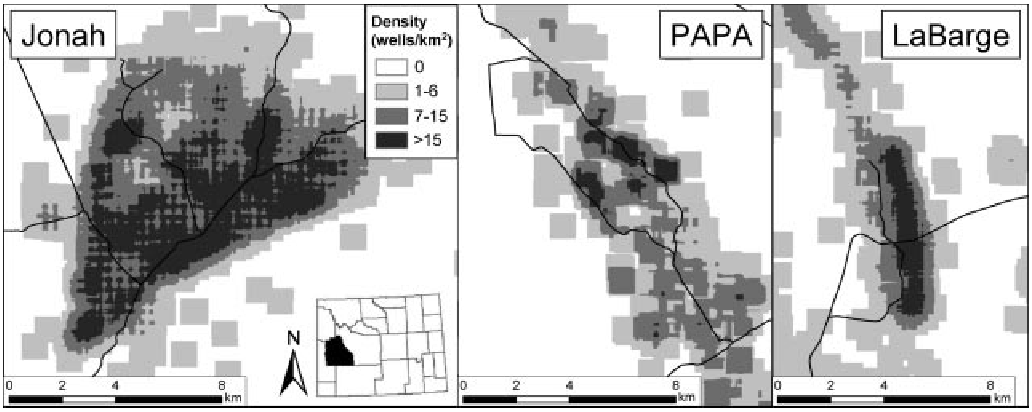

Figure 2. Three energy fields in Sublette County, Wyoming, USA (inset), that we used to examine the relationship between oil and natural gas development and sagebrush songbird abundance and richness, 2008–2009. We used 4 a priori categories of well density (wells/km^2) to stratify point count sampling sites, represented by light to dark shading.

(Petersen and Best 1985*a*,*b*; Chalfoun and Martin 2009). Within each development strata at each study area, we chose the first 5 randomly selected sites that met these habitat criteria for placement of our point count clusters. Clusters consisted of 4 points in the shape of a square with 200-m spacing between points; if habitat minimums at points were not met, we adjusted points outward with a maximum spacing of 400 m. By selecting sites that met habitat minimums we sought to survey only potentially suitable nesting and foraging habitat within areas of differing energy development intensity.

Avian Abundance and Species Richness

We evaluated avian abundance and species richness using point count sampling (Reynolds et al. 1980) from May through July, 2008–2009. We surveyed 20 clusters per energy field (with 5 point count clusters in each of the 4 well density strata), for a total of 240 points. During each 10-min survey we recorded all birds seen or heard and distance to observer using digital rangefinders, taking care to avoid double-counting individuals. We recorded flyovers but excluded them from analyses. Surveys began at sunrise on mornings without rain or strong winds and were completed within 3 hr. We repeated surveys 3 times in 2008 and twice (due to persistent rain) in 2009, varying observer and time of visit among surveys. We surveyed the same sites in both years, except where creation or expansion of drilling infrastructure encroached on 7 point count clusters (2 in PAPA and 5 in Jonah) in 2009, which required relocation of 10 survey points. In most cases, we moved just one point per cluster and reassessed well density for the cluster for that year. We could not resurvey 2 additional clusters in PAPA in 2009 because the entire cluster area was developed, and we excluded those clusters from analyses.

We used Program DISTANCE (Thomas et al. 2010) to fit detection-probability functions for species with sufficient detections at each study area. We pooled data across years, truncated the furthest 10% of distances, and fit detection functions for a uniform model with cosine expansions, a uniform model with simple polynomial expansions, and a half-normal model with hermite polynomial expansions (Somershoe et al. 2006, Thomas et al. 2010). We used Akaike's Information Criterion (Burnham and Anderson 2002) to select the model with the best relative fit and adjusted our relative abundance estimates using the model-generated detection probabilities (Table 1). However, the low-calculated detection probabilities for Brewer's sparrows (0.224–0.298) produced unrealistically high abundance estimates, based on minimum territory sizes of approximately 0.5 ha (Wiens et al. 1985, Chalfoun and Martin 2007). We therefore truncated the Brewer's sparrow data at 100 m rather than the furthest 10% of detections. We summarized adjusted detections for each species by cluster, averaged over the number of visits each year. We summarized species richness as the average number of breeding songbird species detected per cluster visit in each year.

Table 1. Detection probabilities for the 5 most common songbird species we detected at 3 energy fields in southwestern Wyoming, USA, 2008–2009, calculated using Program DISTANCE.

Species	Jonah	PAPA[a]	LaBarge
Brewer's sparrow	0.378	0.384	0.448
Sage sparrow	0.423	0.300	0.359
Sage thrasher	0.361	0.323	0.493
Vesper sparrow	0.432[b]	0.432	0.565
Horned lark	0.508	0.555	0.581

[a] Pinedale Anticline Project Area.
[b] Detections at Jonah were insufficient ($\leq$50 individuals) for estimation of vesper sparrow detection probabilities, so we assumed this value was similar to that of the adjacent energy field (PAPA).

Energy Development and Habitat Characteristics

We used well density as a proxy for energy development intensity. Using aerial imagery and geographic locations of wells, we calculated the number of well locations within a 1-km^2 area (564-m radius) around each point count center using ArcGIS 9.2 software and averaged these values to estimate well density for each cluster.

Because abundance of sagebrush songbirds is influenced by habitat characteristics at breeding sites, we quantified habitat variation at our sampling sites to control for habitat when examining energy development effects. We measured habitat attributes within 5-m-radius circular plots (Martin et al. 1997; Chalfoun and Martin 2007, 2009) placed at 2 locations with randomly selected direction and distance up to 50 m from each point count center. We completed habitat measurements during a 3-week period beginning mid-July of each year, surveying half of each cluster in 2008 and the remainder in 2009. We quantified shrub cover using the line intercept method (Lucas and Seber 1977) along two 10-m transect lines oriented in the cardinal directions. For each intersected shrub we measured 1) height of the main crown (cm) and 2) percent crown vigor (proportion of the crown that was live). In each quadrant designated by the transect lines, we recorded total shrub density and the density of potential nest shrubs (PNS density), which we defined as shrubs with the proper quantitative and qualitative attributes to potentially accommodate a nest of a Brewer's sparrow (Chalfoun and Martin 2007, 2009), the most common species at our sites. We averaged habitat data collected at each point count cluster, combined across years, to obtain 1 value per cluster for each habitat variable.

Correlation analysis revealed significant positive relationships between many of our habitat variables (Table 2). For sparrows in sagebrush habitat, shrub vigor has merit as a proxy for increased insect food abundance and nest concealment, 2 critical resources for shrub-nesting birds (Rich 1980, Knopf et al. 1990, Wenninger and Inouye 2008). Shrub vigor is also important in identifying nest shrubs used by both Brewer's sparrows and sage sparrows (Petersen and Best 1985*a*,*b*). We therefore chose average shrub vigor as our habitat covariate for most species. For Brewer's sparrows, however, we used PNS density instead of shrub vigor, as PNS density influences nest site selection and reproductive success of Brewer's sparrows (Chalfoun and Martin 2007, 2009) and PNS density was correlated with most other habitat characteristics (Table 2). For horned larks (*Eremophila alpestris*), a ground-nesting species more associated with grasslands than shrublands (Beason 1995), we used shrub cover as our habitat covariate, as we anticipated that horned lark abundance would be inversely related to big sagebrush cover.

Statistical Analyses

After we checked abundance and species richness data for normality and homogeneity of variances, we analyzed abundance of each species and overall species richness across energy development gradients using repeated-measures general linear mixed models in SPSS 17 (SPSS Inc., Chicago, Illinois). We treated year as a repeated measure on the experimental units (clusters), using cluster identification as a random effect to acknowledge the potential correlation in songbird abundance at locations across years. We included site as a fixed factor, and well density/km^2 as our covariate of interest. To account for habitat effects, we included a covariate representing habitat characteristics (PNS density for Brewer's sparrow, average shrub cover for horned larks, average shrub vigor for all others). Dependent variables were average species detections (adjusted) and average species richness per cluster per survey visit.

RESULTS

We conducted 1,184 point count surveys during 2008–2009. The most common species were, in order of abundance: Brewer's sparrow, horned lark, sage sparrow, vesper sparrow (*Pooecetes gramineus*), and sage thrasher. These 5 species accounted for 95% of songbird detections. Detection probabilities ranged from 0.300 to 0.581 (Table 1). Other breeding songbird species included in species richness calculations were Brewer's blackbird (*Euphagus cyanocephalus*), green-tailed towhee (*Pipilo chlorurus*), loggerhead shrike (*Lanius ludovicianus*), western meadowlark (*Sturnella neglecta*), and white-crowned sparrow (*Zonotrichia leucophrys*).

Well density had negative effects on abundance of 3 of our most common species: Brewer's sparrow ($F_{1,52} = 5.247$, $P = 0.026$), sage sparrow ($F_{1,53} = 7.995$, $P = 0.007$), and vesper sparrow ($F_{1,53} = 3.055$, $P = 0.086$; Table 3). Because we observed significant site effects in abundance models for all 5 species and richness (Table 3), and because we were interested in which types of energy fields may influence bird populations most strongly, we further analyzed responses individually by site. Sage sparrows, sage thrashers, horned larks, and species richness lacked a significant year × site interaction (Table 3); for these, we pooled data across years and analyzed site responses using general linear models.

Brewer's sparrow abundance decreased most steeply at the Jonah natural gas field ($\beta_{2008} = -0.311 \pm 0.102$, $P = 0.008$; $\beta_{2009} = -0.348 \pm 0.174$, $P = 0.063$; Table 4) with increasing well density; average decreases at all sites were greater in 2009 than in 2008 (Table 4, Fig. 3). For sage sparrow, the strongest declines also occurred at Jonah ($\beta = -0.294 \pm 0.070$, $P \leq 0.001$; Table 4), and the other 2 sites showed similar decreases, though not significant (Table 4, Fig. 3). Vesper sparrow abundance at PAPA decreased in response to increasing well densities

Table 2. Correlation matrix of habitat measurements we collected at 3 energy fields in southwestern Wyoming, USA, 2008–2009, averaged per point count cluster (1 cluster = 4 points). Data are 2-tailed Pearson correlation (*r*) and *P*-values; $n = 118$.

	PNS density[a]		Shrub height		Shrub cover		Shrub density	
Habitat metric	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Shrub vigor	0.212	0.021	0.017	0.857	−0.166	0.072	0.147	0.112
PNS density[a]			0.305	0.001	0.619	≤0.001	0.553	≤0.001
Shrub height					0.149	0.106	0.258	0.005
Shrub cover							0.461	≤0.001

[a] Potential nest shrub density.

Table 3. Between-subjects effects (top 3 lines) and within-subject contrasts (lower 3 lines) from repeated measures general linear mixed models examining effects of energy development density (wells/km^2) on abundance of the 5 most common passerine species and species richness at 3 energy fields in southwestern Wyoming, USA, 2008–2009. $n = 57$ point count clusters for Brewer's sparrow and $n = 58$ for all other species and richness.

		Brewer's sparrow		Sage sparrow		Sage thrasher		Vesper sparrow		Horned lark		Richness	
Variable	*df*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Well density	1	5.247	0.026	7.995	0.007	0.144	0.706	3.055	0.086	0.795	0.377	0.430	0.515
Habitat[a]	1	2.437	0.125	1.786	0.187	1.059	0.308	0.682	0.413	0.030	0.864		
Site	2	38.871	≤0.001	6.953	0.002	7.722	≤0.001	36.175	≤0.001	19.78	≤0.001	12.663	≤0.001
Year	1	14.218	≤0.001	0.01	0.920	0.088	0.768	0.601	0.442	0.037	0.847	13.556	0.001
Year × Well Density	1	0.745	0.392	0.071	0.792	0.848	0.361	0.064	0.802	0.162	0.689	3.662	0.061
Year × Site	2	13.97	≤0.001	0.673	0.515	0.613	0.546	4.265	0.019	0.346	0.709	0.169	0.845

[a] Potential nest shrub density for Brewer's sparrow, shrub cover for horned lark, and average shrub vigor for other species and richness.

($\beta_{2008} = -0.043 \pm 0.152$, $P = 0.407$; $\beta_{2009} = -0.141 \pm 0.331$, $P = 0.136$; Table 4), with mixed responses at LaBarge across years and consistently low detections at Jonah (Table 4, Fig. 3). We found increased horned lark abundance with increasing well density at PAPA ($\beta = 0.125 \pm 0.056$, $P = 0.031$; Table 4), but no significant responses at Jonah or LaBarge (Table 4, Fig. 3). Abundance of sage thrashers was unrelated to well density ($F_{1,53} = 0.144$, $P = 0.706$; Table 3), and direction of responses differed among study sites (Table 4, Fig. 3). Species richness at clusters was unrelated to increasing well density (Table 3, Fig. 3); this response was consistent among study sites (Table 4). Habitat covariates did not influence responses of any of the 5 species we evaluated (Table 3).

DISCUSSION

Increased energy development intensity, as estimated by well density/km^2, was associated with decreased abundances of Brewer's sparrows, sage sparrows, and vesper sparrows. Declines were strongest for Brewer's sparrows and sage sparrows at the Jonah field, with an average decrease of 0.3 individuals per additional well/km^2 (Table 4). This translates to average losses of 2.5 individuals at clusters with densities of 8 wells/km^2 for both these sagebrush-obligates. Approved spacing of 16 well pads per 2.6-km^2 section at Jonah (USDI 2006) readily yields these and higher well densities.

Sage thrashers did not respond significantly to increased well density in our study, despite sage thrashers being the largest-bodied species with the largest average territory size of those we studied. Sage thrashers have also shown a lack of response to other disturbances such as fire treatments (Castrale 1982, Knick and Rotenberry 2000), suggesting they may be less sensitive to habitat change. An alternative explanation is high annual site fidelity (Wiens and Rotenberry 1985, Knick and Rotenberry 2002), regardless of habitat changes, though this hypothesis requires explicit testing. If site fidelity is strong, population responses could take longer to detect due to turnover times of individuals creating a lag effect, which has been shown in greater sage-grouse population responses to energy development (Walker et al. 2007, Harju et al. 2010). Site fidelity within altered habitats, moreover, could reduce population size in the future if these habitats are of lower quality and result in lower fitness of remaining individuals.

We provide evidence that not all energy fields are created equal; significant site effects for all species evaluated suggest that characteristics of an energy development field may influence avian species responses. Effects were typically stronger in the Jonah and PAPA natural gas fields, developing energy fields that contained multiple disturbance sources, in contrast to the LaBarge oil field that had been

Table 4. Parameter estimates (β), standard errors (SE), and P-values for effects of well density (wells/km^2) at 3 energy fields in southwestern Wyoming, USA, 2008–2009 on the abundance of the 5 most abundant passerine species and species richness by year and site from repeated measures general linear mixed models, or by site with years combined from general linear models.

		Jonah			PAPA[a]			LaBarge		
Species	Year	β	SE	*P*	β	SE	*P*	β	SE	*P*
Brewer's sparrow	2008	−0.311	0.102	0.008	−0.011	0.148	0.943	−0.017	0.097	0.865
	2009	−0.348	0.174	0.063	−0.147	0.133	0.286	−0.070	0.143	0.629
Sage sparrow		−0.294	0.07	≤0.001	−0.060	0.096	0.536	−0.144	0.094	0.134
Sage thrasher		0.057	0.053	0.296	−0.062	0.067	0.358	0.077	0.055	0.168
Vesper sparrow	2008	0.001[b]	0.006	0.929	−0.043	0.051	0.407	−0.139	0.092	0.149
	2009	−0.012[b]	0.009	0.183	−0.141	0.089	0.136	0.024	0.085	0.781
Horned lark		−0.024	0.151	0.739	0.125	0.056	0.031	0.005	0.068	0.937
Richness		−0.013	0.008	0.096	−0.002	0.008	0.816	−0.018	0.015	0.248

[a] Pinedale Anticline Project Area.
[b] Parameter estimates for vesper sparrow at Jonah based on very low numbers of detections (<20 individuals over 2 years).

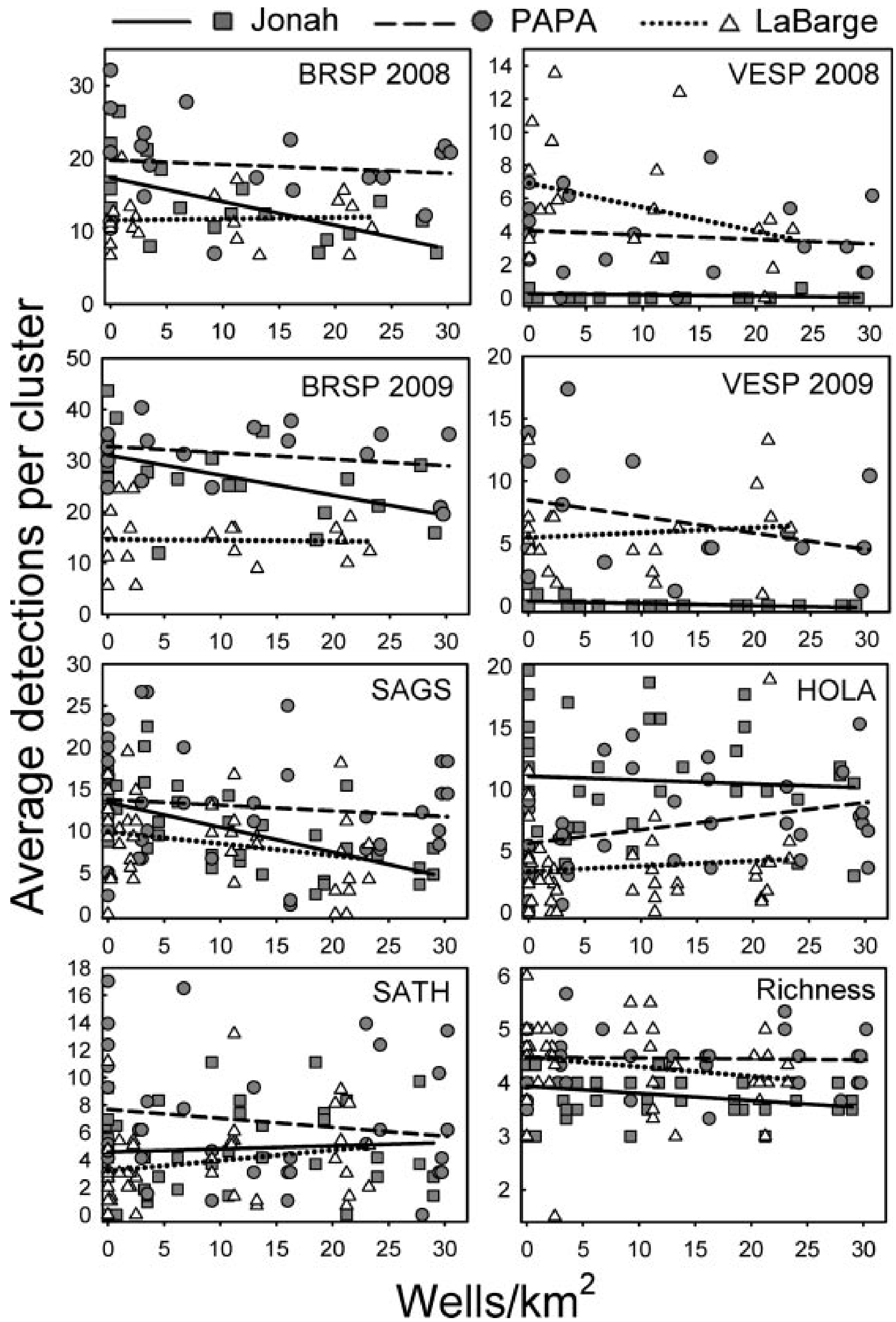

Figure 3. Relative abundance of Brewer's sparrow (BRSP), sage sparrow (SAGS), sage thrasher (SATH), horned lark (HOLA), and vesper sparrow (VESP), and passerine species richness in relation to well density at the Jonah (circles and solid lines), PAPA (squares and dashed lines), and LaBarge (triangles and dotted lines) energy fields, southwestern Wyoming, USA, 2008–2009. Open symbols designate oil fields, shaded symbols are natural gas fields. Data are average number of individuals or species detected per survey visit per cluster (sum of four 100-m radius point counts), adjusted for detection probabilities.

in production for several decades (McDonald 1976, Holloran 2005). Time since the initiation of development, spatial configuration of energy fields (Fig. 2), and higher human activity levels and drilling infrastructure presence may contribute to patterns of songbird abundance.

Human activity and vehicle traffic levels, for example, are highest on active drilling pads (Sawyer et al. 2009) and varied between our energy fields. On the growing PAPA and Jonah natural gas fields, manned drilling rigs were common on the landscape throughout the breeding season. In contrast, such rigs were rare in LaBarge during our study. Likewise, traffic volume around an active well pad in the PAPA averaged 112 vehicles per day (Sawyer et al. 2009), and traffic on main haul roads in Jonah has exceeded 600 vehicles per day (Ingelfinger and Anderson 2004), whereas traffic at LaBarge rarely exceeded 5 vehicles per day during our study (M. Gilbert, University of Wyoming, personal observation).

Field age or spatial configuration may factor into response differences between the PAPA and Jonah natural gas fields. Development began on PAPA approximately 10 years ago and the northern portion of the field was configured in a linear band of development (Fig. 2), primarily employing directional drilling technology with multiple wells drilled on a well pad (Sawyer et al. 2009). Approximately 30 km^2 of our 170-km^2 PAPA study area contained moderate to high well densities of $\geq$8 wells/km^2. The Jonah field, where species declines were steepest, was situated directly south of PAPA but was older, with development authorized in the late 1990s, and had a wide central area that was densely developed (Fig. 2), particularly where infill drilling occurred among existing wells (USDI 2006). As a result, nearly 70 km^2 of our 210-km^2 Jonah study area contained moderate to high well densities ($\geq$8 wells/km^2). Interestingly, overall abundance estimates for several species at the LaBarge field, the oldest of our study areas, were lower than at the other 2 sites (Fig. 3), suggesting that effects may compound over time at energy fields rather than showing patterns of acclimation or recovery after initial disturbances. The specific effects of such anthropogenic disturbance on wildlife are still unclear. Other studies have shown that mule deer (*Odocoileus hemionus*) avoidance of well pads on PAPA increased with higher levels of traffic (Sawyer et al. 2009), and greater noise at energy development facilities reduced passerine density and altered songbird community composition (Bayne et al. 2008, Francis et al. 2009). Even so, some species may show partial acclimation to human activity over time, thus long-term effects at the community level are unknown.

Our results corroborate those of other studies showing decreased occurrence and abundance of several grassland birds near oil and gas development edges and decreased sagebrush songbird density adjacent to natural gas development roads (Ingelfinger and Anderson 2004, Linnen 2008). Higher well densities result in a greater number and proportion of well pads, roads, and other anthropogenic infrastructure, which can intensify edge effects and may negatively impact songbirds via decreased nest success or altered species interactions (Fletcher 2005). Horned larks can be associated with disturbed vegetation communities (Knick and Rotenberry 2002), and the increased horned lark abundance we observed at PAPA, coupled with decreased sparrow populations, could signal a fundamental change in the bird assemblage of shrubsteppe habitats surrounding energy development.

Songbird population declines may be driven by increased nest predation risk as generalist predators become more abundant in human-altered areas (Chalfoun et al. 2002). Common ravens (*Corvus corax*) are widespread and effective nest predators (Andren 1994), and energy field encroachment upon undeveloped sagebrush areas appears to facilitate increases in breeding raven abundance (Bui et al. 2010). Increased raven numbers in sagebrush systems negatively affects nest survival of greater sage-grouse, another sagebrush obligate, particularly in areas with sparse shrub cover (Coates and Delehanty 2010). Data on the identification, abundance, and distribution of dominant nest predators in relation to energy development would shed light on nest predation as a potential mechanism for decreased sagebrush songbird abundance in energy fields.

Landscape-scale habitat alteration associated with energy development may also lead to songbird population declines via decreased food availability (Howe et al. 1996). Reduction of the amount of intact sagebrush habitat surrounding territories via conversion can limit foraging opportunities. Alternatively, if the condition of remaining sagebrush patches is altered, associated insect prey assemblages could decrease in abundance. Breeding songbirds rely heavily on such insect prey for their own maintenance and ability to provision young. We found no significant relationship between the habitat characteristics we measured and sagebrush obligate abundance, but this is likely an artifact of selecting our sampling locations above set minimums of shrub cover and vigor. That we found significant effects of energy development while simultaneously accounting for important microhabitat components suggests, moreover, that energy development independently affects non-game birds.

In conclusion, we documented a pattern of declining sagebrush songbird abundance with increasing well densities in energy development fields. An important next step is to examine the consequences of energy development for songbird demographic and population processes to clarify mechanisms for declines. Understanding patterns of population responses coupled with specific causes for declines will facilitate the development of effective management strategies for the maintenance of sagebrush bird communities.

MANAGEMENT IMPLICATIONS

Sagebrush-obligate songbirds are an important component of the biodiversity of the western United States and can serve as barometers of sagebrush ecosystem integrity due to their dependence on sagebrush and sensitivity to habitat alteration (Dobkin and Sauder 2004). The long-term impact of oil and natural gas development on songbirds in sagebrush habitat is unknown (Ingelfinger and Anderson 2004), but our data suggest that increasing energy development intensity will further exacerbate regional declines of sagebrush songbirds.

For oil and natural gas fields in early development stages, or expansions to existing fields such as the anticipated addition of 4,399 wells on up to 600 well pads in the PAPA (USDI 2008), it will be imperative for future studies to evaluate well placement configurations so as to assess their impacts on wildlife. Furthermore, explicit hypothesis tests focused on impacts to important limiting resources such as refugia from nest predation and food availability will be critical for determining underlying mechanisms through which energy development impacts songbirds and ultimately for developing appropriate mitigation strategies.

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LITERATURE CITED

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat—a review. Oikos 71:355–366.

Bayne, E. M., L. Habib, and S. Boutin. 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conservation Biology 22:1186–1193.

Beason, R. C. 1995. Horned Lark (*Eremophila alpestris*). Account 195 in A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Beck, J. L., and D. L. Mitchell. 2000. Influences of livestock grazing on sage grouse habitat. Wildlife Society Bulletin 28:993–1002.

Braun, C. E., M. F. Baker, R. L. Eng, J. S. Gashwiler, and M. H. Schroeder. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin 88:165–171.

Braun, C. E., O. O. Oedekoven, and C. L. Aldridge. 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 67:337–356.

Bui, T.-V. D., J. M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65–78.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Castrale, J. S. 1982. Effects of 2 sagebrush control methods on non-game birds. Journal of Wildlife Management 46:945–952.

Chalfoun, A. D., and T. E. Martin. 2007. Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. Animal Behaviour 73:579–585.

Chalfoun, A. D., and T. E. Martin. 2009. Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. Journal of Animal Ecology 78:497–503.

Chalfoun, A. D., F. R. Thompson, III, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16:306–318.

Coates, P. S., and D. J. Delehanty. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management 74:240–248.

Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. Wildlife Biology 3:229–234.

Dobkin, D. S., and J. D. Sauder. 2004. Shrubsteppe landscapes in jeopardy: distributions, abundances, and the uncertain future of birds and small mammals in the Intermountain West. High Desert Ecological Research Institute, Bend, Oregon, USA.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187–195.

Fletcher, R. J. 2005. Multiple edge effects and their implications in fragmented landscapes. Journal of Animal Ecology 74:342–352.

Francis, C. D., C. P. Ortega, and A. Cruz. 2009. Noise pollution changes avian communities and species interactions. Current Biology 19:1415–1419.

Harju, S. M., M. R. Dzialak, R. C. Taylor, L. D. Hayden-Wing, and J. B. Winstead. 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. Journal of Wildlife Management 74:437–448.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Howe, F. P., R. L. Knight, L. C. McEwen, and T. L. George. 1996. Direct and indirect effects of insecticide applications on growth and survival of nestling passerines. Ecological Applications 6:1314–1324.

Ingelfinger, F., and S. Anderson. 2004. Passerine response to roads associated with natural gas extraction in a sagebrush steppe habitat. Western North American Naturalist 64:385–395.

Knick, S. T., and J. T. Rotenberry. 2000. Ghosts of habitats past: contribution of landscape change to current habitats used by shrubland birds. Ecology 81:220–227.

Knick, S. T., and J. T. Rotenberry. 2002. Effects of habitat fragmentation on passerine birds breeding in intermountain shrubsteppe. Studies in Avian Biology 25:130–140.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. van Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611–634.

Knopf, F. L., J. A. Sedgwick, and D. B. Inkley. 1990. Regional correspondence among shrubsteppe bird habitats. Condor 92:45–53.

Linnen, C. G. 2008. Effects of oil and gas development on grassland birds. Prepared for Petroleum Technology Alliance Canada. Northern Envirosearch Ltd., Saskatoon, Saskatchewan, Canada.

Lucas, H. A., and G. A. F. Seber. 1977. Estimating coverage and particle density using the line intercept method. Biometrika 64:618–622.

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.

Martin, T. E., C. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD field protocol. Biological Resources Division. Montana Cooperative Wildlife Research Unit, Missoula, USA.

McDonald, Robert. E. 1976. Big Piney-LaBarge producing complex, Sublette and Lincoln counties, Wyoming. AAPG Memoir 24:91–120.

Monsen, S. B., and N. L. Shaw. 2000. Big sagebrush (*Artemesia tridentata*) communities—ecology, importance and restoration potential. Pages 255–270 *in* 2000 Billings Land Reclamation Symposium. Reclamation Research Unit Publication No. 00-01, Bozeman, Montana, USA.

Naugle, D. E., K. E. Doherty, B. L. Walker, M. J. Holloran, and H. E. Copeland. 2011. Energy development and sage-grouse. Studies in Avian Biology. In press.

Paige, C., and S. A. Ritter. 1999. Birds in a sagebrush sea: managing sagebrush habitats for bird communities. Partners in Flight Western Working Group, Boise, Idaho, USA.

Petersen, K. L., and L. B. Best. 1985*a*. Brewer's sparrow nest-site characteristics in a sagebrush community. Journal of Field Ornithology 56: 23–27.

Petersen, K. L., and L. B. Best. 1985*b*. Nest-site selection by sage sparrows. Condor 87:217–221.

Reynolds, R. T., J. M. Scott, and R. A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309–313.

Rich, T. 1980. Nest placement in sage thrashers, sage sparrows, and Brewer's sparrows. Wilson Bulletin 92:362–368.

Rich, T. D., M. J. Wisdom, and V. A. Saab. 2005. Conservation of priority birds in sagebrush ecosystems. Proceedings from the Third International Partners In Flight Conference: A Workshop on Bird Conservation Implementation and Integration. USDA Forest Service General Technical Report PSW-GTR-191. Albany, California, USA.

Rotenberry, J. T., and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North-American steppe vegetation—a multivariate analysis. Ecology 61:1228–1250.

Saab, V. A., and T. D. Rich. 1997. Large-scale conservation assessment for neotropical migratory land birds in the interior Columbia River basin. USDA Forest Service General Technical Report PNW-GTR-399, Portland, Oregon, USA.

Sauer, J. R., J. E. Hines, and J. Fallon. 2008. The North American Breeding Bird Survey, results and analysis 1966–2007. Version 5.15.2008. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation—a review. Conservation Biology 5:18–32.
Sawyer, H., M. J. Kauffman, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.
Somershoe, S. G., D. J. Twedt, and B. Reid. 2006. Combining breeding bird survey and distance sampling to estimate density of migrant and breeding birds. Condor 108:691–699.
Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.
U.S. Geological Survey. 2001. SAGEMAP: a GIS database for sage grouse and shrubsteppe management in the Intermountain West. <http://SAGEMAP.wr.usgs.gov>. Accessed 28 Aug 2009.
U.S. Department of the Interior [USDI]. 2006. Final environmental impact statement: Jonah infill drilling project, Sublette County, Wyoming. Pinedale Field Office, Pinedale, Wyoming, USA.
U.S. Department of the Interior [USDI]. 2008. Final supplemental environmental impact statement for the Pinedale Anticline oil and natural gas exploration and development project, Sublette County, Wyoming. Pinedale Field Office, Pinedale, Wyoming, USA.
U.S. Department of the Interior [USDI]. 2009. Number of producible acres on federal lands, FY 1988-FY 2008. <http://www.blm.gov/wo/st/en/info/newsroom/Energy_Facts_07/statistics.html>. Accessed 18 Dec 2009.
Vander Haegen, W. M. 2007. Fragmentation by agriculture influences reproductive success of birds in a shrubsteppe landscape. Ecological Applications 17:934–947.
Vander Haegen, W. M., F. C. Dobler, and D. J. Pierce. 2000. Shrubsteppe bird response to habitat and landscape variables in eastern Washington, USA. Conservation Biology 14:1145–1160.
Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.
Weller, C., J. Thomson, P. Morton, and G. Aplet. 2002. Fragmenting our lands: the ecological footprint from oil and gas development. The Wilderness Society, Washington, D.C., USA.
Wenninger, E. J., and R. S. Inouye. 2008. Insect community response to plant diversity and productivity in a sagebrush–steppe ecosystem. Journal of Arid Environments 72:24–33.
Western Regional Climate Center. 2010. Western U.S. climate historical summaries page. <http://www.wrcc.dri.edu/summary/climsmwy.html>. Accessed 15 Feb 2010.
Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51:21–41.
Wiens, J. A., and J. T. Rotenberry. 1985. Response of breeding passerine birds to rangeland alteration in a North-American shrub-steppe locality. Journal of Applied Ecology 22:655–668.
Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1985. Territory size variations in shrubsteppe birds. Auk 102:500–505.
Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48:607–615.
Wyoming Geographic Information Science Center. 2009. Wyoming GeoLibrary: Oil and Gas Leases Authorized for Wyoming. <http://www.wygisc.uwyo.edu/data.html>. Accessed 28 Aug 2009.

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POLICY PERSPECTIVE

License to kill: reforming federal wildlife control to restore biodiversity and ecosystem function

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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;

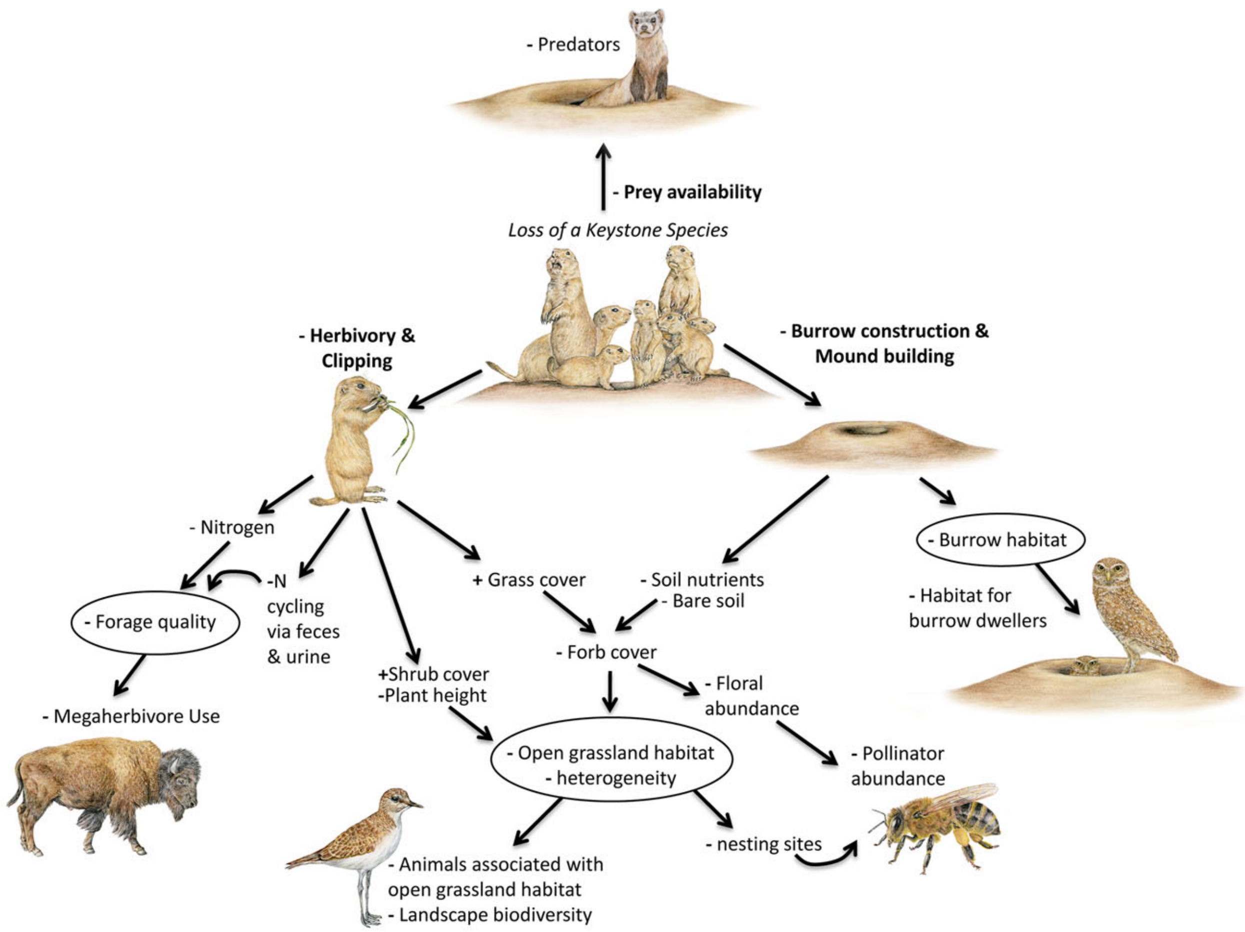

Figure 1 Conceptual diagram illustrating how the loss of a keystone species cascades throughout an ecosystem, using the black-tailed prairie dog (*Cynomys ludovicianus*) in North America's central grasslands as an example. Declines in prairie dogs result in the loss of their trophic (herbivory, prey) 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).

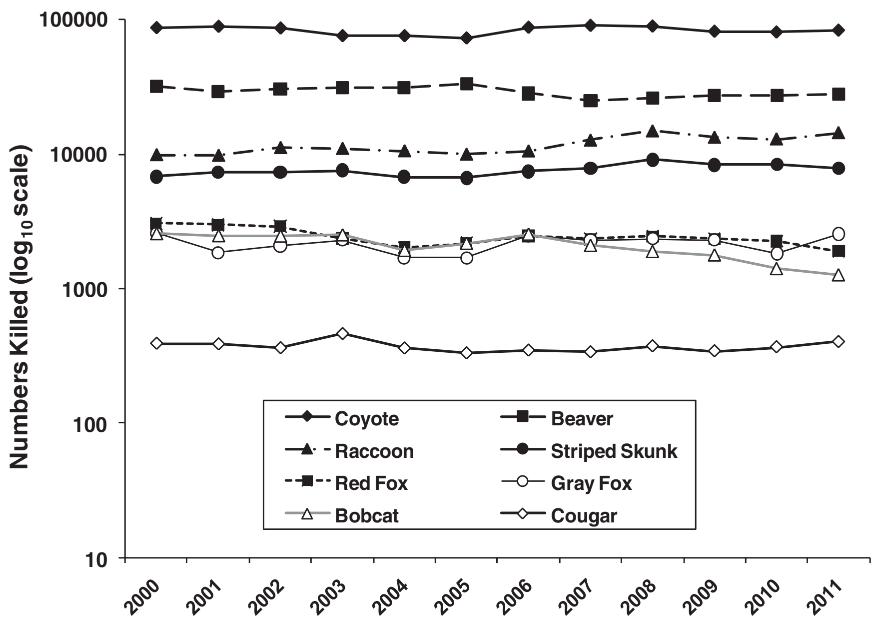

Figure 2 Numbers of the top seven species of native carnivores, plus beavers (*Castor canadensis*), killed annually by USDA-APHIS Wildlife Services from 2000 through 2011 (WS 2012a). Note: coyote (*Canis latrans*), beaver, raccoon (*Procyon lotor*), and striped skunk (*Mephitis mephitis*), in descending 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 ≤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

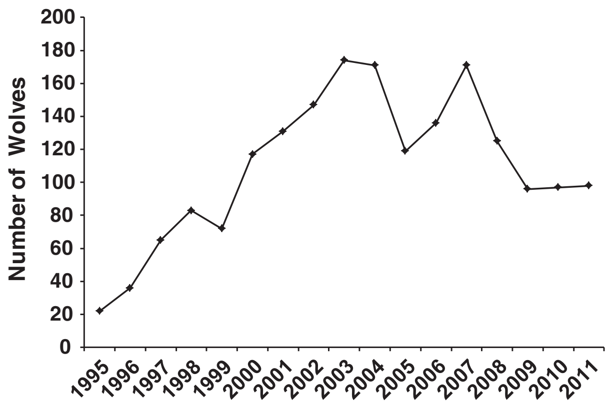

Figure 3 Annual numbers of wolves in Yellowstone National Park from initial reintroduction in 1995 and 1996 through 2011 (winter counts; data from NPS 2011; USFWS 2012b).

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.

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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.

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.

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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.

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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 $\pm 5\%$. 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*;

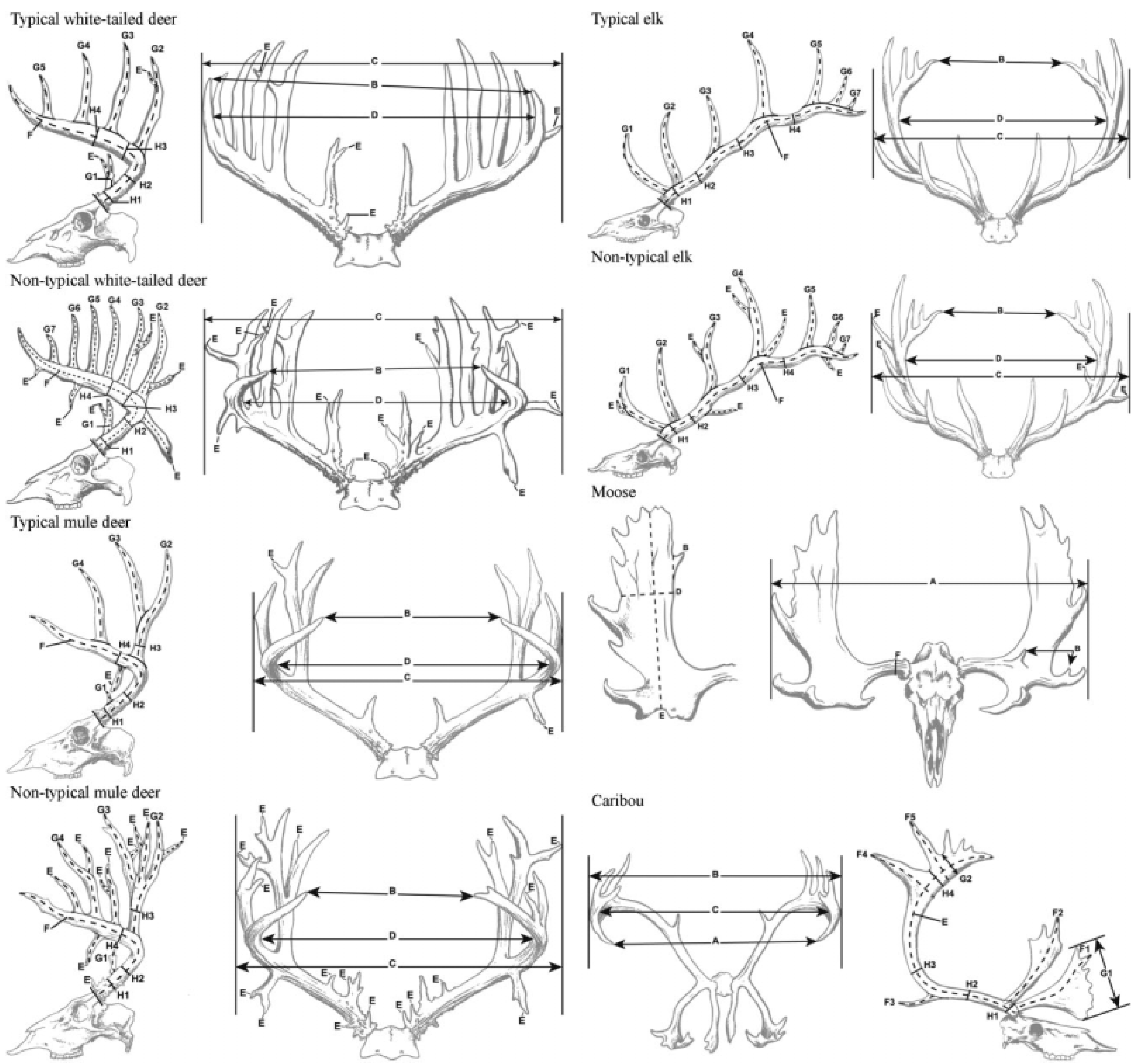

Figure 1. Illustrations of measurements of antlered game according to the Boone and Crockett scoring system. For all antlered categories except moose and caribou, total antler size comprised the sum of all D, E, F, G, and H measurements. Total antler size comprised the sum of measurements A, D, E, F, 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;

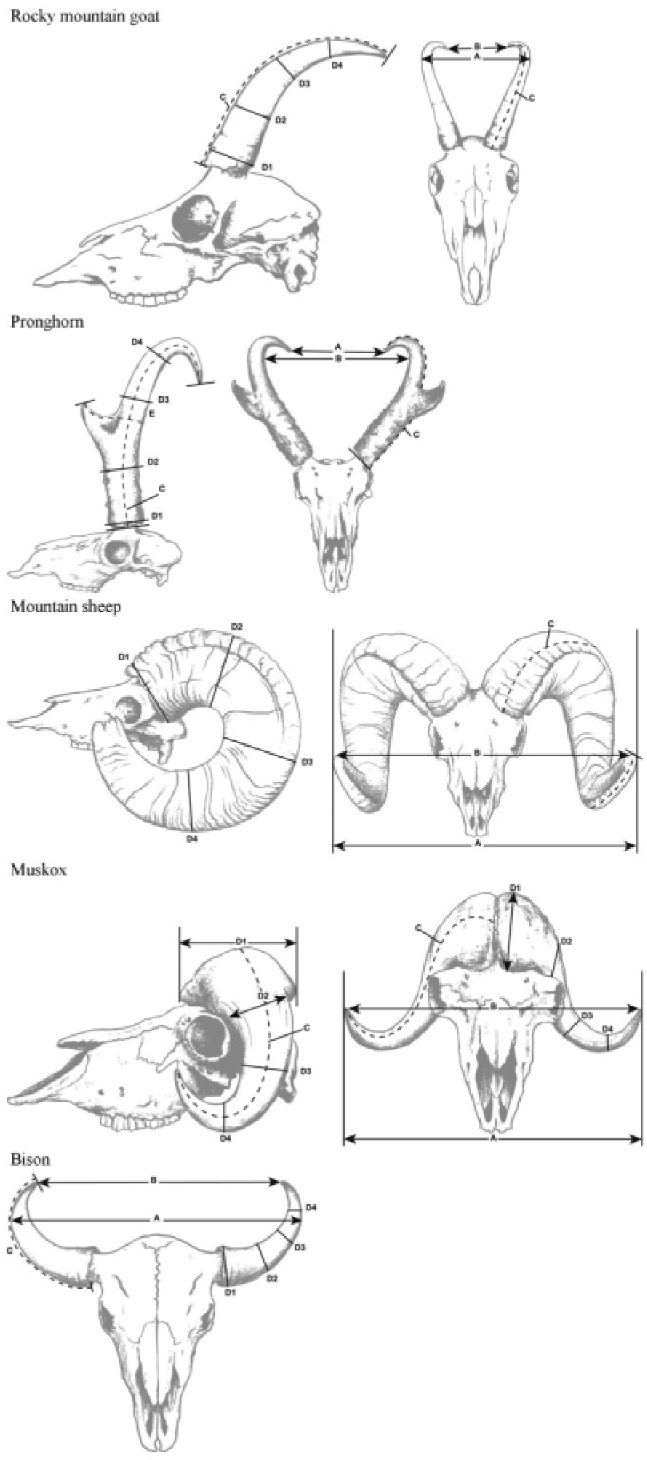

Figure 2. Illustrations of measurements of horned game according to the Boone and Crockett scoring system. Horn size comprised the sum of C and D measurements for all horned game with the exception of pronghorn, where measurement E (length of prong) was added.

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

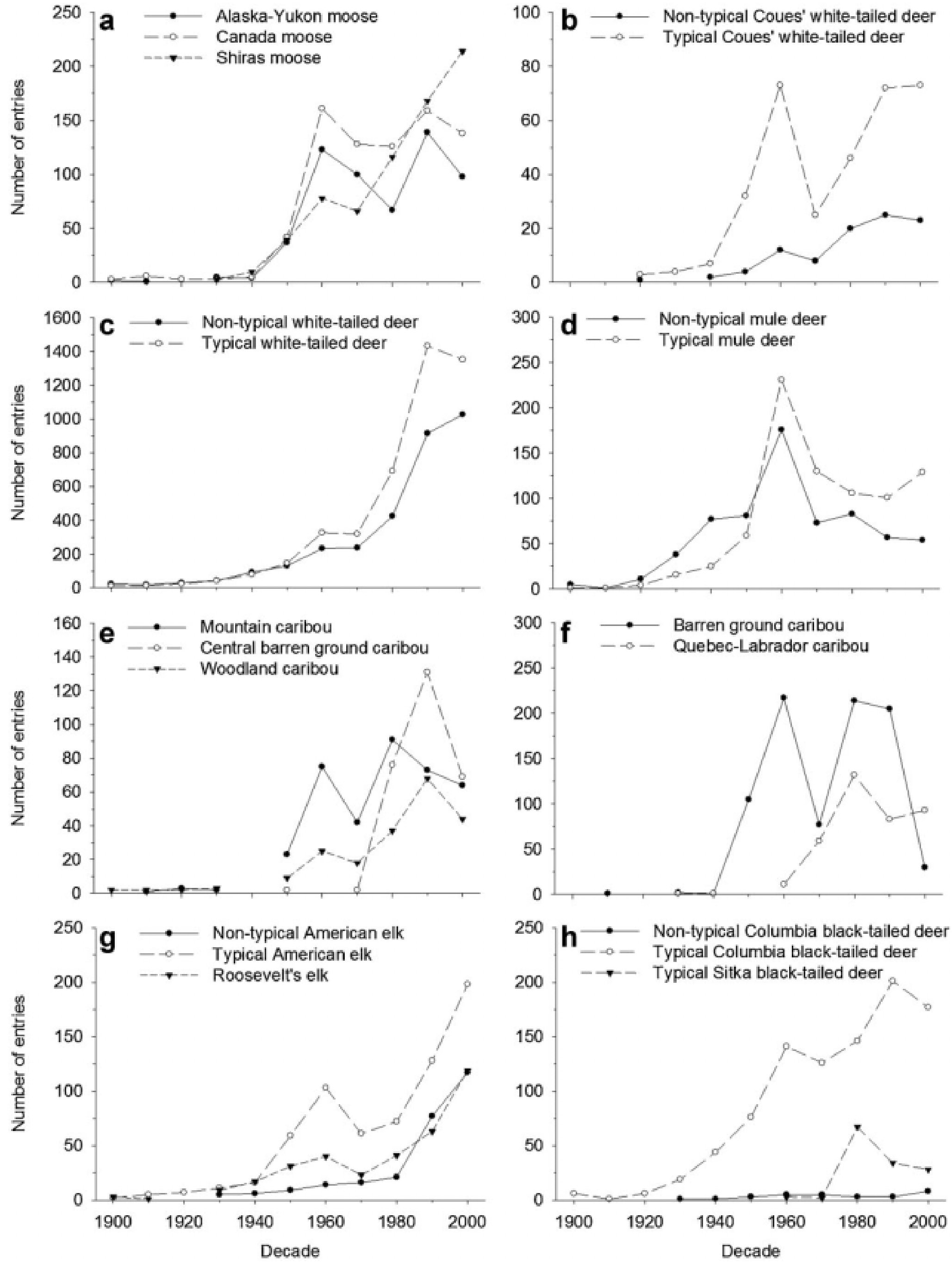

Figure 3. Decadal entries of antlered trophies recorded in Records of North American Big Game. Data points represent total number of entries for each trophy category that exceeded the highest minimum size requirement for eligibility established by the Boone and Crockett Club during the past century.

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

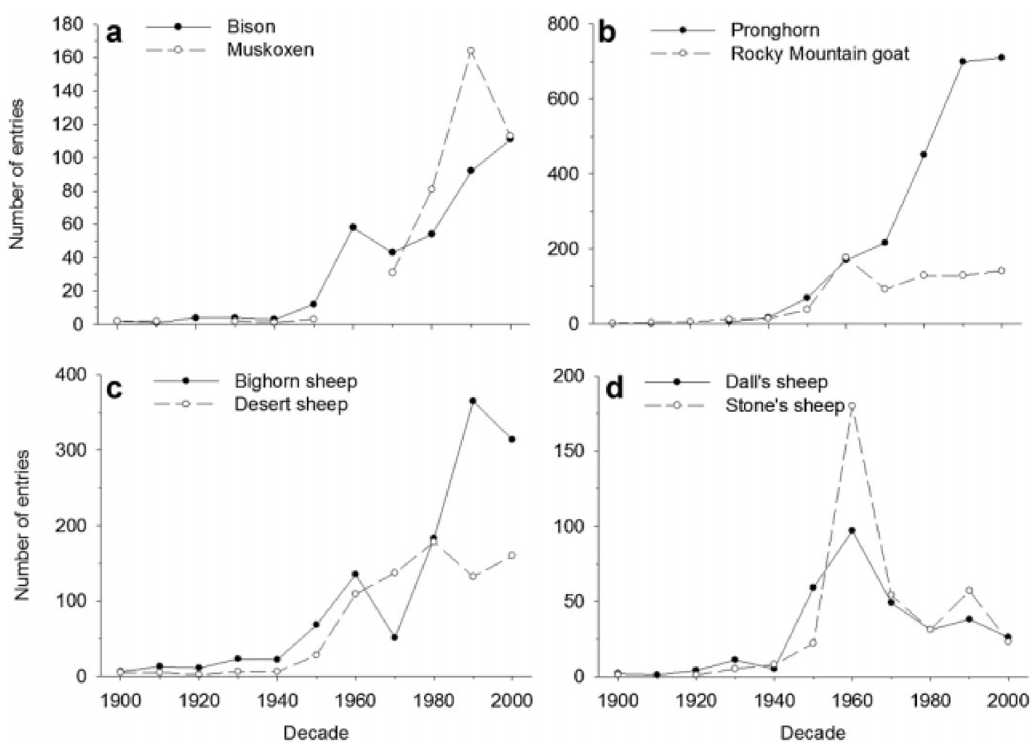

Figure 4. Decadal entries of horned trophies recorded in Records of North American Big Game. Data points represent total number of entries for each trophy category that exceeded the highest minimum size requirement for eligibility established by the Boone and Crockett Club during the past century.

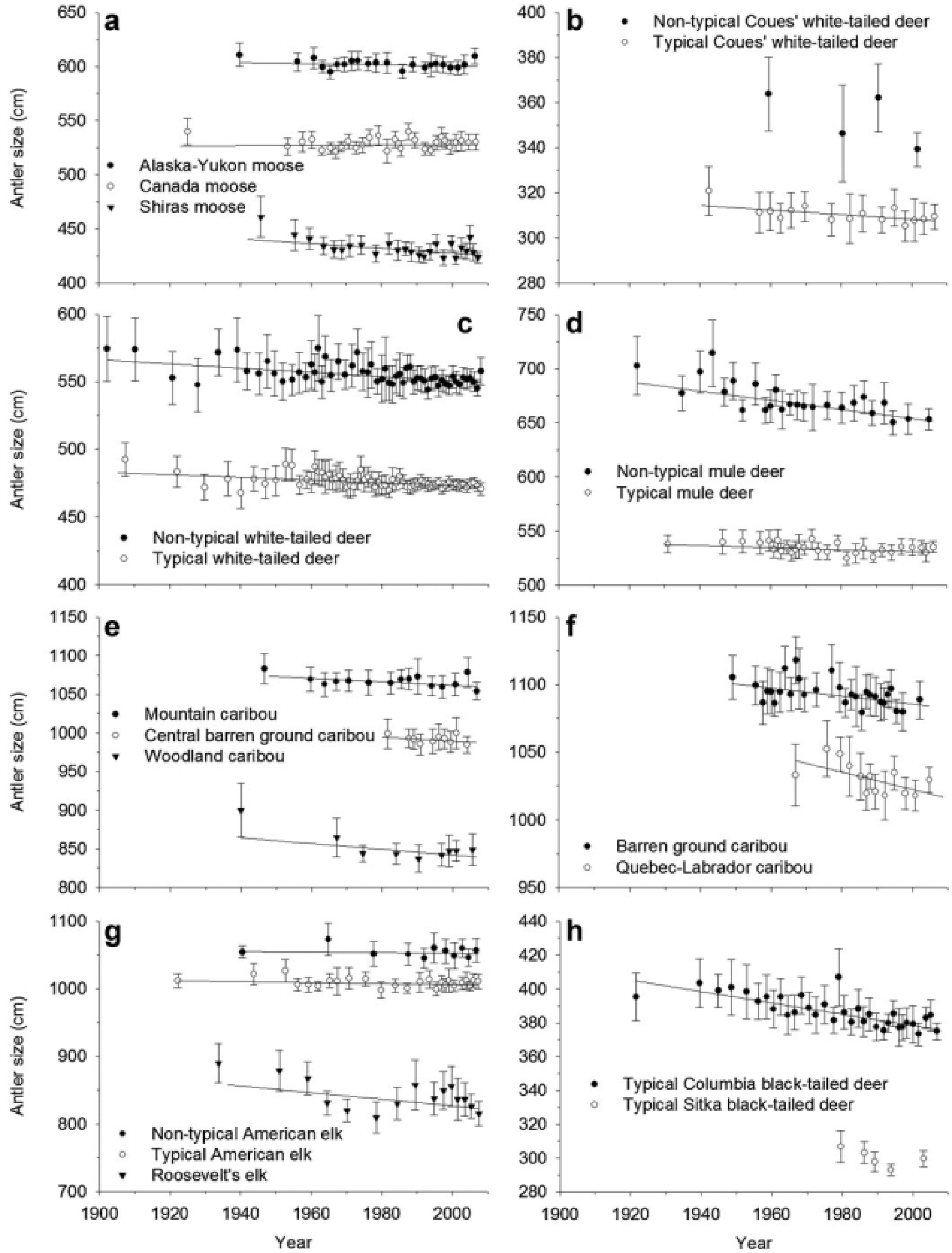

Figure 5. Temporal trends in antler size of trophies recorded in Records of North American Big Game during the past century. Data points represent mean (±95% CI) antler size (cm) of temporal bins containing a minimum of 20 samples; minimum bin size was 1 year. Lines represent fitted least-squares regressions 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).

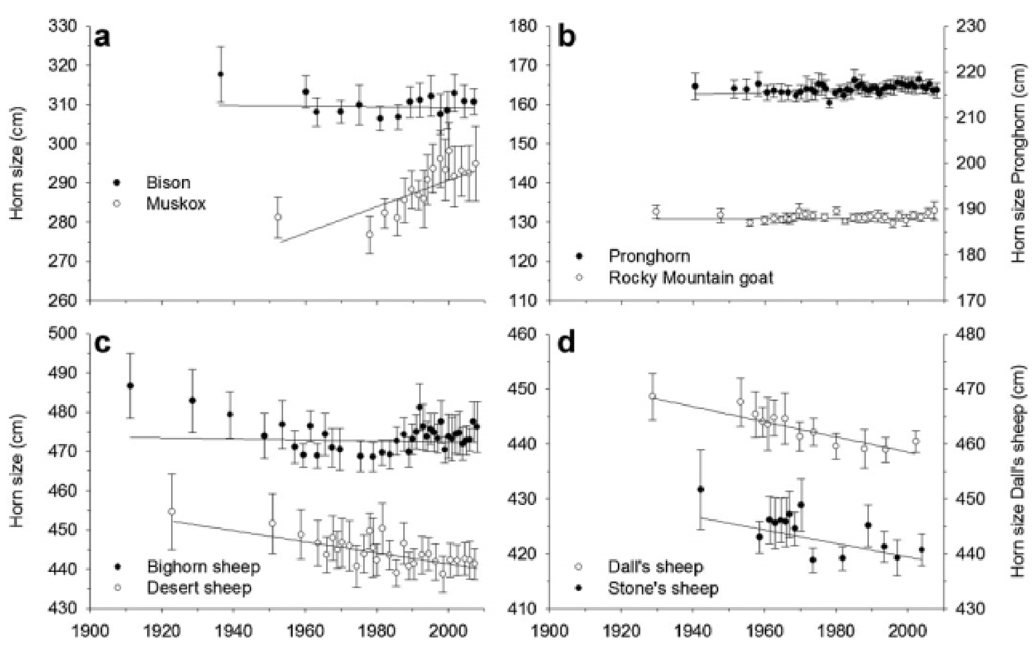

Figure 6. Temporal trends in horn size of trophies recorded in Records of North American Big Game during the past century. Data points represent mean (±95% CI) horn size (cm) of temporal bins containing a minimum of 20 samples; minimum bin size was 1 year. Lines represent fitted least-squares regressions 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

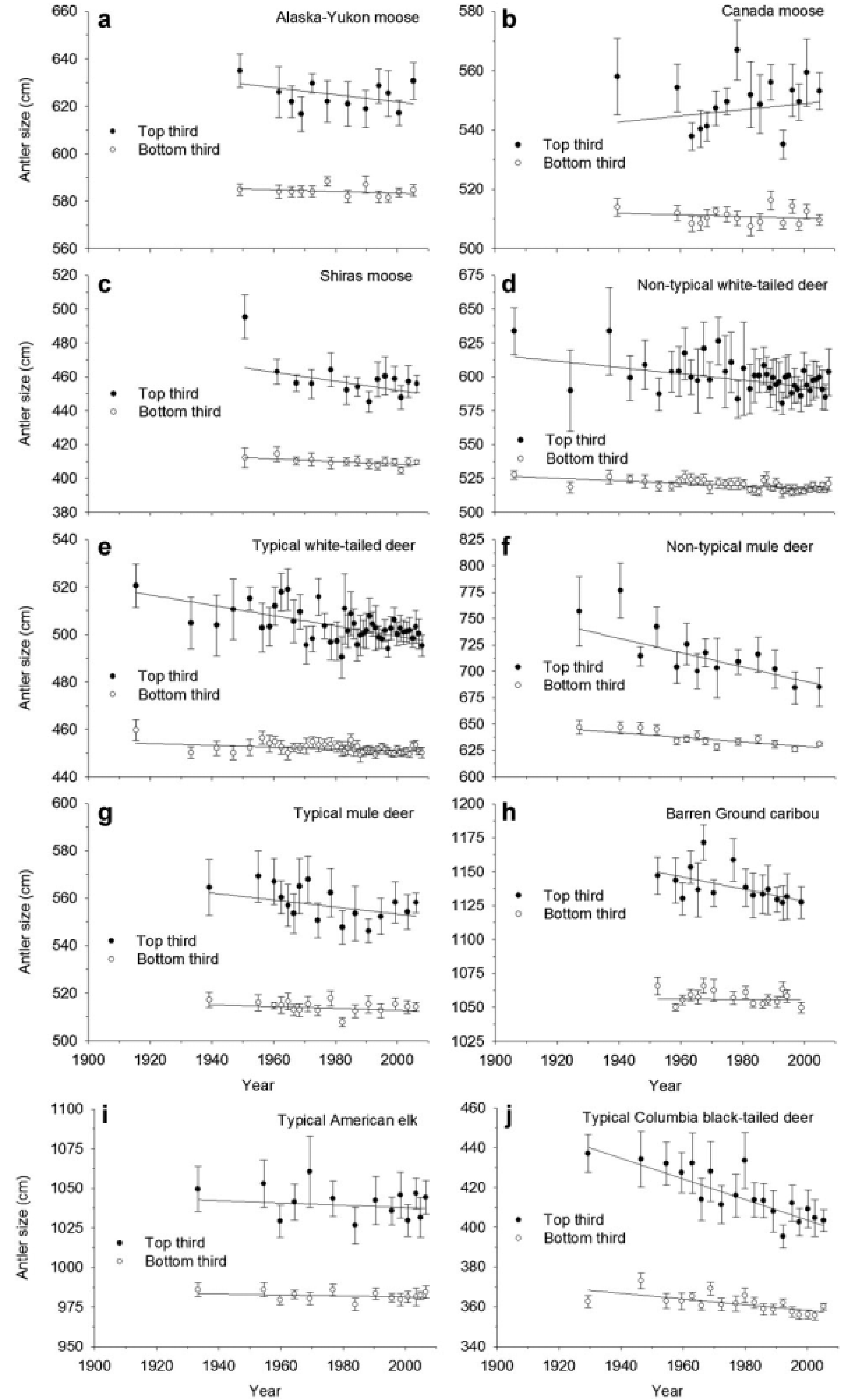

Figure 7. Temporal trends in antler size of the largest and smallest third of trophies recorded in Records of North American Big Game during the past century. Data points represent mean (±95% CI) antler size (cm) of temporal bins containing a minimum of 13 samples; minimum bin size was 1 year. Lines represent fitted least-squares regressions weighted by the inverse of the variance associated with each bin.

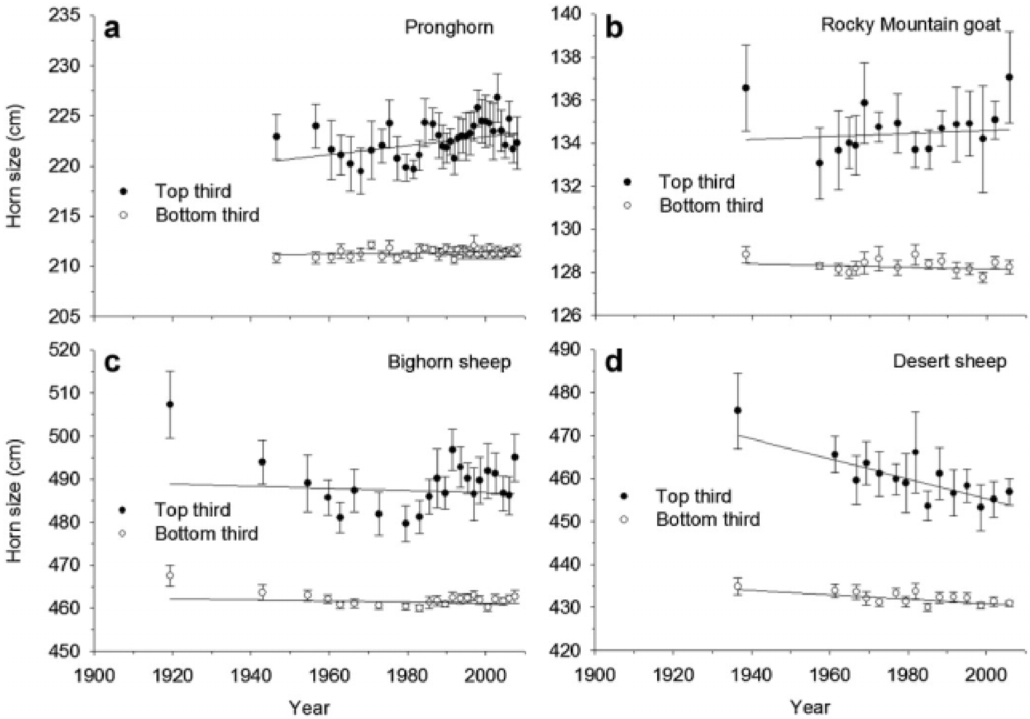

Figure 8. Temporal trends in horn size of the largest and smallest third of trophies recorded in Records of North American Big Game during the past century. Data points represent mean (±95% CI) horn size (cm) of temporal bins containing a minimum of 13 samples; minimum bin size was 1 year. Lines represent 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.

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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.

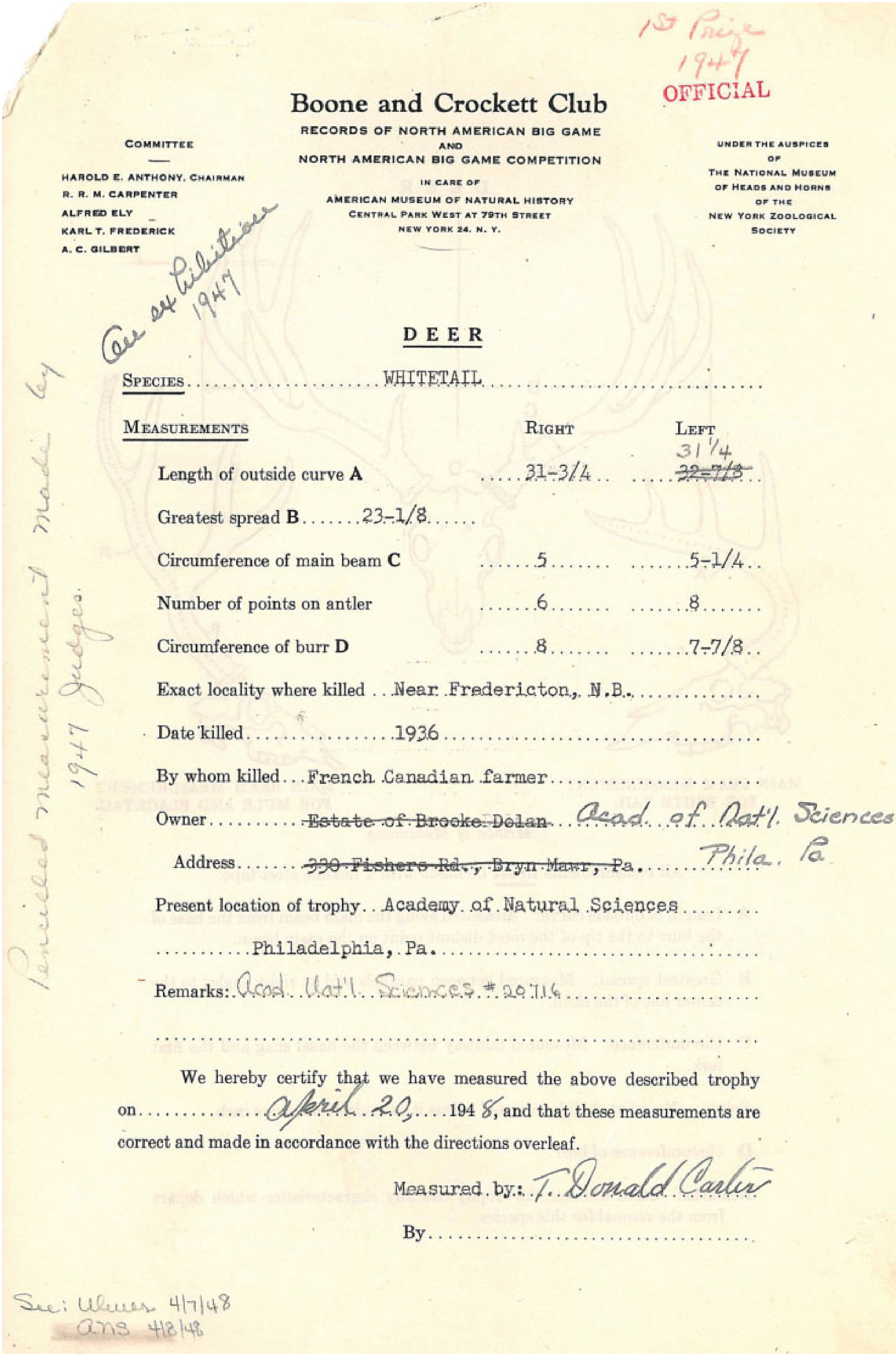
Williamson, L. F. 1987. Evolution of a landmark law. Pages 1–17 *in* H. Kallman, C. P. Agee, W. R. Goforth, and J. P. Linduska, editors. Restoring America's wildlife 1937–1987. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

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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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,....194 8, 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.

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Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone

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Research

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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.

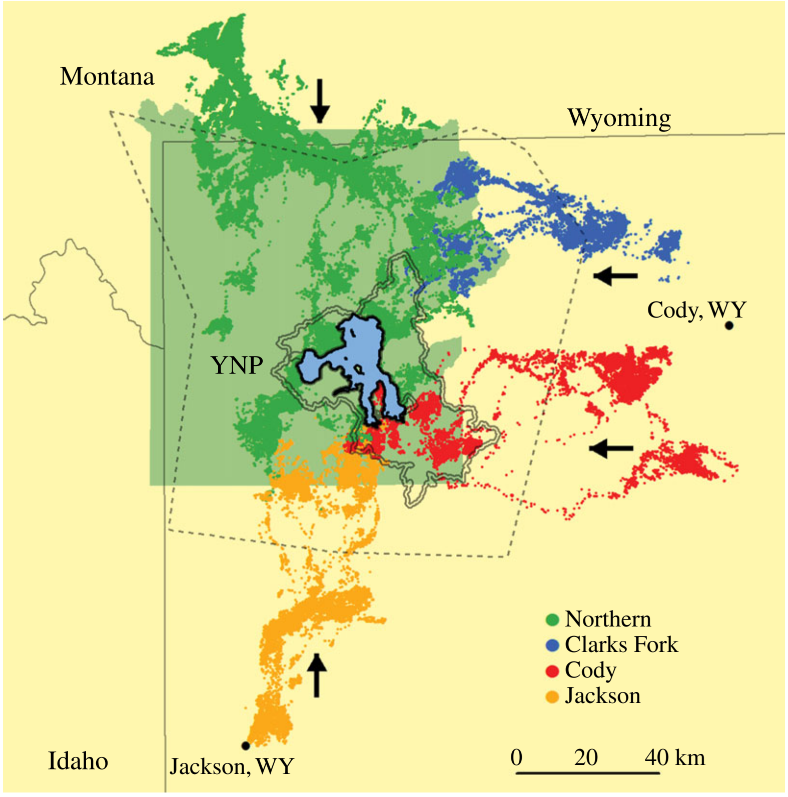

Figure 1. Individuals in four elk populations migrate each spring from outlying areas of the GYE to high-elevation summer ranges in and around the watershed of Yellowstone Lake. Here, the year-round movements of 5–10 individuals in each population are pooled to illustrate migratory movements, with a 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.

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).

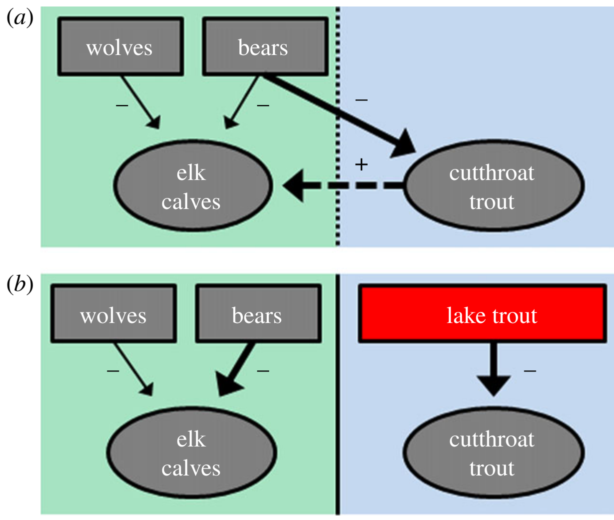

Figure 2. Focal food web interactions (*a*) before and (*b*) after the lake trout invasion in Yellowstone Lake. Predation by lake trout has driven a precipitous decline in the number of native cutthroat trout. Unlike cutthroat trout, which migrate up shallow streams to spawn, lake trout spawn on the lake bottom. Thus, the lake trout invasion has disrupted a major aquatic subsidy to terrestrial consumers, such as the grizzly bear.

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

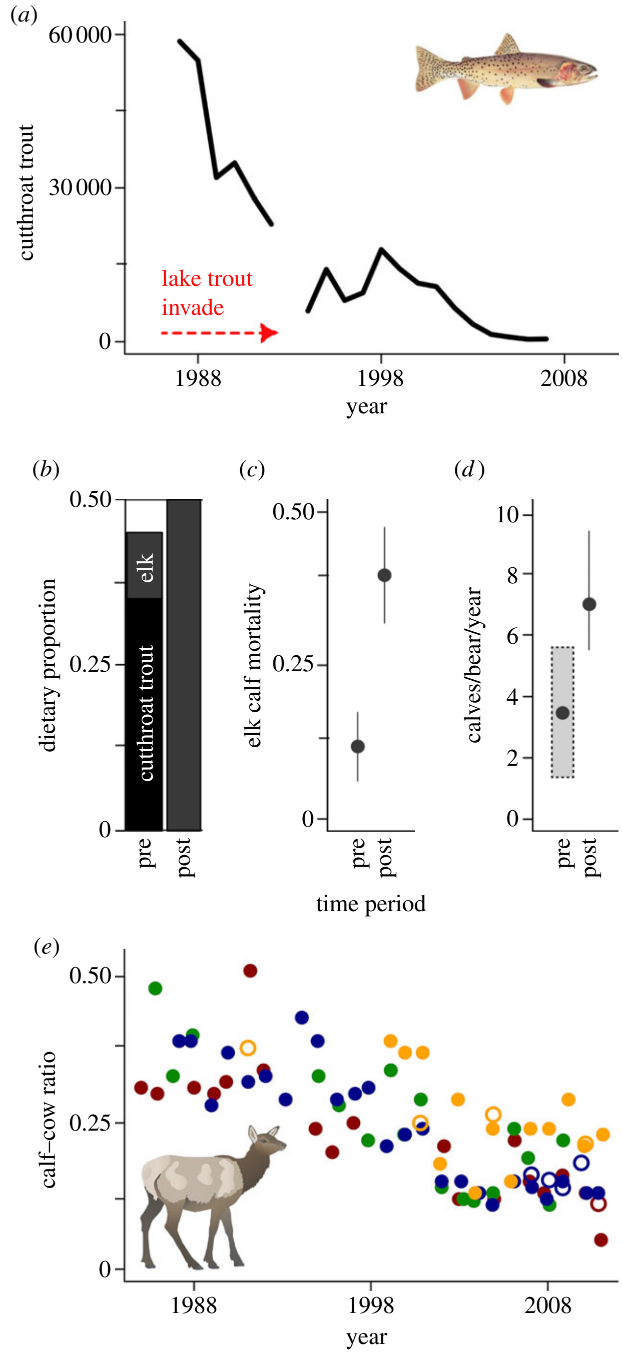

Figure 3. (*a*) Since the late 1980s, the number of spawning cutthroat trout counted each spring at Clear Creek (YNP's primary long-term monitoring site) has declined. We broadly define the 'pre-decline period' as before 1998, and the 'post-decline period' as after 1998. (*b*) In studies conducted during 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).

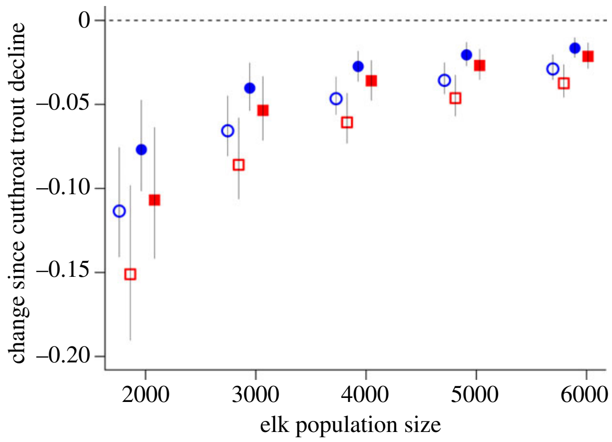

Figure 4. Predicted changes in elk calf–cow ratios (open symbols) and population growth rate (λ, closed symbols) owing to the cutthroat trout decline, using estimates based on estimated kill rates (red squares) and biomass replacement of trout with elk calves (blue circles). Elk were modelled over a 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 $\pm$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 cerebralis*, 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.

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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.

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The Malthusian–Darwinian dynamic and the trajectory of civilization

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Two interacting forces influence all populations: the Malthusian dynamic of exponential growth until resource limits are reached, and the Darwinian dynamic of innovation and adaptation to circumvent these limits through biological and/or cultural evolution. The specific manifestations of these forces in modern human society provide an important context for determining how humans can establish a sustainable relationship with the finite Earth.

Malthus, Darwin, and population dynamics

In 1798 Thomas Malthus laid out the concept of exponential population growth that became the foundation of demography and population biology. He noted that the 'increase of population is necessarily limited by the means of subsistence.' Population growth can thus continue only as long as environmental conditions remain favorable. As numbers increase, sooner or later environmental limits cause birth rates to decrease and/or death rates to increase, ultimately leading to an end to population growth. These concepts profoundly influenced Charles Darwin half a century later: because more offspring are born than can survive, only the fittest individuals reproduce and pass their superior traits on to their offspring. The result is adaption or innovation in the form of either genetic or cultural evolution.

The Malthusian dynamic pushes a population to increase until it reaches its environmental limits. The Darwinian dynamic pushes against these limits by incorporating new traits and technologies that enhance survival and reproduction. There are restrictions to this Malthusian–Darwinian Dynamic (MDD), however: it is logically, physically, and biologically impossible for exponential growth to continue indefinitely within a finite world.

Ecological and historical perspective on the rise of human civilization

Humans are an exceptional species. Our population has increased almost continuously from less than a million individuals in sub-Saharan Africa 50 000 years ago to a current population of 7 billion spanning the entire globe. The human population is projected to reach between 9 and 10 billion by 2050 [1]. In the process, humans have created complex social, technological, and economic systems. We have transformed the atmosphere, water, land, and biodiversity of the planet. We have become the most dominant single species the earth has ever seen. Our success to date is a consequence of our ability to continually develop new innovations that push back environmental limits and to transfer this information across generations (Figure 1). Operating in this way, the MDD has led to rapid cultural evolution and made possible the transition from hunter–gatherer to agricultural to industrial–technological–informational economies.

A central feature of human ecology has been the positive feedback between growth and innovation. As populations grew and aggregated into larger and more complex social groups, more information was acquired and processed. This led to new technologies that further pushed back ecological limits, allowing for continued population growth. The result has been an ascending spiral of exponential processes feeding back on each other: population growth and aggregation begot technological innovation, which in turn allowed for more resource extraction and a greater ability to overcome ecological constraints, begetting still more population growth and socioeconomic development [2].

Our ability to evade local resource shortages and population crashes through trade, migration, and innovation has allowed for continued growth not just of the global population but also of its resource use and economic activity [3]. For more than 200 years, so-called Malthusians [4] have argued, however, that this cannot indefinitely continue because essential resources supplied by the finite Earth will ultimately become limiting. This Malthusian perspective has historically been countered by so-called Cornucopians, who have argued that there is no hard limit to human population size and economic activity because human ingenuity and technological innovation provide an effectively infinite capacity to increase resource supply [5].

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Keywords: resource limitation; behavioral constraints; sustainability science; macroecology; evolutionary biology.

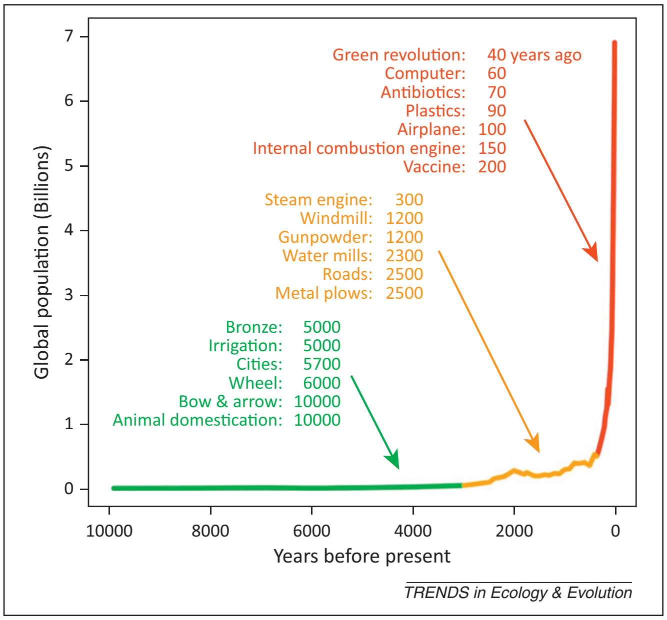

Figure 1. Global human population over the last 10 000 years. Data are based on estimates from [11], the US census bureau, and http://en.wikipedia.org/wiki/World_population_estimates. Average estimates of population size across these sources are plotted. Examples of major innovations that have helped to expand human carrying capacity (based in part on [12]) are listed for three time periods in years before present (ybp): 10 000–3000 ybp (green), 3000–300 ybp (orange), and 300 ybp–present (red).

Box 1. The MDD and challenges to global sustainability

Although the MDD has spurred innovations and adaptations that have allowed us to colonize the entire planet, it has also shaped our biological makeup, selecting for traits and behaviors that favor selfishness and may ultimately make us ill-equipped to act in concert to address global issues.

Natural selection generates the tendency for individuals to preferentially promote themselves and their families. Social groups often establish acceptable behaviors to minimize the inherent conflict between such individual self-interest and group welfare. Although disobeying group rules can result in increased individual fitness, this is counteracted by the detection and punishment of cheaters by social groups. Whether through luck or drive, some will still manage to possess a disproportionate share of resources. Although the degree of inequality can be moderated, highly asymmetric wealth distributions have proven robust to the best efforts of social philosophies and political movements to impose more egalitarian patterns [13].

All of these factors contribute to the tragedy of the commons, which occurs when selfish individuals reap the benefits from shared resources while spreading the costs across the group [14]. The increase in global atmospheric CO_2 concentrations and the reduction in global fisheries stocks (Figure 2) both represent pressing global environmental issues related to this mechanism. In the case of CO_2 emissions, individuals benefit from using carbon-based energy while global society is burdened by the costs related to increased atmospheric CO_2 concentrations. Similarly, a single fishing vessel has no incentive to curb harvests because the costs of reduced stocks are paid for by humanity as a whole. Efforts to implement and enforce international regulations to moderate these two activities have failed because of the selfishness of countries and individuals in combination with the difficulty of detecting cheating at the global scale [15].

Malthus warned of population and economic collapse in the British Isles because the exponentially increasing population would eventually outstrip linearly increasing food supplies. Although millions did die from widespread famines in Ireland and the Scottish Highlands in the mid-19th century, more widespread starvation was averted because of newly acquired agricultural technologies and emigration of people to overseas colonies [2]. As a result, the British economy did not collapse and by 1900 had become the dominant global empire. In the 1960s and 1970s Malthusians again warned that the global human population was nearing its environmental limits. Outbreaks of famine and disease did occur, but advances in agriculture, medicine, technology, and commerce – most notably the green revolution and economic globalization – pushed back the limits again and our population has more than doubled from approximately three billion in 1960 to more than seven billion today [1].

Our ability to evade previous environmental limits through the MDD should not imply, however, that such outcomes are inevitable. First, although the MDD has served as the engine for our extraordinary success, it also contains within it the potential seeds for our ultimate downfall. Motives driven by the MDD, such as selfishness and cheating, benefit individuals at the expense of society as a whole (Box 1). Second, because natural selection can only operate on current conditions, there is little tendency to recognize approaching environmental limits and curb growth before resources are overexploited [6]. Third, the assertion that adaptation and innovation will always prevent collapse – because they have in the past – is logically untenable and akin to the statistical fallacy of extrapolating beyond a data set. Whether we wish to acknowledge it or not, there are hard limits to innovation: according to the first law of thermodynamics, we cannot create energy or matter; according to the second law of thermodynamics, large energy inputs are required to maintain highly organized systems.

The ruins of Mohenjo Daro, Mesopotamia, Egypt, Greece, Rome, the Maya, Hohokam, Angkor Wat, and Easter Island are enduring evidence that many earlier societies were unable to innovate their way out of local limits and therefore collapsed despite attaining dense populations and advanced cultures. Although the proximate causes of these declines are debated and undoubtedly differ, the ultimate causes lie in an inability to sustain resource supplies and protect against parasites, diseases, and other human groups [7].

Until now, both Malthusians and Cornucopians have been correct: some populations have crashed and cultures have vanished, but our species has endured because these events have been localized. However, behavioral changes and technological innovations over the last century now intricately interconnect us in a single global society. As a result, local perturbations currently have the ability to reverberate across all of humanity. For instance, the 2008 meltdown of the USA real estate and mortgage markets and the 2011 Tōhoku earthquake and tsunami in Japan both led to global interruptions in economic activity, impacting most individuals in some way.

Within the context of our now highly globalized society, the essential question is how much potential exists for the

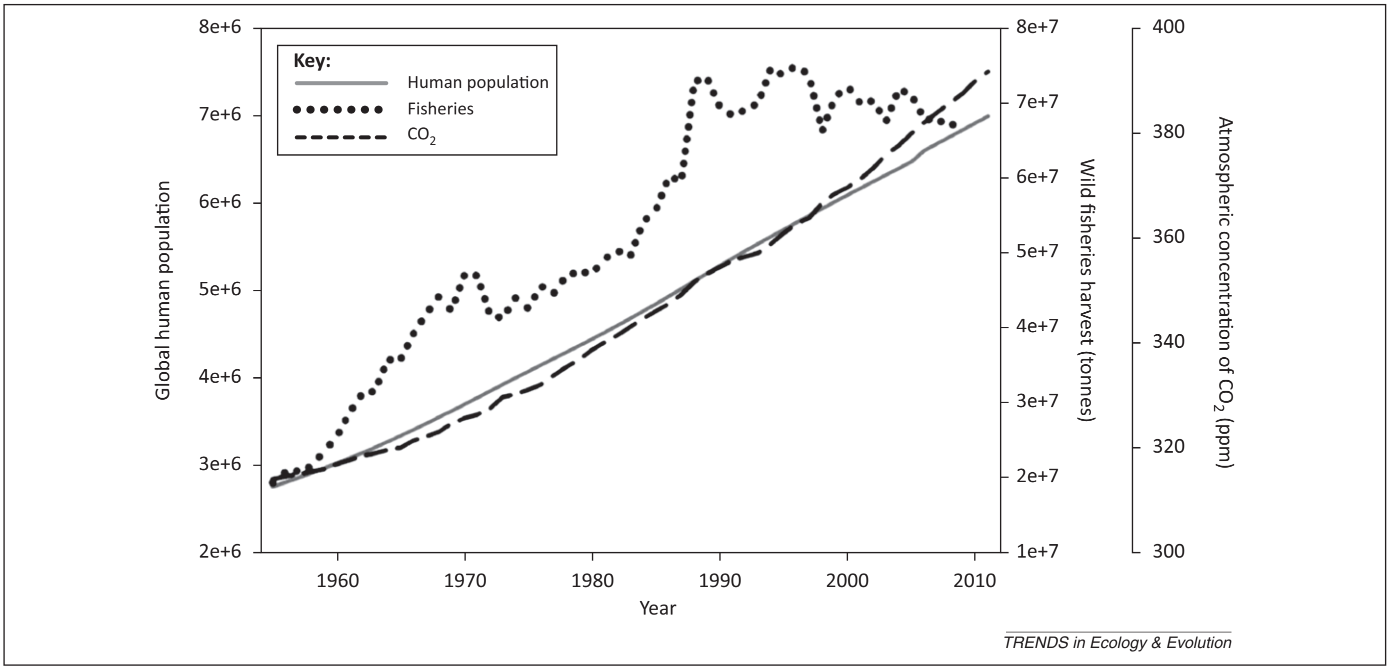

Figure 2. The trajectories of atmospheric CO_2 and wild fisheries harvest in relation to global population since 1955. Note that the increase in CO_2 concentration has accelerated, whereas fisheries harvest reached a peak in the 1990s and has since declined. The world population size is from the World Resources Institute (http://earthtrends.wri.org). The wild fisheries harvest data are from the FAO Fishery Statistical Collection Global Capture Production Database (http://www.fao.org/fishery/statistics/global-capture-production/en) and are limited to diadromous and marine species. Yearly mean CO_2 concentrations as measured at the Mauna Loa Observatory were obtained from ftp://ftp.cmdl.noaa.gov/ccg/co2/trends/co2_annmean_mlo.txt.

Darwinian side of the MDD to allow for continued adaptation and innovation to push back against global scale constraints. Many are now asking questions such as 'What are the limits to growth?' and 'What will happen when these limits are met?' [5,8].

The road forward

We cannot provide definitive answers to these questions. Contemporary human civilization is a complex adaptive system, maintained far from thermodynamic equilibrium largely via the throughput of vast quantities of increasingly exhausted fossil fuel stocks [9]. This system also requires other essential and non-substitutable commodities such as metal ores, radionucleotides, rare earth elements, phosphate fertilizer, arable land, and fresh water that are becoming ever more scarce [10]. The dynamics of such systems are highly unpredictable. Small perturbations can cause wholesale changes, including total collapse.

The bad news is that the MDD has left humans ill prepared to make the necessary ecological and behavioral changes required to avoid civilization collapse. The universal underlying biological imperatives of the MDD lie at the root of many of the most challenging impediments to long-term sustainability: exponential population growth, exploitation of all available resources, and the expression of behaviors that promote the competitive abilities of individuals, their families, and social groups over the species as a whole.

However, the good news is that the MDD may also provide valuable insights into potential solutions from both natural (in particular evolutionary biology and ecology) and social (in particular economics and sociology) science perspectives. We must recognize that a sustainable future will ultimately require: (i) negative population growth for a number of generations, followed by zero growth; (ii) a steady-state economy based on sustainable use of renewable energy and material resources; and (iii) new social norms that favor the welfare of the entire global population over that of specific individuals and groups. It is also essential that we recognize that humanity has not yet evolved the genetic or cultural adaptations needed to accomplish these tasks.

Our exceptional brains give us the ability to appreciate the present situation and envision alternate futures before catastrophe occurs. The challenge will be to facilitate a rapid cultural evolution that, for the good of the entire species, rewards individual sacrifices in fitness and quality of life. Genuine collaboration between natural and social scientists will be essential to inform society as a whole – and policy makers specifically – of this difficult but necessary adaptation required to accommodate our species in a finite and now full world.

References

1 Bongaarts, J. (2009) Human population growth and the demographic transition. *Philos. Trans. R. Soc. B: Biol. Sci.* 364, 2985–2990
2 Boserup, E. (1981) *Population and Technological Change*, University of Chicago Press
3 Hall, C.A.S. and Klitgaard, K.A. (2011) *Energy and the Wealth of Nations: Understanding the Biophysical Economy*, Springer
4 Ehrlich, P.R. (1968) *The Population Bomb*, Sierra Club/Ballantine Books
5 Simon, J.L. (1981) *The Ultimate Resource*, Princeton University Press
6 Levin, S.A. (2000) *Fragile Dominion: Complexity and the Commons*, Perseus Publishing
7 Tainter, J.A. (1988) *The Collapse of Complex Societies*, Cambridge University Press
8 Heinberg, R. (2011) *The End of Growth: Adapting to Our New Economic Reality*, New Society Publishers

9 Smil, V. (2008) *Energy in Nature and Society: General Energetics of Complex Systems*, MIT Press
10 Burger, J.R. *et al.* (2012) The macroecology of sustainability. *PLoS Biol.* 10, e1001345
11 Durand, J.D. (1977) Historical estimates of world population: an evaluation. *Popul. Dev. Rev.* 3, 253–296
12 Vermeij, G.J. and Leigh, E.G., Jr (2011) Natural and human economies compared. *Ecosphere* 2, art39
13 Chatterjee, A. *et al.*, eds (2005) *Econophysics of Wealth Distributions*, Springer Verlag
14 Hardin, G. (1968) The tragedy of the commons. *Science* 162, 1243–1248
15 Ostrom, E. *et al.* (1999) Revisiting the commons: local lessons, global challenges. *Science* 284, 278–282

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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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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*!

* * * * *

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.