Carnivore Repatriation and Holarctic Prey: Narrowing the Deficit in Ecological Effectiveness

JOEL BERGER

Teton Field Office, Wildlife Conservation Society, P.O. Box 985, Teton Valley, Idaho 83455, U.S.A., email jberger@wcs.org

Abstract: *The continuing global decline of large carnivores has catalyzed great interest in reintroduction to restore populations and to reestablish ecologically functional relationships. I used variation in the distribution of four Holarctic prey species and their behavior as proxies to investigate the pace and intensity by which responses are lost or reinvigorated by carnivore repatriation. By simulating the presence of wolves (*Canis lupus*), tigers (*Panthera tigris*), and brown bears (*Ursus arctos*) at 19 transcontinental sites, I assayed three metrics of prey performance in areas with no large terrestrial carnivores (the polar islands of Greenland and Svalbard), extant native carnivores (Eastern Siberian Shield, boreal Canada, and Alaska); and repatriated carnivores (the Yellowstone region and Rocky Mountains). The loss and reestablishment of large carnivores changed the ecological effectiveness of systems by (1) dampening immediate group benefits, diminishing awareness, and diminishing flight reaction in caribou (*Rangifer tarandus*) where predation was eliminated and (2) reinstituting sensitivity to carnivores by elk (*Cervus elaphus*) and moose (*Alces alces*) in the Yellowstone region to levels observed in Asian elk when sympatric with Siberian tigers and wolves or in Alaskan moose sympatric with wolves. Behavioral compensation to reintroduced carnivores occurred within a single generation, but only the vigilance reaction of bison (*Bison bison*) in Yellowstone exceeded that of their wolf-exposed conspecifics from boreal Canada. Beyond these overt responses by prey, snow depth and distance to suitably vegetated habitat was related to heightened vigilance in moose and elk, respectively, but only at sites with carnivores. These findings are insufficient to determine whether similar patterns might apply to other species or in areas with alien predators, and they suggest that the presumed excessive vulnerability of naïve prey to repatriated carnivores may be ill-founded. Although behavior offers a proxy to evaluate ecological effectiveness, a continuing challenge will be to understand how naïve prey respond to novel or introduced predators.*

Keywords: bison, brown bears, caribou, carnivore repatriation, ecological effectiveness, elk, Holarctic prey, moose, predator–prey relationships, reintroduction, tigers, wolves

Repatriación de Carnívoros y Presas Holárticas: Reducción del Déficit de Eficacia Ecológica

Resumen: *La declinación global de carnívoros mayores ha catalizado gran interés en la reintroducción para restaurar poblaciones y reestablecer relaciones funcionales ecológicamente. Utilicé variación en la distribución de cuatro especies de presas Holárticas y su respuesta como aproximación para investigar el paso y la intensidad a la que se pierden o refuerzan respuestas a la repatriación de carnívoros. Mediante la simulación de la presencia de lobos (*Canis lupus*), tigres (*Pathera tigris*) y osos pardos (*Ursus arctos*) en 19 sitios transcontinentales, evalué tres medidas del funcionamiento de presas en áreas sin carnívoros terrestres mayores (las islas polares de Groenlandia y Svalbard), carnívoros nativos (Siberia Oriental, Canadá boreal y Alaska) y con carnívoros repatriados (la región de Yellowstone y las Montañas Rocallosas). La pérdida y reestablecimiento de carnívoros mayores cambió la eficacia ecológica de los sistemas mediante (1) la afectación de los beneficios grupales inmediatos, disminución de alerta y pérdida de reacción de huída en caribúes (*Rangifer tarandus*) donde se eliminó la depredación, y (2) la restitución de la sensibilidad a carnívoros en alces (*Cervus elaphus* y *Alces alces*) en la región de Yellowstone a niveles observados en alces Asiáticos en simpatría con tigres y lobos Siberianos o en alces en simpatría con lobos en Alaska. La compensación conductual a carnívoros reintroducidos ocurrió en una sola generación, pero solo la reacción vigilante de bisontes (*Bison bison*) en Yellowstone*

Paper submitted May 24, 2006; revised manuscript accepted February 20, 2007.

Conservation Biology Volume 21, No. 4, 1105–1116

DOI: 10.1111/j.1523-1739.2007.00729.x

excedió la de sus congéneres expuestos a lobos en Canadá boreal. Más allá de estas respuestas de las presas, la profundidad de la nieve y la distancia a un hábitat con vegetación adecuada se relacionaron con mayor vigilancia en alces solo en sitios con carnívoros. Estos hallazgos son insuficientes para determinar si patrones similares aplican a otras especies o en áreas con depredadores introducidos, y sugieren que la supuesta vulnerabilidad excesiva de presas ingenuas a carnívoros repatriados puede estar mal fundamentada. Aunque la conducta es una aproximación para evaluar la eficacia ecológica, la comprensión de cómo responden presas ingenuas a depredadores nuevos o introducidos continuará siendo un reto.

Palabras Clave: alces, bisonte, caribú, eficacia ecológica, lobos, osos pardos, presas holárticas, reintroducción, relaciones depredador – presa, repatriación de carnívoros, tigres

Introduction

The repatriation of large carnivores to their native ecosystems will always be an emotionally charged and culturally divisive issue. Humans who incur few if any burdens associated with carnivores generally favor restoration; those living in closer proximity have greater antipathy. From perspectives steeped in conservation biology, there are two broad reasons for reintroduction: facilitation of species persistence and restoration of ecological functionality. Given at least 175 global carnivore reintroductions, remarkably few have concentrated on the latter, particularly whether the responses of prey have achieved some level of equilibrium (Gittleman & Gompper 2001). Although large carnivores have been reintroduced into fenced reserves, their repatriation has been especially divisive in the American West. Concerns have focused on the potential erosion of human harvest of big game due to losses by brown bears (*Ursus arctos*) and wolves (*Canis lupus*), and that prey naïve of carnivores may be slaughtered (Berger et al. 2001*a*). Beyond North America, however, these large carnivores are increasing in Scandinavia, France, Italy, and Eastern Europe, where concerns remain similar (Linnell et al. 2000). In Australia and elsewhere behavioral deficiencies in prey figure prominently in vulnerability to introduced predators (Short et al. 2002; Jones et al. 2004).

An understanding of the cessation and resurrection of predation as a process is relevant at three levels. First, where predation has been dampened or lost, it will remain impossible to gauge the potential for ecological recovery unless information on the magnitude of associated changes is available. This is because templates are necessary with which to compare ecological processes and assess the degree to which they deviate from "normative" conditions. In the case of carnivore repatriation one metric might be the restitution of a "normalized" relationship between prey and predator (Fig. 1). Second, given a desire to bolster biological diversity through carnivore recovery (Soulé et al. 2003), understanding mechanisms of prey readjustment can yield insights about food-web dynamics, trophic relationships, and the pace at which prey realterations, if any, occur. For instance, the extirpation of wolves and most brown bears from the Yellowstone ecosystem reduced the abundance of avian Neotropical migrants through a series of ecological cascades that involved prey release from predation, subsequent increases in herbivory, and reduced functionality of riparian systems (Berger et al. 2001b). With wolves biological diversity has increased, in part because prey are no longer as sedentary and habitat preferences have changed (Ripple et al. 2001; Fortin et al. 2005). Finally, by developing baseline information on prey ecology at sites with either extirpated or restored predators, it becomes increasingly possible to predict how systems will respond to native or alien predators (Novaro et al. 2000).

It remains unknown how Nearctic and Palearctic prey respond to the changing milieu of carnivores, for example, in Scandinavia, where raccoon dog (*Nyctereutes procyonoides*) ranges are expanding (Helle & Kauhala 1991); subcontinental Asia, where tigers (*Panthera tigris*) are being replaced locally by either leopards (*P. pardus*) or dholes (*Cuon alpinus*) (Woodroffe & Ginseberg 2005); or where the relaxation of predation serves as a selection force (Berger 1998; Blumstein et al. 2004). Irrespective of whether the process is predation or something else (Redford & Feinsinger 2002), a critical component of restoration is understanding processes by which recovery aims can be assessed.

My goal is to further this discussion by offering data on the potential for Holarctic prey to adjust to the reintroduction of large carnivores. I provide a data set that bears on ecological effectiveness by (1) comparing prey performances at replicated sites with and without repatriated carnivores, (2) conducting manipulative field experiments that alter prey perceptions of landscapes, and (3) concentrating on prey species spanning a spectrum of body sizes and associated vulnerabilities.

Rationale and Major Questions

Processes affected by predation vary from instantaneous responses of individuals to ecological dynamics and evolutionary change. At a proximate level prey behavior offers an index to assay effects of carnivore loss and restoration.

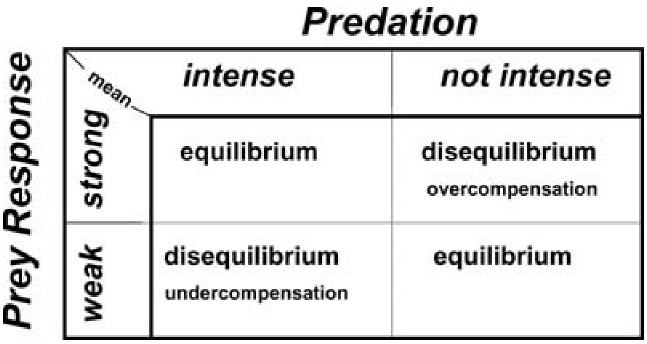

Figure 1. Predicted steady-state relationships in systems with relaxed or continuing predation. With repatriated carnivores, behavioral overcompensation may initially occur, whereas a failure to adjust (e.g., undercompensation) may result in an initial blitzkrieg.

The extent to which equilibrium conditions between prey and predator exist can be depicted by a simple model (Fig. 1). The intensity of predation and the response of prey can vary independently; thus two states arise. Equilibrium conditions reflect those in which prey are broadly adjusted to predation. A disequilibrium reflects either hypersensitivity (e.g., response cost >> response benefit) or hyposensitivity (an insufficient response). Each condition characterizes diverse species (Caro 2005) with lax or exaggerated reactions (Blumstein & Daniel 2005; Sand et al. 2006).

The issue of conservation interest, however, is not prey behavior per se but the relative responses of environments to carnivore extirpation or reintroduction. The variation between unmanipulated, intact prey–predator systems and systems lacking predation represents a deficit, the difference between what once existed and what currently exists. To detect whether equilibrium conditions exist requires comparisons of the strength of potential prey–predator interactions between areas with intact faunas and areas that have been severely altered.

To establish baseline values for putative equilibrium and disequilibrium states (Fig. 1), I measured three discrete but common antipredator behaviors: vigilance, rapid clustering of individuals when alarmed, and immediate flight. These, respectively, exemplify predator awareness, perception of individual risk, and avoidance behaviors.

The central questions I posed were, To what extent does prior intensity of predation affect prey responsiveness? and What is the strength of response to repatriation of carnivores? Answers to these questions should facilitate an understanding of what has been lost and what needs to be restored when the conservation target is the maintenance or resuscitation of prey–predator interactions.

Methods

Species, Study Areas, and Carnivore Status

I selected four Holarctic species for study based on their present occurrence in areas with and without native large carnivores (Fig. 2). Although common names vary geographically among continents, for consistency, I adopt the following: caribou (*Rangifer tarandus*); elk (*Cervus elaphus*); moose (*Alces alces*); and bison (*Bison bison*) (order reflects increasing body size).

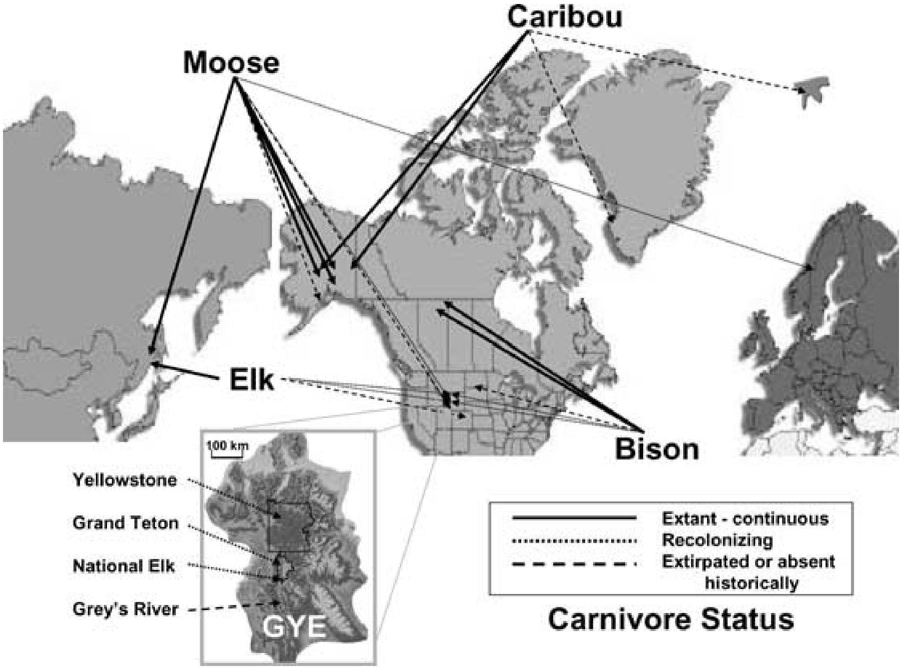

Figure 2. Overview of study regions and carnivore status by prey. Extant carnivore distribution as follows: Russian Far East, tigers, brown bears, and wolves; Alaska, wolves and brown bears except Kalgin Island; northern Alberta, wolves (additional details in Table 1). Inset is Greater Yellowstone Ecosystem (GYE).

I defined control sites operationally as those with a continuous, full suite of native large carnivores. At least two replicates were available for each species (Table 1; Fig. 2), although spatial scale may affect interpretation of true replication. For instance, Wood Buffalo National Park (WBNP) (over 44,000 km^2) is five times the size of Yellowstone National Park (YNP). If, however, bison from YNP and adjacent Grand Teton National Park (GTN) are treated as different sampling units, then bison within WBNP sampled 100 km apart can also be viewed as replicates. For elk I accessed only a single control site; a nonglaciated region of the Eastern Siberian Shield with tigers, brown bears, and wolves (Miquelle et al. 2005). Experimental sites were those with no large carnivores, either because of extirpation by humans or because of geographical isolation. For instance, caribou in southwestern Greenland and the Svalbard Archipelago have been predator free for at least 4000 years (Tyler & Oritsland 1989; Boving & Post 1997).

Sites of carnivore reintroduction or recolonization can also legitimately be considered experimental. To avoid confusion I simply refer to them as repatriated sites, of which two existed. The first was the 60,000 km^2 Greater Yellowstone Ecosystem (GYE), which includes YNP and GTN, four national wildlife refuges, and six national forests. Wolves were reintroduced to YNP in 1995, they recolonized GTN late in November 1997 and have since expanded in all directions (Smith et al. 2003). Brown bears have recolonized former ranges naturally (Pyare et al. 2004). The second repatriated site was the Dalarma–Hedmark region along the Norwegian–Swedish border (Swenson et al. 1998).

To judge the pace and strength of possible change among ungulates in the GYE, I gathered data from areas in and away from wolf settlement and contrasted results within and between control and experimental sites. Field work was conducted in the following locations and on the following species: bison, elk, and moose in the GYE (1995–2001); moose and elk in the Russian Far East (1996); elk in Colorado (2002); caribou in Alaska (1999), Greenland (2000), and Svalbard (2001); and bison in South Dakota (1996) and Canada (1998). The timing, status of carnivores, and degree of predation is summarized in Table 1 and Fig. 2.

The presumption that predation is truly relaxed when brown bears and wolves are absent will be untrue if juvenile or adult survival is reduced as a consequence of mesocarnivore release. That this is not the case has been verified for caribou, moose, and bison by studies in YNP, GTN, and adjacent regions; Alaska; mainland Norway; the Svalbard Archipelago; Sweden; Canada; and Greenland (Table 1). For elk the situation is more complex. At GTN, predation by black bears (*U. americana*) and coyotes (*C. latrans*) operates synergistically to remove about 15% of the calves per year (Smith & Anderson 1996). In Yellowstone, and presumably in Rocky Mountain National Park (RMP), these smaller carnivores and cougars (*Felis concolor*) exert some influences as well (Gese & Grothe 1995; Smith et al. 2003).

Assumptions, Experimental Protocols, and Statistical Analyses

Given islands as a model, terrestrial prey become naïve to predation risk when predators have been absent for relatively long periods (Byers 1997; Blumstein & Daniel 2005). At experimental sites I predicted prey would be less vigilant, less likely to cluster, and less prone to flight than at control sites. Covariates, such as snow depth, distance to a potential predator, and group membership each differentially influence vulnerability to predation (Hebblewhite 2005). Therefore, assuming that carnivore loss affects behavior, effects of such factors should be dampened at experimental sites. With other factors equal, support for an equilibrium model (Fig. 1) will arise if prey responses to carnivores at control and repatriated sites become similar and if prey at experimental and repatriated sites diverge.

I tested these predictions by conducting auditory playbacks and by recording individual prey responses at all sites except Dalarma–Hedmark. Sounds (approximately 90–100 db at 1 m distance of wolves, howler monkeys, running water, and tigers; Berger 1999) were broadcast from a speaker connected to a 40 W amplifier and powered by a 12-volt battery. I conducted playback sessions on windless days during late winter or early spring except in the Russian Far East (fall) and South Dakota (early summer). It may appear odd to use sounds to assay prey responses when hunting carnivores rarely advertise presence. Yet, because prey use their senses to enhance predator detection, this approach seems reasonable (Cheney & Seyfarth 1990; Gil-da-Costa et al. 2002). Only the responses of adult females were noted due to the potential confounding effects of human harvest on males, which render them more wary.

In national parks females were not hunted; beyond park boundaries hunting was either prohibited or light at my sites in Greenland, Svalbard, the Russian Far East, and the Grey's River region. Only in GTN was the shooting of elk legal. Nevertheless, for all species, except bison at Badlands, human harvest was a remote possibility because seasonal movements could transcend protected borders. My study design, which capitalized on prey reactions before and after carnivore repatriation at GTN and the National Elk Refuge and where human harvest did not change, enabled a test of the effects of wolves.

I used the procedures of Berger (1999) and Berger et al. (2001a): familiar and unfamiliar sounds as described above were broadcast in random order, each for 25 seconds. A blank no-stimulus control (Blumstein 2006) served as baseline, and these data were gathered prior to playbacks. When relevant I included as a covariate the distance to nearest cover, defined as vegetation adequate for

Table 1. Summary of carnivore status at study locations.

Species	*Site*[a]	*Carnivore(s)*	*Repatriation*	*Evidence (source)*[b]
Elk	Grand Teton National Park, WY, USA, & adjacent regions	none[c]	no, 60-year absence	sampled before wolf reintroduction (1); approximately 15%/year neonatal mortality due to coyotes & black bears (2)
	National Elk Refuge, WY, USA	none[c]	no, 60-year absence	sampled before wolf reintroduction
	Rocky Mountain National Park, CO, USA, & adjacent regions	none[c]	no, 90-year absence	(3)
	Grand Teton National Park, WY, USA & adjacent regions	wolves, brown bears	yes, November 1997	wolf diet approximately 90–95% elk starting in 1999 (4)
	National Elk Refuge, WY, USA	wolves	yes, January 1998	wolf diet approximately 90–95% elk starting in 1999 (4)
	Yellowstone National Park, WY, USA, & adjacent regions	wolves & brown bears	yes, 1995	wolf diet approximately 90–95% elk, about half being calves (5)
	Sikote-Alin Range, Primorski Krai, RU	tigers, wolves, brown bears	continuous	tiger diet approximately 60% red deer (6)
Caribou	Kangerluusquag, GL	none	no, over 4000-year absence	wolves may have never reached this region (7)
	Nordenskiold, Svalbard, NO	none	no, 5000-year absence	wolves never occurred; predation by polar bears infrequent (8)
	Denali National Park & Reserve, AK, USA	wolves & brown bears	continuous	wolves & brown bears take approximately 35% of neonates (9)
	Tetlin Wildlife Refuge & Mentasta Mountains, AK, USA	wolves & brown bears	continuous	wolves & brown bears take approximately 45% of neonates from adjacent study regions (10)
Bison	Badlands National Park, SD, USA	none	no, 90-year absence	(11)
	Grand Teton National Park, WY, USA	none	no, 90-year absence	sampled before wolf reintroduction (11)
	Yellowstone National Park, WY, USA	wolves & brown bears	yes, 1995	mean of 3.5 bison killed/year between 1995—and 1999 (12)
	Grand Teton National Park, WY, USA	wolves	yes, November 1997	not more than 3 known kills between 1997–2004 (13)
	Wood Buffalo National Park, AB & NWT, CA	wolves	continuous	two discrete areas sampled; attacks on calves not infrequent and predation inferred as strong (14)
Moose	Kalgin Island, AK, USA	none	no, 90-year absence	population introduced on predator-free island (1, 15)
	Grand Teton National Park, WY, USA & adjacent regions to south	none[c]	no, 60-year absence	sampled before wolf reintroduction (1); neonate survival to 60 days approximately 90% from 1995–99 (16)
	Grey's River & adjacent areas beyond park, WY, ID, USA	none[c]	no, 60-year absence	sampled before wolf & during wolf recolonization to the north
	Talkeetna Mountains, AK, USA	wolves & brown bears	continuous	approximately 80 – 90% neonate mortality (17)
	Denali National Park & Reserve, AK, USA	wolves & brown bears	continuous	approximately 90% neonate mortality (18)
	Grand Teton National Park, WY, USA	wolves & brown bears	yes, November 1997	recolonizing wolves and bears, increased predation on juveniles and adults (1, 19)
	Dalarma-Hedmark, N0, SE	wolves & brown bears	yes, gradually by 1990s	recolonizing bears after a 100-year absence (20), increased predation success on naïve adults (1)
	Kolumbe River Basin, Primorski Krai, RU	tigers, wolves, brown bears	continuous	moose in tiger diet (6)

[a] *Abbreviation: WY, Wyoming; CO, Colorado; RU, Russia; GL, Greenland; NO, Norway; AK, Alaska; SD, South Dakota; AB, Alberta; NWT, Northwest Territory; CA, California; ID, Idaho; SE, Sweden.*

[b] *Sources: (1) Berger 1999; (2) Smith & Anderson 1996; (3) Hess 1993; (4) Jiminez, unpublished data, U.S. Fish and Wildlife Service; (5) Smith et al. 2003; (6) Miquelle et al. 2005; (7) Melgaard 1986; Boving & Post 1997; (8) Aanes et al. 2003; Derocher et al. 2000; (9) Mech et al. 1998; (10) Orians et al. 1997; (11) Berger & Cunningham 1988; (12) Smith et al. 2000; (13) Cain unpubl, National Park Service; (14) Carbyn & Trottier 1987; Joly & Messier 2004; (15) Bowyer et al. 1999; (16) Berger unpublished data; (17) Testa 2004; (18) Bowyer et al. 1999; (19) Pyare et al. 2004; (20) Swenson et al. 1998.*

[c] *Cougars present.*

concealment, and controlled for variation in habitat with partial correlation. Only moose in GTN, Grey's River, and the Talkeetnas and elk and bison in the GTN National Elk Refuge complex were individually identifiable by distinct collars. To avoid the possibility of pseudoreplication, unidentified animals were sampled in different geographical regions within the same study site by conducting playbacks beyond the daily distances in which individuals generally move during late winter. Individuals were the sampled unit. During each playback the time an animal spent being vigilant (head up, ears erect, scanning, or standing still) per 180 seconds was noted, as was the frequency of clustering in a group and immediate site abandonment.

Two caveats about sampling protocol are relevant. First, I terminated playbacks to elk in GTP when site abandonment occurred due to deep snow. I felt it unethical to continue to add additional stress when variance in response was low and the sample ($n = 24$) appeared adequate. Second, I censored data on the effects of group size on clustering or flight at the National Elk Refuge because supplementary feeding occurs for 3–4 months a year when groups in excess of 1000 form.

I used general linear models (Norusis 2002) with a nested design in a stepwise procedure to explore the effect of study treatment (control, experimental, and repatriated). To stabilize variance for parametric tests because a large proportion of bouts were recorded as no vigilance, I added 0.5 and transformed data by square root (Zar 1996). I examined effects of covariates with multiple regression and analysis of variance and with multinomial logistic regression (χ^2 statistic and a −2 log-likelihood ratio) when dependent variables were categorical (e.g., prey clustered or did not, remained or fled). The χ^2 is the difference between the final and reduced model (Norusis 2002).

Results

Prey at Sites with and without Carnivores

Debits in the trade-off between foraging and vigilance created by the loss of predation were substantive (Figs. 3 & 4). For instance tigers, which are the primary predator of elk in the Sikote Alin Mountains, elicited the most extreme vigilance, a mean (unadjusted) response over 5 times greater than conspecifics in predator-free regions. With covariates controlled (Table 2), the difference was 8.5 times greater ($p < 0.0001$). Although Sikote Alin elk may have responded to tigers as a consequence of their diverse carnivore community, rates of vigilance before the playbacks (blind control) and among-site contrasts in vigilance behavior involving the sounds of water and howler monkeys were an order of magnitude less. Importantly, responsiveness in other systems lacking large carnivores was similarly reduced (Figs. 3 & 4; Table 2). Both caribou and moose from predator-free regions were about 3.5 times less vigilant to wolves than at control sites ($p < 0.0001$).

Bison also varied in their response to playbacks, although the magnitude of variation was low. Vigilance in bison from boreal Canada (wolves present), Badlands, and GTN (data for the latter are before wolf reintroduction) differed ($p < 0.029$); 95% confidence intervals did not

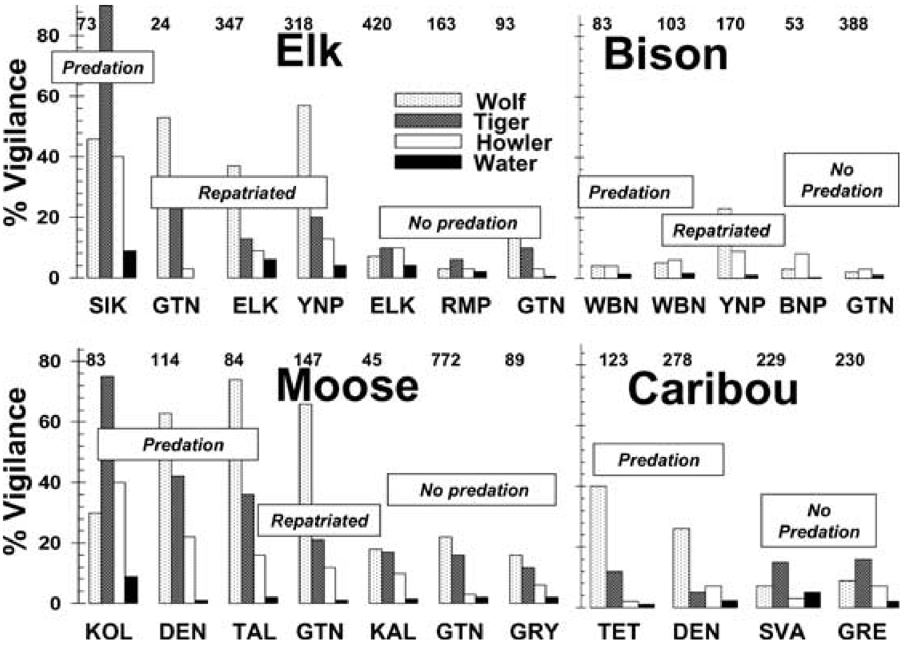

Figure 3. Untransformed mean vigilance responses of prey species to playbacks of wolves, tigers, howler monkeys, and water. Samples sizes are indicated above bars. Standard errors under all conditions for each species and site never exceeded 4.07. Site abbreviations: SIK, Sikote Alin; GTN, Grand Teton National Park (after wolves), ELK, Elk Refuge (after wolves); YNP, Yellowstone National Park; ELK, Elk Refuge (before wolves); RMP, Rocky Mountain; GTN, Grand Teton (before wolves); WBN, Wood Buffalo National Park (two sites); BNP, Badlands National Park; KOL, Kolumbe River; DEN, Denali National Park; TAL, Talkeetna: GRE, Grey's River; TET, Tetlin; SVA, Svalbard; GRE, Greenland.

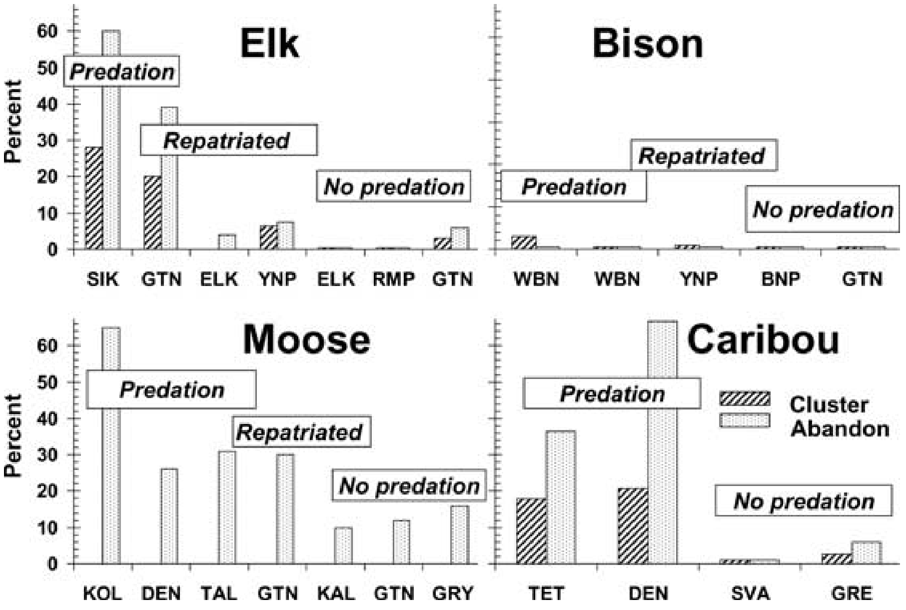

Figure 4. Percentage of prey responses to playbacks of wolves (except for Sikote Alin and Kolumbe, where tigers replaced wolves). Abbreviations of study sites are defined in the legend of Fig. 3.

overlap (wolves present: 3.4–12 CI; wolves absent −1.8 to 3.3%). The biological relevance of the small absolute differences (<10%; Fig. 3) is less clear, although these findings parallel those from the same Canadian and Badlands sites almost 20 years earlier (Berger & Cunningham 1988).

Overall, the loss of predation has resulted in decreases in both overt and subtle effects at all sites and for each prey species. The mean relative difference in response to the primary predator (Table 2) was as follows: vigilance in elk, moose, caribou, and bison—866%, 332%, 356%, and 1290%, respectively (Fig. 3); clustering in elk, caribou, and bison—1400%, 950%, and 230%, respectively (Fig. 4) (moose were excluded because they are generally asocial); and site abandonment in elk, moose, caribou, and bison—2000%, 226%, 1700%, and no difference, respectively. In addition, repatriated and control populations were more likely to cluster and abandon local sites during predator playbacks (Fig. 4; Table 3).

These results reflect immediate adjustments by prey to carnivore presence. Covariates that differed between control and experimental sites were snow depth (for

Table 2. Differences in vigilance rates (from Fig. 3) of prey species at control and experimental sites.*

Playback sound	*Species*	*Group size*		*Distance to speaker (m)*		*Snow depth (m)*		*Distance to cover (m)*		*Carnivore presence* F	n	p
Wolf	elk	3.75	0.061	4.51	0.035	—		1.65	0.200	62.59	199	0.000
	bison	0.00	0.991	5.07	0.025	0.85	0.358	3.51	0.062	4.84	222	0.029
	caribou	5.93	0.016	10.00	0.002	0.47	0.491	2.04	0.154	27.74	267	0.000
	moose	0.30	0.588	18.75	0.000	3.68	0.057	0.53	0.466	30.79	207	0.000
Tiger	elk	1.53	0.217	9.39	0.003	—		0.285	0.594	88.53	143	0.000
	bison	—		—		—		—				
	caribou	0.15	0.697	9.07	0.003	0.54	0.462	1.89	0.170	3.13	184	0.079
	moose	5.48	0.012	16.23	0.000	1.95	0.165	2.03	0.157	26.94	114	0.000
Howler monkey	elk	0.98	0.323	4.15	0.043	—		0.19	0.660	2.58	187	0.116
	bison	2.32	0.371	18.93	0.001	0.86	0.353	0.03	0.857	0.61	200	0.437
	caribou	0.04	0.835	1.83	0.178	4.80	0.003	0.59	0.442	0.41	123	0.743
	moose	3.45	0.065	14.20	0.001	0.67	0.414	0.73	0.395	12.29	112	0.001
Water	elk	0.41	0.519	30.10	0.001	—		8.03	0.005	11.25	179	0.001
	bison	4.31	0.040	0.66	0.415	1.21	0.273	0.00	0.950	0.03	136	0.859
	caribou	0.92	0.398	0.98	0.322	0.22	0.634	0.64	0.424	1.38	252	0.248
	moose	1.27	0.261	0.10	0.752	2.42	0.122	0.01	0.928	0.15	124	0.695

**Within-cell values under the third through the sixth columns of covariates are* F *and significance levels, respectively, with other factors held constant. The main factorial effect of predation treatment (carnivore presence or absence) is reflected in the last three columns (with* F *and* p *values as shown) and is based on a generalized linear model univariate procedure as described in Methods. Tiger sounds were not played to bison.*

Table 3. Effects of playback of carnivore sounds on two categorical response variables (cluster or not, abandon site or remain) examined with multinomial logistic regression (from Fig. 4).[a]

		Experimental vs. control[b]			*Experimental vs. repatriated*[b]			*Repatriated vs. control*[b]		
Species	*Response*	χ^2	*p*		χ^2	*p*		χ^2	*p*	
Elk	cluster	10.44	0.0001	0.001^{*}	0.72	0.397	0.03^{**} $0.001^{\ddagger}$	0	0.03^{*}	$0.001^{\ddagger}$
	abandon	27.03	0.0001	0.032^{*}	9.83	0.002	0.001^{**}	28.60	0.0001	0.001^{**} $0.017^{\ddagger}$
Bison	cluster	0	$0.001^{\dagger}$		0			0	$0.002^{\dagger}$	
	abandon	0			0			0		
Caribou	cluster	18.98	0.0001	0.001^{**}, $0.001^{\ddagger}$	not estimated			not estimated		
	abandon	21.02	0.0001	0.001^{*}, $0.001^{\dagger}$, 0.007^{*}	not estimated			not estimated		
Moose	cluster	insufficient response			insufficient response			insufficient response		
	abandon	6.70	0.01	$0.012^{\dagger}$	8.13	0.004		3.31	0.191	

[a] *All sites involved wolf playbacks except the Russian Far East (tigers). Main factorial effect of predation treatment is shown.*

[b] *For covariates, only statistically significant responses are shown:* **, group size;* ***, distance to habitat cover;* †*, snow depth;* ‡*, distance to speaker. Insufficient response (moose) reflects a partially nonaggregating species; zeroes (bison) indicate that site abandonment never occurred; for caribou sites of repatriation are lacking.*

caribou response to howlers); distance to vegetation cover (for elk response to water); playback distances, which affected all prey during carnivore playbacks, although effects were less for the sounds of howlers and water; and group size. Influences were, however, generally weak and significant only for caribou during wolf playbacks and for moose with tiger playbacks (Table 2). In addition, group sizes were low for caribou on polar islands; 18% and 29% of the female groups on Svalbard and Greenland (respectively, $n = 99$, 126) had two or fewer females. Solitary females and dyads did not occur at Alaskan sites. Hence, the factor that consistently discriminated between site-specific behavioral or ecological responses was coexistence in a community with large carnivores.

Prey at Sites with Carnivore Repatriation

If a component of ecological effectiveness is to be achieved by carnivore repatriation and if behavior is a reasonable proxy, then prey at sites with reintroduced (or recolonizing) predators should converge in their responsiveness to conspecifics at sites with large carnivores. During wolf playbacks each of the three species at repatriated sites became vigilant at rates equal to or in excess of those at control sites (Fig. 3). Hence, support for the above prediction is as follows. (1) For moose, despite among-site differences ($F_{2,108} = 37.60$, $p < 0.0001$), behavior of those from GTN failed to differ from either those in Denali (pairwise comparisons; $p = 0.45$) or Talkeetna ($p = 0.70$) sites. The single covariate affected by carnivore status was distance to the speaker ($F_{1,108} = 55.48$, $p < 0.0001$). (2) For elk the pattern was similar. Among-site differences in vigilance occurred ($F_{3,303} = 3.09$, $p = 0.027$), although responses to wolves did not differ among the Sikote Alin population relative to GTP ($p = 0.12$), YNP ($p = 0.97$), or the Elk Refuge ($p = 0.21$). Only group size was influenced by the treatment ($F_{1,303} = 49.87$, $p < 0.0001$). (3) Site-specific variation occurred in bison ($F_{3,131} = 6.99$, $p < 0.001$), but this was a consequence of heightened sensitivity in YNP animals to wolves ($p < 0.001$) and not due to variation between sampling regions in northern Alberta ($p = 0.994$; Fig. 3).

Although hunting by humans might confound interpretation of responses, this appears unlikely. If human harvest interacts with wolf predation to affect vigilance, differences in prey between sites with and without human hunting should be reflected as wolves invade. Nevertheless, responses by elk to wolf howls from the Elk Refuge and GTN (before wolves, hunting permitted) and RMP (no wolves and no hunting) did not differ (Fig. 3; $F_{2,166} = 0.623$, $p = 0.538$; GLM univariate model with a post hoc test for site effects). Likewise, moose at KAL and GRY (no wolves and light hunting) and GTN (before wolves and no hunting) also did not differ with wolf playbacks ($F_{2,39} = 1.745$, $p = 0.189$) and water ($F = 0.106$, $p = 0.900$). These results suggest human harvest history has not exacerbated responses to wolf recolonization.

Discussion

Ecological Effectiveness and Behavioral Deficits

A system is ecologically effective if the functional relationships among its species are maintained (Pyare & Berger 2003; Soulé et al. 2003). Although precise definitions are difficult to delineate, examples are many (Ripple et al. 2001; Smith et al. 2003). For mammalian carnivores these include trophic-level consequences resulting from the cessation of predation by species such as sea otters (*Enhydra lutris*) and jaguars (*P. onca*) (Terborgh et al. 2001; Estes et al. 2004). Similar empirical support exists for temperate and boreal landscapes (McLaren & Peterson 1994; Berger et al. 2001b; Ray et al. 2005).

Each of the three prey species I examined in areas repatriated by carnivores showed evidence of rapid responses to carnivore presence, despite their subtle and large differences in body size, social systems, and ecological relationships. For moose, behavior changed within a single generation, approximating the responsiveness found in Alaskan control populations. For elk and bison similar changes occurred following repatriation, although appropriate spatial and temporal baselines were not established in YNP. Nevertheless, data were collected before wolves and brown bears were reestablished at GTN and other regions south or west of Yellowstone. In addition, both elk and bison in areas of wolf repatriation displayed increased reactions relative to conspecifics in predator-free zones (Figs. 3 & 4). Fine-grained observations of foraging rates in bison and elk in and away from wolf home ranges in Yellowstone are similarly consistent with behavioral modifications (Laundre et al. 2001). In YNP and GTN, where wolf densities are relatively high (Smith et al. 2003; Berger & Smith 2005), levels of vigilance among elk approximate those in Russia.

The presence of carnivores does not, however, guarantee instantaneous changes in prey for at least two reasons. First, ecological interactions may be threshold dependent (Estes & Duggins 1995). Where carnivore densities are excessively low, prey responses may be limited, a topic for which theory outstrips empiricism. Second, even where carnivore densities approximate some threshold for ecological effectives, responses may be species specific. Moose, for instance, that lost neonates to sources other than predation, despite sympathy with wolves, responded to cues in ways similar to moose living without predation (Berger et al. 2001a). This point underscores the frailty of tacit assumptions involving carnivore repatriation and ecological effectiveness. If ample diverse prey are available yet predators specialize on one form, then the fuller suite of interactions anticipated for other species may not occur, at least swiftly. In Grand Teton and on the National Elk Refuge, high elk densities apparently buffer moose and bison from predation. Hence, despite sympatry with large carnivores the latter two species are not very vigilant. On the other hand, ecological effectiveness may involve substantive time lags as one species becomes rare and another favored, as hypothesized to explain the shift in the prey by killer whales from seals to otters (Estes et al. 2004).

Prey responses to carnivores may approach conditions that deviate far from or reflect a broad level of relative adjustment (Fig. 1). Undercompensation (a disequilibrium situation) must initially be occurring along carnivore colonizing fronts or with carnivore reintroduction, as suggested by exacerbated predation rates on adult moose by brown bears and naïveté toward wolves (Berger et al. 2001a). But, overcompensation also occurs (Figs. 3 & 4; Table 2). At some point, however, as with African ungulates, excessive wariness subsides (Fitzgibbon 1989; Caro 1999) as once overvigilant prey return to a more typical nonchalant situation unless under direct attack. This sort of behavioral transition may explain the reduced vigilance rates of boreal bison that have coexisted with wolves relative to conspecifics in Yellowstone.

Insights from Systems with Alien and Repatriated Carnivores

Relaxed predator-induced selection affects the behavior of island forms (Blumstein et al. 2002; Blumstein & Daniel 2005). The changes I describe, however, arose in terrestrial systems but not as a consequence of prolonged geological or geographic isolation; rather, these changes occurred within 10–20 prey generations. Nevertheless, naïveté remains an important issue in the conservation of biodiversity, primarily because the global proliferation of nonnative carnivores continues (Reed 1999; Short et al. 2002).

Beyond desires to reestablish ecologically functioning systems by carnivore repatriation, this goal may be unrealistic in many if not most systems. Nevertheless, understanding predator recognition by prey is relevant to conservation in two principal ways (Table 4). First, with appropriate data on the capacity of prey to respond to predators, native or not, decisions can be rendered about how best to commit time and resources to problem solving. On Svalbard and Greenland, for example, caribou are relatively oblivious to the cues of predators with which they coevolved but have now been long isolated (Melgaard 1986; Van der Knap 1986). Yet, in southeastern Quebec, where wolves were recently replaced by coyotes, predation rates on the calves of coyote-naïve caribou are relatively high (Crete & Desrosiers 1995). If caribou mothers are at a behavioral disadvantage, demographic consequences will be severe. Second, where antipredator responses persist as a consequence of multiple predators rather than a single specialist (Blumstein 2006), concerns about devastating alien effects may be dampened because recognition of a general predator is possible (see Table 4 for further examples). Knowing whether this occurs will help enable predictions about possible adaptive responses or enhanced vulnerability of prey species, particularly given the challenges of future systems with increasing arrays of alien carnivores (Table 4).

Ecological Effectiveness and Carnivore Repatriation

In areas where carnivores have been lost, repatriation is generally favored as the most efficient means to restore ecological processes (Soulé et al. 1999; Ripple & Beschta 2004), although other tools are available (Ray et al. 2005). When large carnivores facilitate but do not control biodiversity, there may be routes to ecological effectiveness other than repatriation. First, apparent guild redundancy may occur in communities where one predator has been replaced by another (Woodroffe & Ginseberg 2005), and, in some circumstances, these may be simple cases of mesocarnivore release (Crooks & Soule 1999). Whether carnivore turnover alters prey responsiveness

Table 4. Behavior or demographic responses of mammalian prey to carnivore loss, repatriation, or replacement.[a]

Carnivore species (source)[b]	*Predation pressure*	*Prey species*	*Location*[c]	*Response*	*Comment*	*Evidence*	*Ecological insight*
Wolves* (1)	relaxed	caribou	Greenland & Svalbard	group size effects, reduced vigilance & flight	habitat productivity unmeasured	experimental, comparative	possible predation-mediated density through grouping
Thlyacines (2)	relaxed	kangaroos & wallabies	Australia & small associated isles	group size effects variable	effects of different predators tested	experimental, comparative	unclear
Tigers & leopards (3)	relaxed	macaques	Sumatra, Indonesia	group size effect	habitat quality not examined	comparative	unclear
Cougars (4)	recent range expansion	porcupines	Great Basin Desert, USA	population extirpation	behavioral capacity unclear	observational	population persistence challenged
Coyotes (5)	recent range expansion	caribou	Southern Quebec, Canada	high neonate mortality	behavioral capacity unclear	observational	population persistence challenged
Lynx (6)	repatriated	roe deer	Alps, Switzerland	high mortality along colonizing front	behavior unclear	observational	possible alterations in behavior
Leopards (7)	repatriated	vervet monkey	Amboseli, Kenya	high initial mortality	subsequent behavioral adjustment	observational	possible habitat use modified by foraging-predation trade-offs
Brown bears* (8)	repatriated	moose	Southern GYE, USA	olfactory astuteness	mothers with neonate loss only	experimental & observational	Habitat use modified by predation
Brown bears (9)	repatriated	moose	Darma-Hedmark, Scandinavia	high initial mortality	naïveté presumed	observational	possible alterations in behavior
Wolves* (9)	repatriated	moose	Alaska & GYE	vigilance enhanced	mothers with neonate loss only	experimental & observational	habitat use modified by predation
Wolves* (10)	repatriated	elk	Yellowstone Park, USA	altered habitat use & movement	hypersensitive behavior	experimental & observational	modified habitat use facilitates trophic cascade
Wolves* (11)	repatriated	bison	Yellowstone Park, USA	modified vigilance		experimental & observational	unclear
Harpy eagle (12)	repatriated	howler monkey	Barro Colorado, Panama	modified vigilance		experimental	possible habitat use modified by predation
Humans (13)	replacement	moose	Norway & Alaska, USA	change in aggressiveness		observational	possible habitat use modified by predation
Dingo (14)	naturalized or alien?	tammar wallaby	Australia & New Zealand	loss of group size effect	auditory & recognition models	experimental	possible habitat use modified by predation
Red fox (15)	alien	eastern quolls	Tasmania	reduced recognition capabilities		experimental	population persistence challenged
Red fox (16)	alien	wallabies & bettongs	Multiple sites, Australia	surplus killing common	behaviorally naïve	historical	population persistence challenged
Lions, hyenas, & humans (17)	recent (alien ?)	black rhinos	Etosha, Namib Desert, Namibia	increased flight to humans	hypersensitive to humans	comparative	possible redistribution across landscapes

[a] *Predation pressure is species specific.*

[b] *Sources: (1) Boving & Post 1997; (2) Blumstein et al. (2005); (3) van Schaik & von Noordwijk 1985; (4) only males remained, population functionally extinct, Sweitzer et al. 1997; (5) Crete & Desrosiers 1995; (6) Breitenmoser & Haller 1993; (7) Isbell 1990; (8) Pyare & Berger 2003; (9) Berger et al. 2001a; (10) Creel & Winnie 2004; Fortin et al. 2005; (11) Laundre et al. 2001; (12) Gil-da-Costa et al. 2002; (13) Sand et al. 2006; (14) Blumstein et al. 2002; (15) Jones et al. 2004; (16) Short et al. 2002; (17) Berger & Cunningham 1995; asterisk (*) indicates data from this study.*

[c] *Greater Yellowstone Ecosystem, GYE.*

at one tier and ecological effectiveness at a broader level awaits investigation. Second, replacement of carnivores by humans occurs globally (Festa-Bianchet 2003), and these substitutions are often used to justify us as predators. If humans are functionally redundant behaviorally and ecologically, then by definition prey should respond similarly. Evidence suggests that where hunting by humans occurs, prey became hypersensitive (Bender 1999; Caro 1999). Nevertheless, stunning variation also occurs in the timing, extent, and strength of predation by human hunters and by carnivores. Large dissimilarities in ecological effectiveness are the consequence (Berger 2005).

Although carnivore restoration is often desirable, it is no longer feasible in most landscapes. Where impossible, perhaps the best that can be done for restoring operationally functional systems is to recognize what can and what cannot be achieved and, subsequently, to face the difficult decision about where best to allocate efforts that matter most. Where repatriation is possible, however, the approach outlined here offers one way to judge the first signs of ecological effectiveness.

Acknowledgments

For grant or logistical support, I thank the Charles Engelhard and National Science foundations, the National Park Service (Grand Teton), the U.S. Fish and Wildlife Service (National Elk Refuge), Parks Canada (Wood Buffalo National Park), Wyoming Game and Fish, Alaska Fish and Game, Greenland Department of Home Rule, and the Governor's Office of Svalbard. For additional help I am grateful to R. Aanes, K. Berger, R. T. Bowyer, S. Cain, L. Carbyn, D. Craighead, C. Cunningham, J. Goodrich, M. Reid, T. Roffe, J. W. Testa, W. Weber, K. White, O. Zaumyslova, and the comments of three unknown reviewers.

Literature Cited

Aanes, R. 2003. Synchrony in Svalbard reindeer population dynamics. I: Canadian Journal of Zoology **81:**103–110.

Bender, L. C., D. E. Beyer Jr., and J. B. Haufler. 1999. Effects of short-duration, high intensity hunting on elk wariness in Michigan. Wildlife Society Bulletin **27:**441–445.

Berger, J. 1998. Future prey: some consequences of losing and restoring large carnivores. Pages 80–100 in T. Caro, editor. Behavioral ecology and conservation biology. Oxford University Press, Oxford, United Kingdom.

Berger, J. 1999. Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. Proceedings of the Royal Society **266:**2261–2267.

Berger, J. 2005. Hunting by carnivores and by humans: is functional redundancy possible and who really cares? Pages 316–341 in J. Ray, K. H. Redford, R. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island Press, Covello, California.

Berger, J., and C. Cunningham. 1988. Size-related effects on search times in North American prairie ungulate females. Ecology **69:**177–183.

Berger, J., and C. Cunningham. 1995. Predation, sensitivity, and sex: why female black rhinoceroses outlive males. Behavioral Ecology **9:**57–64.

Berger, J., and D. Smith. 2005. Restoring functionality in Yellowstone with recovering carnivores: gains and uncertainties. Pages 100–109 in J. Ray, K. H. Redford, R. Steneck, and J. Berger, editors. Large carnivores and conservation of biodiversity. Island Press, Covello, California.

Berger, J., J. E. Swenson, and I. Per-Illson. 2001a. Re-colonizing carnivores and naive prey; conservation lessons from Pleistocene extinctions. Science **291:**1036–1039.

Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson. 2001b. A mammalian predator-prey imbalance: grizzly bears and wolf extinction affect avian Neotropical migrants. Ecological Applications **11:**947–960.

Blumstein, D. T. 2006. The multipredator hypothesis and the evolutionary persistence of antipredator behavior. Ethology **112:**209–217.

Blumstein, D. T., and J. C. Daniel. 2005. The loss of anti-predator behaviour following isolation on islands. Proceedings of the Royal Society **272:**1663–1668.

Blumstein, D. T., M. Mari, J. C. Daniel, J. G. Ardron, A. S. Griffin and C. S. Evans. 2002. Olfactory predator recognition: wallabies may have to learn to be wary. Animal Conservation **5:**87–93.

Blumstein, D. T., J. C. Daniel, and B. P. Springett. 2004. A test of the multi-predator hypothesis: Rapid loss of antipredator behavior after 130 years of isolation. Ethology **110:**919–934.

Boving, P. S., and E. Post. 1997. Vigilance and foraging behaviour of female caribou in relation to predation risk. Rangifer **17:**55–63.

Bowyer, R. T., V. Van Ballenberghe, J. G. Kie, and J. A. K. Maier. 1999. Birth site selection by Alaskan moose: strategies for coping with a risky environment. Journal of Mammology **80:**1070–1083.

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.

Breitenmoser, U., and H. Haller. 1993. Patterns of predation by reintroduced European lynx in the Swiss Alps. Journal of Wildlife Management **57:**135–144.

Byers, J. A. 1997. American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Chicago.

Carbyn, L. N., and T. Trottier. 1987. Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. Canadian Journal of Zoology **65:**2072–2078.

Caro, T. M. 1999. Demography and behaviour of African mammals subject to exploitation. Biological Conservation **13:**805–814.

Caro, T. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago.

Cheney, D. L., and R. M. Seyfarth. 1990. How monkeys see the world; inside the mind of another species. University of Chicago Press, Chicago.

Creel, S., and J. A. Winnie Jr. 2004. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behaviour **69:**1181–1189.

Crete, M., and A. Desrosiers. 1995. Range expansion of coyotes, *Canis latrans*, threatens a remnant herd of caribou, *Rangifer tarandus*, in southeastern Quebec. Canadian Field-Naturalist **109:**227–235.

Crooks, K. R., and M. E. Soule. 1999. Mesopredator release and avifaunal extinctions in a fragmented ecosystem. Nature **400:**563–566.

Derocher, A.E., O. Wiig, and G. Bangjord. 2000. Predation of Svalbard reindeer by polar bears. Polar Biology **23:**675–678.

Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska; generality and variation in a community ecological paradigm. Ecological Monographs **65:**75–100.

Estes, J. A., E. M. Danner, D. F. Doak, B. Konar, A. M. Springer, P. D. Steinberg, M. T. Tinker, and T. M. Williams. 2004. Complex trophic interactions in kelp forest ecosystems. Bulletin of Marine Science **74:**621–638.

Festa-Bianchet, M. 2003. Exploitative wildlife management as a selective pressure for life history evolution of large mammals. Pages 191–208 in M. Festa-Bianchet and M. Appolilio, editors. Animal behavior and wildlife management. Island Press, Covello, California.

Fitzgibbon, C. D. 1989. A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. Animal Behaviour **37:**508–510.

Fortin, D., L. Hawthorne, L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology **86:**1320–1330.

Gese E. and S. Grothe. 1995 Analysis of coyote predation on deer and elk during winter in Yellowstone National Park. Wyoming American Midland Naturalist **133:**36–43.

Gil-da-Costa, R., A. Palleroni, M. D. Hauser, J. Touchton, and J. P. Kelley. 2002. Rapid acquisition of an alarm response by a neotropical primate to a newly introduced avian predator. Proceedings Royal Society **203:**605–610.

Gittleman, J. L., and M. E. Gompper. 2001. The risk of extinction—what you don't know will hurt you. Science **291:**997–999.

Helle, E., and K. Kauhala 1991. Distribution history and present status of the raccoon dog in Finland. Holarctic Ecology **14:**278–286.

Hess, K., Jr. 1993. Rocky times in Rocky Mountain National Park. University of Colorado Press, Niwot, Colorado.

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.

Isbell, L. A. 1990. Sudden short-term increase in mortality of vervet monkeys (*Cercopithecus aethiops*) due to leopard predation in Amboseli National Park. Kenya American Journal of Primatology **21:** 41–52.

Joly, D. O., and F. Messier. 2004. Testing hypotheses of bison population decline (1970-1999) in Wood Buffalo National Park: synergism between exotic disease and predation. Canadian Journal of Zoology **82:**1165–1176.

Jones, M. E., G. C. Smith, and S. M. Jones. 2004. Is anti-predator behaviour in Tasmanian Eastern Quolls (*Dasyurus viverrinus*) effective against introduced predators? Animal Conservation **7:**155–160.

Laudre, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: re-establishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology **79:**1401–1409.

Linnell, J., J. Swenson, and R. B. Andersen. 2000. Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators or keystones? Biodiversity and Conservation **9:**857–868.

Mclaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266:1555–1558.

Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. The wolves of Denali. University of Minnesota, Minneapolis.

Melgaard, M. 1986. The Greenland caribou: zoogeography, taxonomy, and population dynamics. Meddelser om Gronland, Bioscience 20. Springer, Berlin.

Miquelle, D. G., P. A. Stephens, E. N. Smirnoff, J. M. Goodrich, O. J. Zaumyslova, and A. Myslenkov. 2005. Tigers and wolves in the Russian Far East: competitive exclusion, functional redundancy, and conservation implications. Pages 179–208 in J. Ray, K. H. Redford, R. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island Press, Covello, California.

Novaro, A. J., M. C. Funes, and R. S. Walker. 2000. Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia—natural versus livestock ranges. Biological Conservation **92:**25–33.

Norusis, M. J. 2002. SPSS 11.0. Guide to data analysis. Prentice Hall, New Jersey.

Orians, G. H., editor. 1997. Wolves, bears, and their prey in Alaska. Biological and social challenges in wildlife management. National Academy Press, Washington, D.C.

Pyare, S., and J. Berger. 2003. Beyond demography and delisting: ecological recovery for Yellowstone's grizzly bears and wolves. Biological Conservation **113:**63–73.

Pyare, S., S. L. Cain, D. Moody, C. Schwartz, and J. Berger. 2004. Grizzly bears in the Yellowstone Ecosystem; loss and re-colonization rates during a century of change. Animal Conservation 7:71–78.

Ray, J., K. H. Redford, R. Steneck, and J. Berger, editors. 2005. Large carnivores and the conservation of biodiversity. Island press, Covello, California.

Redford, K., and P. Feinsinger. 2002. The half empty forest: sustainable use and the ecology of interactions. Pages 370–400 in J. Reynolds, G. Mace, K. Redford, and J. Robinson, editors. Conservation of exploited species. Cambridge University Press, Cambridge, United Kingdom.

Reed, J. M. 1999. The role of behavior in recent avian extinctions and endangerments. Conservation Biology **13:**232–241.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience **54:**755–766.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk, and aspen on Yellowstone National Park, USA. Biological Conservation **102:**227–234.

Sand, H., C. Wikenros, P. Wabakken, and O. Liberg. 2006. Cross-continental differences in patterns of predation: Will naive moose in Scandinavia ever learn? Proceedings of the Royal Society doi:**10** 1098/rspb.2005.3447.

Short, J., J. E. Kinnear, and A. Robley. 2002. Surplus killing by introduced predators in Australia—evidence for ineffective anti-predator adaptations in naive prey species. Biological Conservation **103:**283–301.

Smith, B. L., and S. H. Anderson. 1996. Patterns of neonatal mortality of elk in Northwestern Wyoming. Canadian Journal of Zoology **74:**1229–1237.

Smith, D. W., L. D. Mech, M. Meagher, W. E. Clark, R. Jaffe, M. K. Phillips, and J. A. Mack. 2000. Wolf-bison interactions in Yellowstone National Park. Journal of Mammalogy **81:**1128–1135.

Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. BioScience **53:**330–340.

Soulé, M. E., J. A. Estes, J. Berger, and C. Martinez del Rio. 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology **17:**1238–1250.

Sweitzer, R. A., S. H. Jenkins, and J. Berger. 1997. Near-extinction of porcupines by pumas in the Great Basin and consequences of ecological changes. Conservation Biology **11:**1407–1417.

Swenson, J. E., F. Sandgren, and A. Soderberg. 1998. Geographical expansion of an increasing brown bear population: evidence for presaturation dispersal. Journal of Animal Ecology **67:**819–826.

Terborgh, J., et al. 2001. Ecological meltdown in predator-free forest fragments. Science **294:**1923–1926.

Testa, J. W. 2004. Population dynamics and life history trade-offs of moose (*Alces alces*) in southcentral Alaska. Ecology **85:**1439–1452.

Tyler, N. J. C., and N. A. Oritsland. 1989. Why don't Svalbard reindeer migrate? Holarctic Ecology **12:**369–376.

Van Der Knaap, W. O. 1986. On the presence of reindeer (*Rangifer tarandus* L) on Edgoya, Spitsbergen, in the period 3800–5000 BP. Circumpolar Journal **2:**3–10.

Van Schaik, C. P., and M. A. von Noorwijk. 1985. Evolutionary effect of the absence of felids on the social organization of the macaques on the island of Simeulue. Folia Primatolgica **44:**138–147.

Woodroffe, R., and J. R. Ginseberg. 2005. King of the beasts? Evidence for guild redundancy among large mammalian carnivores. Pages 154–176 in J. Ray, J. K. H. Redford, R. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island Press, Covello, California.

Zar, J. H. 1996. Biostaistical analyses. Prentice-Hall, Upper Saddle River, New Jersey.