
Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens

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The recent extinction of grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) by humans from 95–99% of the contiguous USA and Mexico in less than 100 years has resulted in dramatically altered and expanded prey communities. Such rampant ecological change and putative ecological instability has not occurred in North American northern boreal zones. This geographical variation in the loss of large carnivores as a consequence of anthropogenic disturbance offers opportunities for examining the potential consequences of extinction on subtle but important ecological patterns involving behaviour and interspecific ecological interactions. In Alaska, where scavengers and large carnivores are associated with carcasses, field experiments involving sound playback simulations have demonstrated that at least one prey species, moose (*Alces alces*), is sensitive to the vocalizations of ravens (*Corvus corax*) and may rely on their cues to avoid predation. However, a similar relationship is absent on a predator-free island in Alaska's Cook Inlet and at two sites in the Jackson Hole region of the Rocky Mountains (USA) where grizzly bears and wolves have been extinct for 50–70 years. While prior study of birds and mammals has demonstrated that prey may retain predator recognition capabilities for thousands of years even after predation as a selective force has been relaxed, the results presented here establish that a desensitization in interspecific responsiveness can also occur in less than ten generations. These results affirm (i) a rapid decoupling in behaviour involving prey and scavengers as a consequence of anthropogenic-caused predator–prey disequilibria, and (ii) subtle, community-level modifications in terrestrial ecosystems where large carnivores no longer exist. If knowledge about ecological and behavioural processes in extant systems is to be enhanced, the potential effects of recently extinct carnivores must be incorporated into current programmes.

Keywords: carnivores; behaviour; wolves; moose; bears; ravens

1. INTRODUCTION

The past and continuing global extinction of large terrestrial carnivores from many of this planet's unprotected ecosystems has resulted in rampant ecological change, partly because the removal of top carnivores can lead to a cascade of community alterations (Terborgh 1987; Wright *et al.* 1994; Estes & Duggins 1995) and because, even with replacement by modern humans, our patterns of prey selection differ dramatically from those of non-humans (Ginsberg & Milner-Gulland 1994). In North America, the most extreme losses of large carnivores have been south of the Canadian border where wolves and grizzly bears were eradicated from some 95–99% of previously occupied regions during the last century (figure 1). Among the consequent changes are the relaxation of predation as a selective force, the eruption of herbivore populations, the spread of disease and diminished biodiversity (Kay 1994; Wilson & Childs 1997; McShae & Rappole 1997; Terborgh *et al.* 1999; Berger 1998).

Nevertheless, the extent to which predator–prey imbalances, whether caused by humans or other factors,

influence the behaviour of either prey species or other members of the same ecological community remains uncertain. However, what is clear is that, with continued anthropogenic disturbance and accelerated extinctions, many previously unexamined interspecific interactions involving ecology and behaviour will be unrecorded. For example, the temporal and spatial patterning of interactions between prey and scavenger guilds is unknown and any putative relationships that might once have existed may be impossible to document after extinctions have occurred. Yet, from both scientific and conservation perspectives, an understanding of such relationships is important because (i) the management, protection or restoration of both pristine and disturbed communities requires knowledge about the ecological dynamics, and (ii) programmes aimed at the restoration of biological diversity through the reintroduction of carnivores, as is occurring in areas of Europe, North America and Africa (Reading & Clark 1996), will be enhanced by understanding not only targeted prey species but how they interact with other community members. Here, I report on evidence of a rapid interspecific behavioural change

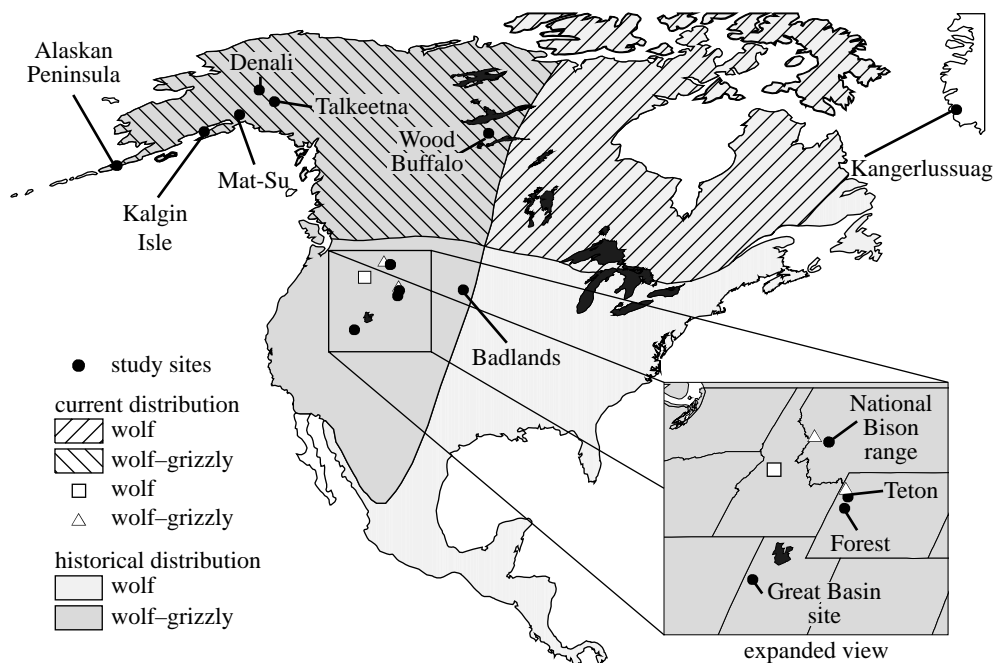


Figure 1. Map showing the past and current distributions of grizzly bears and wolves in North America. The six sites used in this study are as follows: Teton, Forest and Kalgin (grizzly bears and wolves absent) and Denali, Talkeetna and Mat-Su (grizzly bears and wolves present). The other named areas are sites mentioned in the text and table 1 where the effects of predation release on behaviour in North American ungulates have been studied.

involving prey responsiveness to a scavenger species. This disruption of a natural pattern has arisen due to the extinction of large carnivores through the combined effects of modern human hunting and habitat alteration and, concomitantly, the total relaxation of predation as a selective force.

Carnivores and scavengers often live mutualistically, a relationship throughout Holarctic boreal and tundra biomes which includes both mammals and birds (Henry 1986; Vander Wall 1991). For instance, not only do Athabaskan hunters in Alaska locate food by observing the behaviour of ravens but so may wolves and grizzly bears; in contrast, ravens often rely on carnivores to open carcasses with thick hides (Mech 1970; Nelson 1983; Heinrich 1989). Although local recognition of corvids by prey species may occur (Birkhead 1991; Stockwell 1991), the extent to which prey rather than carnivores use scavengers to facilitate behavioural decisions remains uncertain. However, where predation exerts a strong influence on prey demography, individuals often alter their daily behaviour, decisions which include joining groups and changing positions within them (FitzGibbon & Lazarus 1995; Byers 1998), trading access to higher food quality by living in safer areas (Molvar & Bowyer 1994) and shifting to less predator-prone habitats (Berger 1991). But, whether mammalian prey species modify their behaviour either directly or indirectly as a response to scavengers to enhance predator detection is uncertain. Here, I test the prediction that prey are more responsive to cues associated with sympatric scavengers than to sympatric neutral species as a means of enhancing predator detection where predation by large carnivores has not been eliminated.

An adequate test of this prediction cannot be conducted if several ecological conditions do not exist. First, areas that vary in their degree of predation must be available for study. Mere knowledge about the presence or absence of potential predators is likely to be insufficient for concluding anything about predation pressure because

the presence of carnivores does not necessarily indicate that predation exists. For instance, the extinction of grizzly bears and wolves may fail to result in a cessation of predation even though the large carnivores may be extinct as predation on the prey species may still occur by replacement predators. Second, a sufficient time-frame of relaxed selection must exist to enable opportunities for changes in behaviour. To examine the prediction about prey–scavenger recognition, I first tested the fundamental assumption that predation release in moose is a consequence of the absence of grizzly bears and wolves and then, by employing manipulative field experiments, in the very same scavenger–prey systems which varied in predation pressure.

2. METHODS

I gathered data on the proportion of time adult female moose allocated to feeding and vigilance during standardized 180 s time-periods. This measure offers a reasonably sensitive gauge of predation risk (Byers 1997; Hunter & Skinner 1998). These data were collected between 1995 and 1998 at six independent study areas, all with ravens but varying in their degree of large carnivore presence. Three sites had complete carnivore communities and three were lacking in both grizzly bears and wolves (figure 1). The sites with grizzly bears and wolves were Alaska's Talkeetna Mountains, Denali National Park and the Matanuska (Mat-Su) Valley region, each geographically separated from each other by at least 150 km. The areas lacking grizzly bears and wolves were Grand Teton National Park and Bridger-Teton National Forest in north-western Wyoming (each separated by 10–75 km) and Kalgin Island in Alaska's Cook Inlet (figure 1). Due to carnivore extirpations moose have been predator free at the Wyoming sites for *ca.* 50–75 years and on the island for 40 years, where they were introduced and neither grizzly bears nor wolves have occurred due to strong marine undercurrents.

Because assessments of interpopulation variation in the foraging–vigilance dichotomy may be confounded by ecological differences or other variables, it is critical to control for potential

sources of variation so that the possible effects of predation may be examined. Therefore, I gathered additional data on (i) the presence of young since parous females are more vigilant than females without young (Berger & Cunningham 1988), (ii) group size since grouping influences feeding rates (FitzGibbon 1989), (iii) the distance to cues (e.g. sound; see below) which I used as a potential marker of risk of predation, and (iv) the distance to forest or willow canopy because foraging efficiency and distance to concealment cover are inversely related (Molvar & Bowyer 1994).

The behaviour of adult female moose was assessed during experimental playback of sounds and post-playback periods using log-transformed data of the proportion of 180 s feeding bouts that were vigilant (Berger & Cunningham 1988; Berger 1991) under four conditions: (i) a control (i.e. baseline; no overt or experimental disturbance), (ii) 25 s playbacks of raven vocalizations, (iii) 25 s playbacks of red-tailed hawk vocalizations, and (iv) a dummy sound (running water). The use of baseline values enabled an assessment of the extent to which the playbacks may have resulted in heightened vigilance. The running water was used as a simple measure of a familiar but non-threatening sound. The distances between the subjects and sounds (from a JBL Pro-III speaker connected to a 40 W Kenwood amplifier and powered by a 12 V battery) averaged 145 m (s.e. = 6.90, $n = 203$ and range = 30–600 m). All experiments were on calm days to avoid the possibility that wind would obscure the recognition of sound. The effects of predation treatment were explored by general linear models (Norusis 1997) with the study areas nested by predation treatment in ANOVAs and multiple regression and with the effects of the above-mentioned, four covariates (presence of young, group size, distance to cues and distance to canopy) removed. Pairwise post-hoc multiple comparisons were performed with Bonferroni adjustments.

Although I (Berger 1991) and others have made the assumption that the presence of predators suggests a risk of predation, neither that assumption nor the converse may be valid. That is, the loss of large carnivores does not necessarily mean that predation is relaxed because smaller carnivores may be released. For instance, although grizzly bears and wolves are absent at the three putative 'predator-free' study areas, if replacement meso-carnivores (e.g. black bears or coyotes) prey on adult or juvenile moose, as described previously (Franzmann & Schwartz 1986), then predation as a selection force will not have been relaxed and the presumptions about predation-free environments will be invalid. I tested this assumption through monitoring either the survival rates of known calves (Berger 1998; Berger *et al.* 1999) or by comparative analyses using previously collected data from other study areas (see below).

3. RESULTS AND DISCUSSION

Ravens and moose have a circumpolar distribution which, until recently, included sympatry with grizzly bears and wolves in Asia, North America and Europe (Mech 1970; Craighead 1979; Heinrich 1989). Although the presence of predators is often assumed to be equated with predation risk (Magurran 1992), this may not be the case where alternative prey exist or if predator loss is compensated for by replacement predation which, for grizzly bears, may occur by black bears. To verify whether predation had been relaxed, I contrasted the patterns of juvenile moose survival between the study

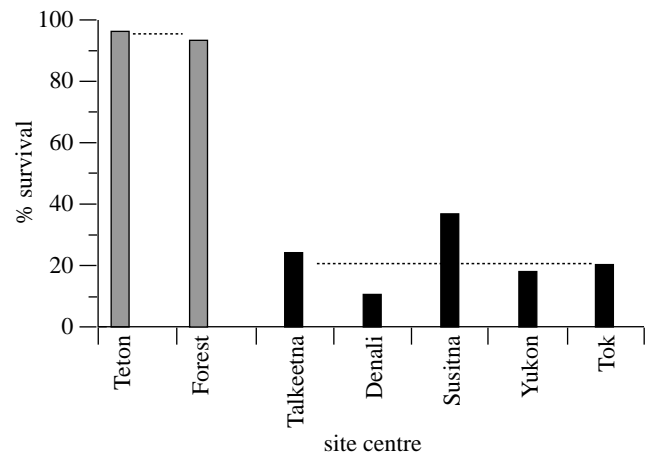


Figure 2. Comparison of the mean survival rates of juvenile moose through their first summer at sites with (black) and without (grey) grizzly bears and wolves. The dotted lines are the means for the respective treatments. Data sources: Teton and Forest (this study), Talkeetna (Testa 1998), Denali (Bowyer *et al.* 1998), Susitna (Ballard *et al.* 1991), Yukon (Larsen *et al.* 1989) and Tok (Gasaway *et al.* 1992; National Research Council 1997).

areas (figure 2). At the Alaskan sites with grizzly bears and wolves, survival averaged less than 30% during the first two months of life; in contrast, survival was more than three times as great where extirpations had occurred (figure 2). If these results were not reflective of long-term patterns, it would be fruitless to argue that predation pressure indeed varies between areas where grizzly bears and wolves are present or absent. Fortunately, additional studies of juvenile survival and population growth at sites differing in predation intensity in both Alaska and Canada's Yukon have confirmed that large carnivores limit recruitment and population growth in prey populations, including moose (Gasaway *et al.* 1992; National Research Council 1997).

Given the consistent and dramatic demographic differences across areas with extant wolves and grizzly bears (figure 2), a basis exists for expecting astuteness in environmental monitoring by prey—that vigilance should be greater at sites with intact carnivore communities. Surprisingly, the evidence is equivocal for multiple species.

Alaskan caribou which are sympatric with wolves are more vigilant than conspecifics from western Greenland where predation by wolves has been absent for 4000 years and pronghorn experiencing carnivore replacement by humans are more wary than those without predation (table 1 and figure 1). However, neither bison under varying predation risk nor pronghorn under relaxed predation from extinct Pleistocene predators fit the model (table 1). In addition, contrasts between the foraging rates of undisturbed female moose from my six study populations, which vary in predation, also showed no variation, nor when they were systematically exposed to the playback sounds of running water (as a control; figure 3a). These data illustrate that, in the absence of disturbance or with exposure to a familiar neutral sound, foraging is independent of predation regime. Clearly, the mere presence of predators within an ecological community may be insufficient as a factor affecting foraging rates.

Table 1. *Summary of the behavioural consequences of relaxation of predation in North American ungulates*

(Replication indicates whether the studies have been repeated at other sites. The effects are changes at sites lacking in predation. The locations are as shown in figure 1. An asterisk indicates Pleistocene extinctions and a double asterisk reflects modern humans.)

variable	species	location	extinct predators	effects	replication	time-frame (years)
group size	pronghorn	National Bison Range, Montana	cheetah, short-faced bear and lion*	no change ^a	no	10 000 +
	pronghorn	Great Basin Desert, Nevada (paired sites)	human** versus none	smaller ^b	no	25
	musk ox	Alaska, Canada and Greenland—19 sites	wolf	smaller ^c	yes	25–50
vigilance	caribou	Peninsula and Kangerlussuag, Alaska and Greenland	wolf	reduced ^d	no	4000 +
	bison	Badlands and Wood Buffalo, South Dakota and Canada	wolf	no change ^e	no	75
location in group	pronghorn	Badlands, South Dakota	wolf and grizzly bear	vigilance differs ^e	no	75
	bison	Badlands and Wood Buffalo, South Dakota and Canada	wolf and grizzly bear	no change ^e	no	75
raven response	moose	Alaska and Wyoming	wolf and grizzly bear	decreased ^f	yes	40–75

^a Byers (1997).

^b Berger *et al.* (1983).

^c Heard (1992).

^d Boving & Post (1997).

^e Berger & Cunningham (1988).

^f This study.

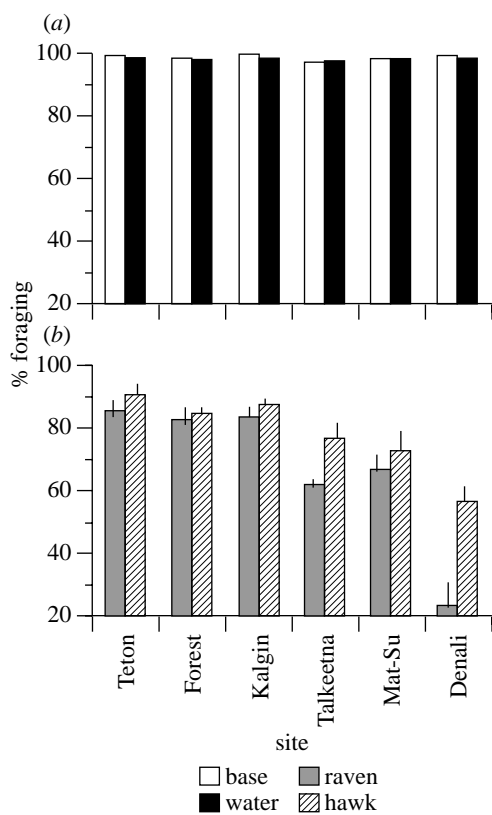


Figure 3. Site-specific mean (and s.e.) foraging rates (vertical bars) of female moose where grizzly bears and wolves were absent or present during (a) the control (baseline) and (b) the experimental (water; raven; hawk) conditions. (a) Without carnivores: $\bar{X}_B = 99$ and $\bar{X}_W = 98$, and with carnivores $\bar{X}_B = 98$ and $\bar{X}_W = 98$. (b) Without carnivores: $\bar{X}_R = 84$ and $\bar{X}_H = 89$, and with carnivores $\bar{X}_R = 49$ and $\bar{X}_H = 67$. Sample sizes (playbacks) per site (in parentheses): Teton (105), Forest (23), Kalgin (12), Talkeetnas (22), Mat-su (22) and Denali (25).

Because both bears and wolves associate with ravens at either carcasses or during attempts to locate food (Mech 1970; Nelson 1983; Henry 1986; Heinrich 1989), prey may be more responsive to scavenger cues as a means of enhancing predator detection in areas where carnivores have not been eliminated. Alternatively, if prey responsiveness is obligatory, vigilance should not vary by site irrespective of the predation regime. To distinguish between these possibilities, I contrasted the baseline vigilance with that during exposure to vocalizations using two sympatric birds, scavengers (ravens) and non-scavengers (red-tailed hawks). Under relaxed predation, females responded only weakly to hawks or ravens (figure 3b), but the reductions in feeding at predator-rich sites were dramatic (figure 3b; $F_{5,200} = 17.68$ and $F = 13.29$, respectively, both $p < 0.0001$). The order of presentation of acoustical cues was not responsible for these differences (at predator-free sites, $F = 0.178$ and $p > 0.50$ and at predator sites, $F = 0.464$ and $p > 0.50$).

Four additional results are consistent with the hypothesis that prey are more responsive or less inured to scavengers at sites with active predation (table 2). First, although group size had no effect on the foraging rates, vigilance was greater for mothers with calves at sites with predation, a relationship that suggests mothers were more apt to trade off feeding to survey environments where they coexist with grizzly bears and wolves ($p = 0.034$). Second, the distance to the sounds of surrogate predators (e.g. to the sites where vocalizations were broadcast) resulted in differences in the moose feeding rates and these varied by predation treatment but were significant only for ravens ($p = 0.048$); at predator-free sites, the distance of avian sounds having no effect on feeding (table 2). Third, vigilance was not related to the distance to canopy during raven or hawk vocalizations at predator-free sites but it was in areas with large carnivores and these relationships differed between

Table 2. Summary of statistical relationships

(Relationships (i) between the feeding rates in female moose at sites with (present) and without (absent) grizzly bears and wolves and covariates, (ii) whether differences between predation treatment (present or absent) exist after the effects of covariates are controlled for by MANOVA and (iii) Bonferroni adjustments for post hoc multiple comparisons of site-specific differences in feeding after playbacks of ravens and hawks. For both raven and hawk calls, the subgroups that differed from one another were (1) Denali, (2) Talkeetnas and Matsu, and (3) Kalgin, Tetons and Forest. For ravens the minimum site differences were significant at $p \leq 0.008$ and for hawks the minimum site differences were at $p \leq 0.034$.)

covariate	experimental variable	large carnivores				predation treatment	
		absent		present		<i>F</i>	<i>p</i>
		<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>		
mother with calf	raven	-1.302	0.195	-2.001	0.049	4.571	0.034
	hawk	1.685	0.100	-1.179	0.243	0.189	0.664
group size	raven	-0.146	0.884	0.757	0.452	0.420	0.518
	hawk	-1.135	0.258	1.369	0.323	0.982	0.323
distance to sound	raven	0.318	0.751	3.565	0.001	3.955	0.048
	hawk	1.127	0.262	3.374	0.001	2.167	0.143
distance to canopy	raven	1.862	0.065	5.242	0.0001	4.537	0.034
	hawk	1.127	0.262	2.322	0.023	0.216	0.643

predation regimes ($p=0.034$; table 2). Finally, the patterns of post-playback feeding differed between the predator-free and predator-rich sites. With the effects of other variables removed, both ravens and hawks elicited greater reductions in feeding where grizzly bears and wolves still existed ($F=19.019$ and $F=20.243$, respectively, both $p < 0.0001$).

While the six areas where the field data were gathered and experiments conducted will clearly vary structurally, it appears as if factors other than predation history can be excluded as possible causes for the observed variation in responses to scavengers. That both the baseline foraging values and responses to playbacks of running water produced no detectable intersite or treatment variation (figure 3a) suggests that the experimental apparatus produced reliable results. In fact, after the effects of covariates were removed, the differences were ascribed more to predation than to environmental noise or other factors (table 2). These findings suggest not only the recent existence of geographical variation in mammalian prey reliance on cues associated with an aerial scavenger but that the variation has arisen as a consequence of recent ecological instability. In this case, it is the human-caused, predator-prey disequilibrium due to the extinction of wolves and grizzly bears.

Why moose from predator-free environments respond less strongly after predation has been relaxed for as little as 40 years (approximately eight to ten generations) is intriguing. Either (i) the cost of non-response (non-vigilance) is low since the chance of predation is zero risk, or (ii) moose have become desensitized to environmental sounds that have little capacity to impact on them biologically, although these predictions need not be mutually exclusive. For instance, ravens in the Teton region occur at the highest known densities in North America (Dunk *et al.* 1994) and, in the absence of predation, there is little apparent incentive for moose to interrupt feeding. In contrast, in ecological communities where carnivores remove a high proportion of young, a surveillance failure could be fatal, which may also explain why moose in environments with

grizzly bears and wolves are also more responsive to sounds such as hawks. However, becoming inured to scavengers is not in itself a sufficient explanation, because predator-free Kalgin Isle moose, where ravens are substantially fewer, were also less responsive than Alaskan conspecifics which coexist with predators (table 2).

In other systems, prey species may be remarkably deft at discriminating between the calls of potential predators. These include primates which recognize the warning calls of conspecifics in distinguishing aerial from terrestrial predators (Cheney & Seyfarth 1990) and ground squirrels which may discern differences between venomous snakes and benign owls (Rowe *et al.* 1986). However, these situations differ from the one I have described above in two important respects. First, predation has not been relaxed through either the direct or indirect effects of human extinction and, even where geographical variation in predation occurs, as is the case of California ground squirrels where rattlesnakes have been locally extinct at some sites but not at others for thousands of generations, some retention of a predator response in ground squirrels still persists (Coss *et al.* 1993). What differs in the boreal web involving grizzly bears, wolves, moose and ravens is that responsiveness to cues associated with an aerial scavenger no longer occurs in a major prey species where large carnivores have been eliminated. Second, the striking reductions occurred not over thousands of generations of relaxed selection but in as few as ten.

An additional possibility which is unrelated to the loss of predation may account for the detectable geographic variation in moose responses to scavengers. Populations may have become genetically isolated after extirpation of predators and genetically hard-wired behaviour may have subsequently been lost through drift or founder effects (Mayr 1970; Magurran *et al.* 1992; Coss 1999). However, this scenario is unlikely because moose are continuously distributed, long-distance dispersal occurs and evidence of rapid genic differentiation is lacking (Cronin 1992; Hundertmark *et al.* 1992).

The abrupt decoupling of a prey–scavenger recognition system raises broader questions about the biological and anthropogenic effects of predator–prey disequilibria. First, where relaxed predation has been substantiated not all prey populations show behavioural plasticity (table 1). The lack of responsiveness in systems where predators have been extinct since the Pleistocene has been termed ‘ghost effects’ (Byers 1997). However, even when predators have been lost intersite variation may not occur as has been found for bison (table 1) or moose (figure 3a), results which may stem not from ghost effects *per se*, but from a lack of immediate attention to the stimuli associated with either predators or scavengers. However, it is now likely, at least for moose and perhaps other prey species, that the monitoring of scavengers may increase abilities to detect large carnivores, an interspecific behavioural response which is obviously labile and may be dropped from a species’ repertoire when predation no longer exists.

Second, although native peoples, hunters and biologists have suggested that carnivores may follow ravens to food sources (Mech 1970; Craighead 1979; Nelson 1983; Heinrich 1989) the evidence has often been equivocal. If, however, as the data in this paper suggest, moose enhance their abilities to detect predators through environmental monitoring of ravens, then there is reason to suspect that carnivores may similarly locate food (Heinrich 1999).

Finally, the desensitization of prey to scavengers at sites lacking predation indicates that subtle, community-level interactions now no longer occur in some boreal ecosystems. Whether other interspecific behaviours and the extent to which interspecific ecological interactions have been compromised or lost as a consequence of the extinction of top carnivores remains an open question. However, given the swift rate at which large carnivores are being eradicated throughout much of the world, rapid decoupling of other prey behaviours may also have occurred although the detection of such potential changes may continue to be masked by an absence of large carnivores. Just as biodiversity is being lost before it is even described (Wilson 1992), so too may interspecific processes involving animal behaviour.

However, progressive conservation efforts may bring optimism. The restoration of carnivores through either reintroduction, such as for cheetahs and lions in parts of African (Hunter & Skinner 1998) and wolves into the Yellowstone ecosystem, or the current geographical expansion of both grizzly bears and wolves into the Teton area, will create opportunities beyond the obvious benefits to tourism and ecosystem health. It will now be possible to examine how the restitution of mammalian predation as a selective force shapes both prey responses to carnivores themselves and possibly to scavengers.

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REFERENCES

- Ballard, W. B., Whitman, J. S. & Reed, D. J. 1991 Population dynamics of moose in southcentral Alaska. *Wildl. Monogr.* **114**, 1–49.
- Berger, J. 1991 Pregnancy incentives, predation constraints, and habitat shifts; experimental and field evidence for wild bighorn sheep. *Anim. Behav.* **41**, 61–77.
- Berger, J. 1998 Some consequences of the loss and restoration of large mammalian carnivores on prey. In *Behavioral ecology and conservation biology* (ed. T. M. Caro), pp. 80–100. Oxford University Press.
- Berger, J. & Cunningham, C. 1988 Size-related effects on search times of North American grassland female ungulates. *Ecology* **69**, 177–183.
- Berger, J., Daneke, D., Johnson, J. & Berwick, S. H. 1983 Pronghorn foraging economy and predator avoidance in a desert ecosystem; implications for the conservation of large mammalian herbivores. *Biol. Conserv.* **25**, 193–208.
- Berger, J., Testa, J. W., Roffe, T. & Montfort, S. L. 1999 Conservation endocrinology: a noninvasive tool to understand relationships between carnivore colonization and ecological carrying capacity. *Conserv. Biol.* **13**, 980–989.
- Birkhead, T. 1991 *The magpies*. London: T. & A. D. Poyser.
- Boving, P. S. & Post, E. 1997 Vigilance and foraging behaviour of female caribou in relation to predation risk. *Rangifer* **17**, 55–63.
- Bowyer, R. T., Van Ballenberghe, V. & Kie, J. G. 1998 Timing and synchrony of parturition in Alaskan moose: long term versus proximal effects of climate. *J. Mamm.* **79**, 1332–1344.
- Byers, J. A. 1997 *American pronghorn; social adaptations and ghosts of predators past*. University of Chicago Press.
- Cheney, D. L. & Seyfarth, R. M. 1990 *How monkeys see the world*. University of Chicago Press.
- Coss, R. G. 1999 Effects of relaxed natural selection on the evolution of behavior. In *Geographical variation in behavior: perspectives on evolutionary mechanisms* (ed. S. A. Foster & J. A. Endler), pp. 180–208. New York: Oxford University Press.
- Coss, R. G., Guse, G. L., Poran, N. S. & Smith, D. G. 1993 Development of anti-snake defenses in California ground squirrels. II. Microevolutionary effects of relaxed selection from rattlesnakes. *Behaviour* **124**, 137–164.
- Craighead, F. C. 1979 *Track of the grizzly*. San Francisco, CA: Sierra Club Books.
- Cronin, M. A. 1992 Intraspecific variation in mitochondrial DNA of North American cervids. *J. Mamm.* **73**, 70–82.
- Dunk, J. R., Cain, S. L., Reid, M. E. & Smith, R. N. 1994 A high breeding density of common ravens in northwestern Wyoming. *Northwest. Nat.* **75**, 70–73.
- Estes, J. A. & Duggin, D. O. 1995 Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecol. Monogr.* **65**, 75–100.
- FitzGibbon, C. D. 1989 A cost to individuals with reduced vigilance in groups of Thomson’s gazelles hunted by cheetahs. *Anim. Behav.* **37**, 508–510.
- FitzGibbon, C. D. & Lazarus, J. 1995 Antipredator behavior of Serengeti ungulates: individual differences and population consequences. In *Serengeti II* (ed. A. R. E. Sinclair & P. Arcese), pp. 274–296. University of Chicago Press.
- Franzmann, A. W. & Schwartz, C. C. 1986 Black bear predation on moose calves in highly productive versus marginal moose habitats on the Kenai Peninsula, Alaska. *Alces* **22**, 139–153.
- Gasaway, W. C., Boertje, R. D., Gravggaard, D. V., Kellyhouse, D. G., Stephenson, R. O. & Larsen, D. G. 1992 The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildl. Monogr.* **120**, 1–59.

- Ginsberg, J. R. & Milner-Gulland, E. J. 1994 Sex-biased harvesting and population dynamics in ungulates; implications for conservation and sustainable use. *Conserv. Biol.* **8**, 157–166.
- Heard, D. C. 1992 The effect of wolf predation and snow cover on musk-ox group size. *Am. Nat.* **139**, 193–204.
- Heinrich, B. 1989 *Ravens in winter*. New York: Random House.
- Heinrich, B. 1999 *Mind of the raven*. New York: HarperCollins.
- Henry, J. D. 1986 *The red fox*. Washington, DC: Smithsonian Institution Press.
- Hundertmark, K. J., Johns, P. E. & Smith, M. H. 1992 Genetic diversity of moose from the Kenai Peninsula, Alaska. *Alces* **28**, 15–20.
- Hunter, L. T. B. & Skinner, J. D. 1998 Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* **135**, 195–211.
- Kay, C. 1994 The impact of native ungulates and beaver on riparian communities in the Intermountain West. *Nat. Res. Environ. Issues* **1**, 23–44.
- Larsen, D. G., Gauthier, D. A. & Markel, R. L. 1989 Causes and rate of moose mortality in the southwest Yukon. *J. Wildl. Mgmt* **53**, 548–557.
- McShae, W. J. & Rappole, J. H. 1997 Herbivores and the ecology of forest understorey birds. In *The science of overabundance* (ed. W. J. McShae, H. B. Underwood & J. H. Rappole), pp. 298–307. Washington DC, USA: Smithsonian Institution Press.
- Magurran, A. E., Seghers, B. H., Carvalho, G. R. & Shaw, P. W. 1992 Behavioural consequences of an artificial introduction of guppies (*Poecilia reticulata*) in N. Trinidad: evidence for the evolution of anti-predator behaviour in the wild. *Proc. R. Soc. Lond.* **B248**, 117–122.
- Mayr, E. 1970 *Population, species, and evolution*. Cambridge, MA: Harvard University Press.
- Mech, L. D. 1970 *The wolf*. Minneapolis, MN: University of Minnesota Press.
- Molvar, E. M. & Bowyer, R. T. 1994 Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *J. Mamm.* **75**, 621–630.
- National Research Council 1997 *Wolves, bears, and their prey in Alaska*. Washington, DC: National Academy Press.
- Nelson, R. K. 1983 *Make prayers to the raven*. University of Chicago Press.
- Norusis, M. J. 1997 *SPSS 7.5, guide to data analysis*. Engelwood Cliffs, NJ: Prentice Hall.
- Reading, R. P. & Clark, T. W. 1996 Carnivore reintroductions: an inter-disciplinary examination. In *Carnivore behavior, ecology, and evolution*, vol. 2 (ed. J. L. Gittleman), pp. 296–336. Ithaca, NY: Cornell University Press.
- Rowe, M. P., Coss, R. G. & Owings, D. H. 1986 Rattlesnake rattles and burrowing owl hisses: a case of acoustic Batesian mimicry. *Ethology* **72**, 53–71.
- Stockwell, C. A. 1991 Behavioural reactions of desert bighorn sheep to avian scavengers. *J. Zool. (Lond.)* **225**, 563–566.
- Terborgh, J. 1987 The big things that run the world—a sequel to E. O. Wilson. *Conserv. Biol.* **2**, 402–403.
- Terborgh, J., Estes J. A., Paquet P., Ralls K., Boyd-Heger D., Miller B. J. & Noss, R. F. 1999 The role of top carnivores in regulating terrestrial ecosystems. In *Continental conservation* (ed. M. E. Soule & J. Terborgh), pp. 39–64. Covello, USA: Island Press.
- Testa, J. W. 1998 *Research progress report, 149*. Anchorage, AK: Alaska Division of Wildlife Conservation.
- Vander Wall, S. B. 1991 *Food hoarding in animals*. University of Chicago Press.
- Wilson, E. O. 1992 *The diversity of life*. Cambridge, MA: Harvard University Press.
- Wilson, M. L. & Childs, J. E. 1997 Vertebrate abundance and the epidemiology of zoonotic diseases. In *Science of overabundance* (ed. W. J. McShea, H. B. Underwood & J. H. Rappole), pp. 224–248, Washington, DC: Smithsonian Institution Press.
- Wright, S., Gompper, M. E. & De Leon, B. 1994 Are large predators keystone species in neotropical forests? The evidence from Barro Colorado Island. *Oikos* **71**, 279–294.

As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.

