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Recolonizing Carnivores and Naïve Prey: Conservation Lessons from Pleistocene Extinctions

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The current extinction of many of Earth's large terrestrial carnivores has left some extant prey species lacking knowledge about contemporary predators, a situation roughly parallel to that 10,000 to 50,000 years ago, when naïve animals first encountered colonizing human hunters. Along present-day carnivore recolonization fronts, brown (also called grizzly) bears killed predator-naïve adult moose at disproportionately high rates in Scandinavia, and moose mothers who lost juveniles to recolonizing wolves in North America's Yellowstone region developed hypersensitivity to wolf howls. Although prey that had been unfamiliar with dangerous predators for as few as 50 to 130 years were highly vulnerable to initial encounters, behavioral adjustments to reduce predation transpired within a single generation. The fact that at least one prey species quickly learns to be wary of restored carnivores should negate fears about localized prey extinction.

The spectacular post-Pleistocene extinctions of many genera of large animals in areas ranging from Australia to North America have been attributed primarily to human overkill as hunters encountered naïve prey—the “blitzkrieg hypothesis” (1)—and/or to climate change (2). An inadvertent consequence of today's extinction of many large carnivores is that prey in otherwise intact areas may lose knowledge about current predators (3, 4). These extinctions, however, offer op-

portunities to assess the generality of components of the blitzkrieg hypothesis and to address concerns about the ecological consequences of carnivore restoration. In Western Europe and the United States (outside of Alaska), wolves (*Canis lupus*) and brown bears (*Ursus arctos*) were eliminated within 100 years from more than 95% of their range. The cessation of predation has released mammalian prey from past selection pressures (3–5), but the current expansion of large car-

nivores into formerly depopulated ecosystems is bringing them into contact with naïve prey, a situation roughly similar to some post-Pleistocene events. Whereas naïve large animals first encountered colonizing paleolithic hunters 10,000 to 50,000 years ago, species such as bison, moose, and elk are now reexperiencing bears and wolves after they had been locally extinct.

To understand the possible susceptibility of extant prey to unfamiliar predators, we focus on two predictions: that naïve prey (i) fail to display appropriate behavior to reduce predation and (ii) experience heightened mortality along colonizing fronts (6). We studied a common circumpolar ungulate, the moose (*Alces alces*), focusing on sites (i) with predators, (ii) lacking predators, and (iii) with recent carnivore recolonization. Two types of macrogeographic contrasts were made: one in Europe, the other in North America. Three Scandinavian sites [(i) Dalarna-Hedmark (Sweden-Norway), (ii) Harjedalen (Sweden), and (iii) Norrbotten (Sweden)] had predator-naïve moose that were becoming reexposed to bears along colonizing fronts (7, 8). In the United States, six sites (four in Alaska and two in Wyoming) were studied. The Wyoming sites included naïve moose in and away from the paths of colonizing wolves and grizzly bears in the southern region of the Greater Yellowstone Ecosystem. Bears, wolves, and moose have overlapped in mainland Alaska for about 9000 years (9), and in these and other systems, juvenile moose mortality is three times greater than when these predators are absent (10, 11).

Predator-naïve individuals may be less sensitive to cues that signify the presence of dangerous carnivores. We examined this idea by comparing (i) vigilance, (ii) predator-directed aggression, and (iii) abandonment of feeding sites by adult female moose during and after systematic playback experiments with novel and familiar auditory and olfactory cues. In Alaska, we used three sites with intact carnivore communities (Talkeetna Mountains, Denali National Park and Preserve, and Matanuska Valley) and three predator-free systems (Kalgin Island in Alaska's Cook Inlet, Grand Teton National Park, and adjacent forest lands); in the latter, prey had

not experienced grizzly bears or wolves for 40 to 75 years (12).

Responses to auditory or olfactory cues were conspicuously less among predator-naïve moose (Figs. 1 and 2). Wolf calls increased vigilance by about 250% in predator-experienced Alaskan populations relative to predator-free ones ($F_{1,221} = 25.771$, $P < 0.0001$) (13). The sound of a control—running water—produced no differences ($F_{1,180} = 0.541$, $P = 0.744$). Additionally, the reactions of predator-experienced moose to raven calls were about six times greater than those of moose in predator-free zones ($F = 44.26$; $P < 0.0001$) (Fig. 1), presumably because these scavengers are highly associated with grizzly bears and wolves (4, 14). Likewise, the odors of wolves and bears generally elicited parallel responses (Fig. 2); a striking absence of site abandonment occurred in naïve moose from either Alaska or Wyoming when they were exposed to wolf urine (abandonment oc-

curred in 0 out of 70 trials; Fig. 3) (15).

One additional measure—the demeanor of moose—also supports the notion that individuals from predator-depopulated regions are more vulnerable to predation. Naïve moose were one-quarter as likely to behave aggressively in response to odor cues than were predator-savvy conspecifics (11 versus 47%, respectively; $N = 86$ naïve animals and 24 predator-savvy animals; $\chi^2 = 22.397$; $P < 0.0001$) (16). The former failed to drop their heads, retract their ears, and piloerect their nape fur—all patterns observed when moose fight off bears or wolves (17, 18). Because naïve moose approached, rather than avoided, odors in 16% of the trials ($N = 86$ trials), but predator-experienced moose never did ($N = 24$ trials, $P < 0.0001$), we can only presume that approaches increase, rather than decrease, the chances of predation.

These data show clear and repeatable

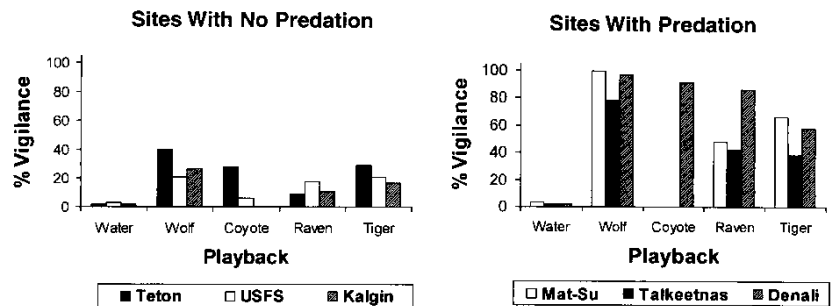


Fig. 1. Descriptive summary of nontransformed mean (cumulative) moose vigilance per 180-s bout during and after experimental playback of sounds. Sounds, sites, and sample sizes per site (followed by SEM in parentheses) were as follows. Water: Grand Teton National Park (Tet), 196 (1.1); U.S. Forest Service (USFS), 30 (1.5); Kalgin Island (Kal), 12 (1.9); Matanuska Valley (Mat), 28 (1.0); Talkeetna Mountains (Tal), 25 (1.4); and Denali National Park (Den), 35 (1.1). Wolf: Tet, 215 (4.3); USFS, 30 (4.3); Kal, 12 (8.7); Mat, 27 (4.6); Tal, 24 (5.9); and Den, 31 (5.1). Coyote: Tet, 137 (5.3); USFS, 21 (2.9); and Den, 26 (4.7). Raven: Tet, 215 (3.2); USFS, 30 (1.6); Kal, 12 (7.3); Mat, 28 (4.8); Tal, 23 (5.4); and Den, 31 (4.9). Tiger: Tet, 187 (4.3); USFS, 20 (6.2); Kal, 12 (6.8); Mat, 22 (5.5); Tal, 18 (5.5); and Den, 27 (5.0).

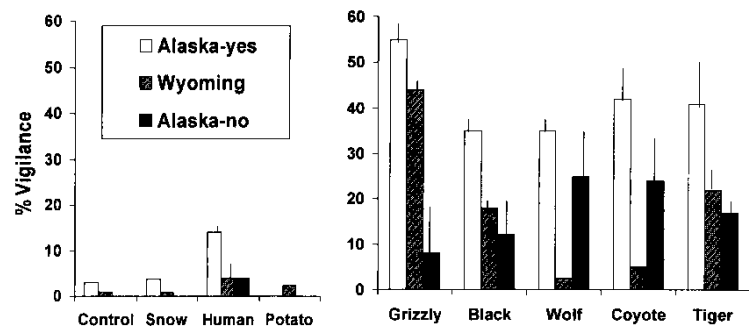


Fig. 2. Descriptive summary of nontransformed mean and SEM of moose responses to odor trials by site. The number of trials with the various substances per site was as follows (numbers appear in parentheses in the following order: Alaska-yes, Wyoming, and Alaska-no): control, observational only (27, 95, 1); snow (24, 78, 1); human urine (18, 59, 7); fermented potato (0, 10, 0); grizzly bear feces (19, 80, 4); black bear feces (6, 31, 6); wolf urine (22, 88, 6); coyote urine (12, 70, 4); tiger feces (12, 59, 3). Alaska-yes indicates sites with predators; Alaska-no indicates a 2500-acre predator enclosure on Kenai Peninsula.

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Table 1. Summary of the major effects of colonizing carnivores on predator-experienced and -naïve moose in Europe and North America. Sample sizes are given in parentheses under the "Predation" heading.

| Dependent variable | Evidence and comment | |
|---|---|----------------------------|
| <i>Anti-predator response [North America: Alaska and Wyoming (USA)]</i> | | |
| Vigilance | Sound and odor playbacks elicit greater responses in predator-experienced (Alaska) than in naïve (Alaska and Wyoming) populations | |
| Site abandonment | As above | |
| Demeanor | Predator-experienced (Alaska) individuals were aggressive to and never approached odors, in contrast to naïve ones (irrespective of either Alaska or Wyoming origins) | |
| <i>Predation [Europe (Sweden and Norway) and North America (USA)]</i> | | |
| | Moose at core of bear areas | |
| | Moose at colonizing fronts | |
| Carcass use (all bears)* | 2.8% (771) | 5.9% (715) |
| Carcass use (male bears)† | 4.7% (450) | 7.8% (503) |
| Predation success/attempts‡ | 0% (15) | 37.5% (8) |
| Predation: total events§ | 0 (Yellowstone; ~30 years) | 10 (Jackson Hole; 5 years) |
| <i>Rapid behavioral adjustments associated with predation (North America)</i> | | |
| Vigilance | Increased in Teton mothers losing offspring to wolves relative to mothers with offspring surviving or lost to other causes | |
| Site abandonment | As above | |
| Birth locations | Mean distance of sites in successive years differs between Alaskan mothers with surviving calves (2.9 km) and nonsurviving calves (4.9 km) (22) | |

*One-tailed statistical test: $\chi^2 = 8.0195$, $P < 0.0046$ (Wald test). †One-tailed statistical test: $\chi^2 = 4.824$, $P < 0.028$. ‡One-tailed statistical test: $P = 0.032$ (Fisher's exact test). §From (20) and this study.

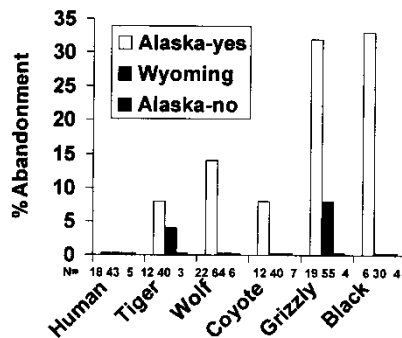


Fig. 3. Frequency of local site abandonment by female moose after odor deposition. The number of trials (N) is as indicated. Alaska-yes data are from Denali and Talkeetnas; Wyoming data are from Grand Teton National Park. Pairwise Alaska-Wyoming contrasts (excluding the Kenai site) are as follows: wolf ($P = 0.016$), wolf and coyote combined ($P = 0.003$), grizzly bear ($P = 0.065$), grizzly and black bear combined ($P = 0.005$), and tiger ($P = 0.553$).

differences in behavior associated with predators but do not indicate whether prey lacking knowledge of either novel or recolonizing predators experience heightened mortality. We examined this possibility using moose in two discrete systems with recolonizing (i) Scandinavian brown bears and (ii) Yellowstone wolves and bears. In the Dalarna-Hedmark area, bears were functionally extinct by 1897. To evaluate the efficiency of bear predation on naïve and experienced moose, we used spatial contrasts, predicting a greater proportion of kills along bear colonizing fronts than in

the center of their range. Bear colonizing fronts typically involve males at low densities, with females more centrally concentrated at higher densities (7, 8).

Our measures reveal that (i) both sexes of radio-marked bears fed on adult moose carcasses along dispersal fronts at more than twice the rate than away from them; (ii) male bears alone did so about two-thirds more often along the front than in the center (Table 1); and (iii), most prominent, predation was more successful along the periphery than at the center (38 versus 0%; Table 1) (19), a pattern that was also repeated in North America. In Yellowstone National Park, where grizzly bears and moose have occurred sympatrically since at least the 1880s, predation on moose was not detected between 1959 and 1992 (20). However, along the current recolonization front in Jackson Hole, at least 10 adult moose were killed between 1996 and 2000. Our findings (Table 1) indicate that naïve individuals are (i) conspicuously lacking in astuteness and (ii) experiencing a blitzkrieg.

If predation has the capacity to be both intense and swift, then how do naïve prey avoid extinction, either now or post-Pleistocene? One survival model posits the rapid development of predator recognition through individual experience. Predator-naïve mothers whose calves were killed by wolves colonizing Jackson Hole elevated their post-playback vigilance to wolf calls by about 500%, and the consequent latency to resumption of feeding increased from a mean of less than 30 s (in years before predation) to more than 6 min after ($F_{1, 89} = 32.516$, $P < 0.0001$); additionally, a fourfold increase in site abandonment accompanied these feeding shifts ($\chi^2 = 5.831$, $P < 0.016$) (21). That such dramatic changes were caused by wolf predation per se and not by other factors is supported by two comparative analyses: (i) Mothers whose calves died because of starvation or collision with vehicles ($N = 3$) had lower vigilance ($\bar{x} = 29$) levels during playbacks than did mothers with wolf experience ($\bar{x} = 92$) ($F_{1, 16} = 24.625$, $P < 0.0001$), and (ii) differences between these control mothers (who had not lost offspring to wolves) and non-wolf-savvy ones ($\bar{x} = 17$) were not detectable ($P = 0.772$). Moreover, mothers who lost young to predators at the Talkeetna (Alaska) site relocated their subsequent birth sites more than 1.75 times the distance from the prior birth site in the next year than did mothers who reared offspring successfully (22).

Our results suggest that offspring loss to predators may cause maternal hypersensitivity, and they illustrate how differences in the detection of cues may contribute to survival. The sounds of wolves elicited much stronger responses, at least after the initial phase of the blitzkrieg south of Yellowstone Park, than did other cues, and the magnitude of reactions exceeded those of predator-experienced Alaskan moose; responses to odors or the calls of scavengers did not (Fig. 4). Although the lack of predator recognition by naïve prey may have been but one of several factors that contributed to reduced post-Pleistocene population viability (6), for the survivors it remains

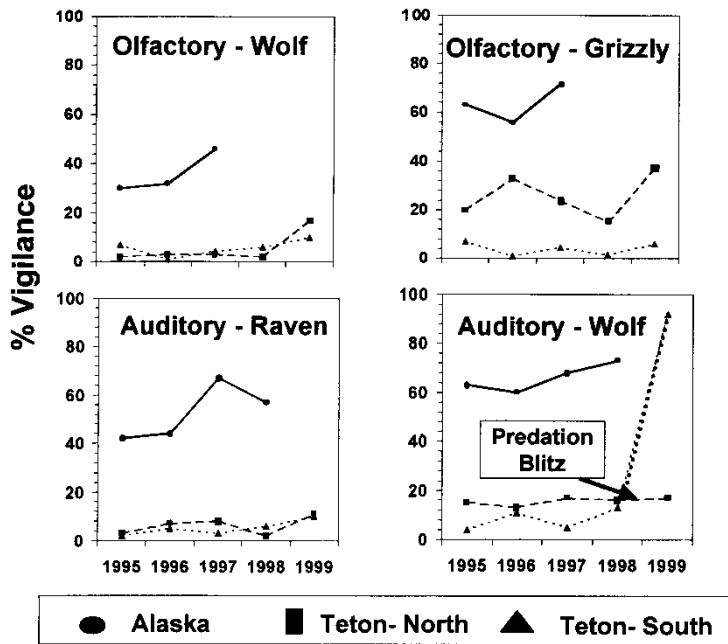


Fig. 4. Summary of comparative mean annual post-playback responses of adult female moose to four cues: olfactory (wolf urine and grizzly bear feces) and auditory (raven calls and wolf howls). The predation blitz is shown once only, but post-blitz responses to all four cues were possible (the differences between females of Teton-South and Teton-North are $F = 24.625$, $P < 0.0001$, and are reflected by the bold dotted line). Data on Alaskan females are as follows: Olfactory, wolf and grizzly (Talkeetnas and Denali); auditory, raven and wolf (Matunsuka, Talkeetnas, and Denali).

unclear whether the acquisition of anti-predatory skills is maintained horizontally or vertically, or if it is just a transitory process (23).

What is evident is that naïve prey have the capacity to process information about predators swiftly—in the case of these moose, in a single generation. Where both young and adults are killed rapidly, opportunities for learning will be diminished and possibilities for local extinction increased. In contrast, where young are primary targets, learning may be transmitted vertically (24, 25), possibly reducing extinction thresholds. Whether behavioral mechanisms some 10,000 to 12,000 years ago retarded or facilitated prey viability as human hunters advanced remains uncertain. Nevertheless, the evidence involving recolonizing brown bears and wolves and moose is partially consistent with a blitzkrieg model but tempered by rapid adaptive learning (Fig. 4 and Table 1). If climate change was not responsible for the Quaternary extinctions (2), then perhaps species that failed to survive post-Pleistocene hunters were simply not quick learners.

Because large native carnivores continue to be reintroduced to parts of Africa, Europe, and North America (26, 27), our findings have conservation relevance. In extant prey, rapid learning may prevent a

complete blitzkrieg, which is something to be welcomed not only by contemporary human hunters but by those of us who favor fewer extinctions.

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12. The reactions of moose were gauged by the proportion of time spent vigilant. Auditory and olfactory playback experiments were conducted using sounds of different species (4) and by presentation of canid urine and bear feces obtained from zoological parks (J. Berger, in preparation). Olfactory trials were done in late winter or spring when temperatures were 0° to 5°C and days were windless. Delivery of olfactory material to within four moose body lengths was accomplished by launching snowballs either soaked in urine or coated with feces from less than 35 m, and

delivery was occasionally facilitated by use of a moose suit.

13. Results do not derive from possible covariates, such as distance to the speaker, group size, distance to cover, or calf presence, all controlled by partial correlation. Data were analyzed by a general linear model [M. J. Norusis, *SPSS 7.5 Guide to Data Analysis* (SPSS, Chicago, IL, 1997)] with a nested design and predation as a treatment, employing data transformed by $x' = \sqrt{x + 0.5}$ because of its variance-stabilizing properties [J. H. Zar, *Biostatistical Analysis* (Prentice-Hall, Upper Saddle River, NJ, 1996)].
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15. The influences of ecological and social variables were examined by multinomial logistic regression on a categorical dependent variable (subject stays or departs) by site and designated covariates, using the chi-square statistic and a $-2 \log$ likelihood ratio as in (13).
16. As in the auditory experiments, regional variation cannot explain the results because a control population of predator-naïve moose in a 2500-acre enclosure on the Kenai Peninsula [C. C. Schwartz, *Alces* (Suppl.) **1**, 177 (1992)] also never abandoned feeding sites when exposed to carnivore odors (Fig. 2), despite the presence of bears and wolves on immediately adjacent lands.
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21. The effects of covariates were not detectable: for calf presence, $F = 0.589$, $P = 0.443$; for distance to cover, $F = 0.000$, $P = 0.987$; for distance to speaker, $F = 1.415$, $P = 0.130$; for group size, $F = 1.89$, $P = 0.665$.
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