Recolonizing Carnivores and Naive 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 naive 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 naive 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 opportunities 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 mamalian prey from past selection pressures (3–5), but the current expansion of large car-

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10. The ΔCH3CN/ΔCO molar ratio refers to the enhancement of these gases compared with background air. The lowest concentrations of CH3CN (140 pptv) and CO (50 ppbv) observed south of the ITZ have been used as background values (ppbv is parts per trillion by volume or pmol/mol, ppbv is parts per billion by volume or ppmv/mole). CH3CN/CO from biomass burning varies according to the fuel type and the burning temperature. The measurements by J. M. Lobert et al. [Global Biogeochem. Cycles, in press] indicate a mean range of 0.13 to 0.25%.
11. We observed a mean molar enhancement of CH3Cl relative to CO of 1.98 × 10-3 in the marine BL, a strong indication of biomass burning emissions; see W. C. Keene et al., J. Geophys. Res. 104, 8429 (1999); J. L. Abell et al., J. Geophys. Res. 104, 8373 (1999). We found high correlations (r2 = 0.9) of CH3Cl with CO, CH4, CH3CN, and CH3NH2, all products from incomplete (biomass) combustion.
13. Ozone measurements were performed from balloons with Electrochemical Concentration Cell sondes coupled to Vaisala radiosondes, on KCO as described by W. D. Komhyr et al. [J. Geophys. Res. 100, 9231 (1995)], and on the R/V Brown as described by D. Klej et al. [Q. J. R. Meteorol. Soc. 123, 2009 (1997)].
15. P. J. Madan et al., Meteorological Analysis During INDOEX Intensive Field Phase—1999 (Centre for Atmospheric Sciences, New Delhi, India, 1999).
16. NO, as measured from the Citation aircraft, was generally below the detection limit of 40 ppbv. On the R/V Brown, NO was generally below 10 ppbv (T. P. Casey, R. R. Dickerson, M. L. Farmer, unpublished data).
22. P. J. Crutzen, M. G. Lawrence, U. Pöschl, Tellus 51A1, 123 (1999). Primary OH production occurs through O3 photodissociation by solar shortwave radiation in the presence of water vapor [the reaction O(1D) + H2O → O(3P) + H2O]. After the initial loss of OH through its reaction with a pollutant gas, e.g., CO, a peroxo radical (e.g., HO2) is formed, which can react with NO, yielding NO2 and generating OH. NO2 subsequently photodissociates and forms O2.
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) Dalarma-Hedmark (Sweden-Norway), (ii) Harjedalen (Sweden), and (iii) Norrbotten (Sweden)] had predatorexperienced 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 occurred 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

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**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).

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**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: snow (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 exclosure on Kenai Peninsula.
Demeanor Predator-experienced (Alaska) individuals were aggressive to and never approached odors, in contrast to naïve ones.

Vigilance Sound and odor playbacks elicit greater responses in predator-experienced (Alaska) than in naïve (Alaska and Wyoming) populations.

Two comparative analyses: (i) Mothers whose calves were killed by wolves (who had not lost offspring to predators) and non–wolf-savvy ones (x² = 8.0195, P < 0.0046 [Wald test]).† One-tailed statistical test: χ² = 4.824, P < 0.028.‡ One-tailed statistical test: P = 0.032 (Fisher’s exact test).§ From (20) and this study.

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

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.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Evidence and comment</th>
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</thead>
<tbody>
<tr>
<td>Anti-predator response [North America: Alaska and Wyoming (USA)]</td>
<td></td>
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<tr>
<td>Vigilance</td>
<td>Sound and odor playbacks elicit greater responses in predator-experienced (Alaska) than in naïve (Alaska and Wyoming) populations.</td>
</tr>
<tr>
<td>Site abandonment</td>
<td>As above</td>
</tr>
<tr>
<td>Demeanor</td>
<td>Predator-experienced (Alaska) individuals were aggressive to and never approached odors, in contrast to naïve ones (irrespective of either Alaska or Wyoming origins).</td>
</tr>
<tr>
<td>Predation [Europe (Sweden and Norway) and North America (USA)]</td>
<td></td>
</tr>
<tr>
<td>Moose at core of bear areas</td>
<td>Moose at colonizing fronts</td>
</tr>
<tr>
<td>Carcass use (all bears)*</td>
<td>2.8% (771) 5.9% (715)</td>
</tr>
<tr>
<td>Carcass use (male bears)†</td>
<td>4.7% (450) 7.8% (503)</td>
</tr>
<tr>
<td>Predation success/attempts‡</td>
<td>0% (15) 37.5% (8)</td>
</tr>
<tr>
<td>Predation: total events§</td>
<td>0 (Yellowstone; −30 years) 10 (Jackson Hole; 5 years)</td>
</tr>
</tbody>
</table>

| Rapid behavioral adjustments associated with predation (North America) | |
| 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: χ² = 8.0195, P < 0.0046 [Wald test].† One-tailed statistical test: χ² = 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).

Fig. 4. Anti-predator response (percentage of trials) and predation (total events) to sound and odor playbacks in predator-experienced (Alaska) and naïve (Alaska and Wyoming) populations. 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).

*One-tailed statistical test: χ² = 8.0195, P < 0.0046 [Wald test].† One-tailed statistical test: χ² = 4.824, P < 0.028.‡ One-tailed statistical test: P = 0.032 (Fisher’s exact test).§ From (20) and this study.
unclear whether the acquisition of anti-
prey 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, opportu-
nities for learning will be diminished and
possibilities for local extinction increased.
In contrast, where young are primary tar-
gets, learning may be transmitted vertically
(24, 25), possibly reducing extinction
thresholds. Whether behavioral mecha-
nisms some 10,000 to 12,000 years ago
retarded or facilitated prey viability as hu-
man hunters advanced remains uncertain.
Nevertheless, the evidence involving recol-
onizing 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 Quater-
nary extinctions (2), then perhaps species
that failed to survive post-Pleistocene hunt-
ers were simply not quick learners.

Because large native carnivores continue
to be reintroduced to parts of Africa, Eu-
rope, 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.

References and Notes
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12. The reactions of moose were gauged by the propor-
tion 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°
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, dis-
tance to cover, or calf presence, all controlled by
partial correlation. Data were analyzed by a gen-
eral 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, em-
ploying data transformed by \( x = \sqrt{x + 0.03} \) because of
its variance-stabilizing properties [J. H. Zar, Biostatis-
cal Analysis (Prentice-Hall, Upper Saddle River, NJ,
1996)].
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York, 1999).
15. The influences of ecological and social variables were
examined by multinomial logistic regression on a
categorical dependent variable (subject stays or de-
parts) 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 popula-
tion of predator-naïve moose in a 2500-acre enclo-
sure on the Kenai Peninsula [C. C. Schwartz, Alces
(Suppl.) 1, 177 (1992)] also never abandoned feeding
sites when exposed to canid odors (Fig. 2), de-
spite the presence of bears and wolves on imme-
diately adjacent lands.
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19. The data derive from 23 predation attempts, deter-
mined from 1306 km of snow tracking in spring in the
three areas, including data from B. Haglund, Viltrey
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Bears of Yellowstone (Island Press, Washington, DC,
1995). Because moose occur at low densities in Yel-
lowstone National Park and the verification of pre-
dation is difficult, it is always possible that predation
was undetected.
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 = 0.189, P = 0.665
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28. Grants or permissions from the U.S. National Science
Foundation, the Norwegian Directorate for Nature
Management, the Swedish Association for Hunting
and Wildlife Management, the Orsa Communal For-
est, the Research Council of Norway, Beringia South,
the Wildlife Conservation Society, Grand Teton and
Denali National Parks, World Wildlife Fund–Sweden,
the Wyoming Game and Fish Department, and the
Alaska Department of Fish and Game facilitated our
research. We thank the students and members of
the Scandinavian Brown Bear Research Project who skied
hundreds of kilometers to follow bear tracks, and for
support, comments, or fieldwork we thank S. Cain, D.
Craighead, C. Cunnington, S. Engelhard, M. Gomp-
er, S. Pyare, K. Redford, M. Reid, T. Roffe, R. Schiller,
White.

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 (Matusnuka, Talkeetnas, and Denali).

10 October 2000; accepted 21 December 2000