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Beyond demography and delisting: ecological recovery for Yellowstone's grizzly bears and wolves

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Abstract

This paper addresses the question, when are threatened or endangered species really recovered? The US Endangered Species Act enables the de-listing of species once demographic criteria are met. In the Greater Yellowstone ecosystem, two protected apex carnivores, grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*), face removal from federal government protection due to population increases, a point at which they are expected to be integrated components of this ecosystem. We tested the assumption that these two carnivores are playing normative ecological roles in the Yellowstone ecosystem by comparing the extent to which wolves and bears have re-instilled anti-predator responses in a primary prey species, moose (*Alces alces*), within wolf and bear recovery zones. As a type of control, we contrasted female moose from two areas in Alaska with different predator regimes to those in Wyoming. Populations from mainland Alaska, a region with a relatively intact carnivore assemblage, responded significantly more to odors of both carnivores. In contrast, a basic anti-predator reaction was lacking in Wyoming; and responses to grizzly bear odor only nominally increased after dependent young experienced heightened mortality. Additionally, the level of response among Alaskan moose living under virtual predator-free conditions for 25+ years closely resembled that of conspecifics in Wyoming. That such striking variation in prey responses exists re-enforces critical ecological differences between predator-intact and -defunct systems. Thus, although grizzly bears and wolves in the Yellowstone area will most likely be de-listed within the next few years, whether such action would be ecologically defensible is arguable. At this point in the recovery process, these predators may currently have limited ecological impacts in large portions of this region, at least as gauged by one potentially important prey species, moose. Although our data suggest ecologically incomplete conditions, other indices of carnivore recovery that include responses of other important prey species such as elk (*Cervus elaphus*), may be more in tune with carnivore activities. We recommend that different types of ecological data available throughout recovery zones be used in consort with demographic criteria to evaluate when endangered carnivores are more fully integrated into their ecosystems. And, in the event of a disparity between these criteria, we also encourage a dialogue focusing on approaches towards bringing ecological conditions in concordance with demographic criteria, irrespective of whether one considers increasing population levels beyond the current target levels required for de-listing,and/or simply, additional time for the recovery process.

Keywords: Carnivores; De-listing; Endangered Species Act; Recovery plans; Greater Yellowstone ecosystem

1. Introduction

Despite the sensational reductions of large carnivores from terrestrial habitats throughout the twentieth century, formal interest in their restitution has only recently become a focal issue in conservation (Gittleman and Gomper, 2001). For instance, federal recovery plans for two prominent carnivores, grizzly bears (*Ursus arctos horribilis*) and gray wolves (*Canis lupus*) have only been in place for approximately 20 years, and until very recently the prospects for formal de-listing from the US Endangered Species list were low. The recovery of these types of large carnivores, in particular, represents a new chapter in conservation and resource management, and de-listing will continue to generate a host of novel issues and challenges for the conservation community, state and federal agencies, local residents, and the public at-large.

What demographic criteria are adequate to ensure the probability of population persistence remains high? This

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question has been asked in one form or another for almost 20 years (Craighead, 1998; Mattson and Craighead, 1994; Schaffer, 1983). For both grizzly bears and wolves, whether the existing number of individuals can be considered sufficient to prevent the species' extinction in the future will undoubtedly remain a contentious issue in the Rocky Mountains of the United States (Clark et al., 1999; Keiter, 1998; USFWS, 1993; Wilcox and Ellenberger, 2000). We believe it is prudent to subject recovery planning for large carnivores to debates about population viability—this will only enhance the long-term effectiveness of conservation strategies by accommodating diverse social, political, and biological criteria. But, we also think that debates that center on population viability have overshadowed efforts to answer a critical underlying question: Will target population levels successfully restore the ecological interactions involving the species in question? Indeed, in the haste to support or refute population estimates and prospects for population viability, the ecological relevance of large carnivores has been viewed as less important to recovery goals. Even when ecological issues have been considered during recovery planning, as had been done prior to the reintroduction of wolves (Cook, 1993), anticipated ecological effects ultimately have not been incorporated into recovery plans. That is, the degree to which a carnivore is expected to interact with other species and alters its ecosystem at-large has not been viewed as a measure worthy of a de-listing benchmark. Major recovery criteria for grizzly bears in the Yellowstone area, for instance, are population-level parameters: the number of unduplicated females with cubs, number of family units, and number of mortalities among both females and the total population (USFWS 1993). Similarly, for wolves, the number of breeding pairs (i.e. 10 for 3 consecutive years) is the criteria required for ESA reclassification and/or de-listing in the Rocky Mountains (Smith et al., 1999; USFWS, 1987).

That an ecological perspective should be viewed as less appropriate than a demographic one in the context of large carnivore recovery is surprising. Research continues to demonstrate that these terrestrial carnivores, perhaps more so than most other threatened or endangered species, have far-reaching consequences for their ecosystems. Not only has predation influenced the evolution and ecology of their prey directly (Caro, 1998; Estes and Duggin, 1995), but it has also had substantive indirect effects on entire ecosystems (Breitenmoser, 1998). Terborgh et al. (1999) summarized anecdotal, empirical, and experimental evidence to illustrate such instances of top-down control. For instance, in addition to affecting the densities of ungulates (Bergerud, 1988; Messier and Crete, 1985; Hatter and Janz, 1994; White et al., 1998), wolves modulate beaver foraging patterns, and consequently have top-down impacts on beaver–plants dynamics (Naiman et al., 1994; Pollock et al., 1995). Wolves have also had such diverse cascading effects as altering growth rates of balsam-fir and aspen-willow communities via impacts on browsing ungulates (McLaren and Peterson, 1994; Messier, 1994; Ripple et al., 2001), as well as affecting mesocarnivore and scavenging communities in Yellowstone National Park (Crabtree and Sheldon, 1999a,b; Stahler, 2000). And, the loss of grizzly bears and wolves has caused a cascade of interactions that ultimately decreased the diversity and nesting densities of Neotropical avian migrants via herbivory-induced effects in willow (*Salix* spp.) communities (Berger et al., 2001a). The possibility of such ecological effects had not been completely ignored during recovery planning: Cook (1993) discussed ecological issues prior to the reintroduction of wolves into Yellowstone National Park. From a heuristic perspective, it seems appropriate to ask why ecological criteria were not more explicitly incorporated in recovery plans for these types of important species?

One obvious reason is based on the conventional interpretation that the Endangered Species Act solely prevents species' extinctions or declines through population-level monitoring (Clark, 1994). Closer examination of the Act's language, however, suggests that the Act was designed with a broader intent and more flexible approach:

> The purposes of this act are to provide a means whereby the *ecosystems* upon which endangered species depend are conserved; and
>
> The Secretary, in developing and implementing recovery plans, shall provide *objective, measurable criteria* which, when met, would result in a determination . . .that the species be removed from the list. (From the Endangered Species Act of 1973)

Thus, the Act is an implicit recognition of the importance of restoring species *and* associated ecological processes to defunct ecosystems. A complementary interpretation of the Act, therefore, appears to support an approach that would include, at least in part, the monitoring of ecological processes associated with recovering species, so long as these processes are measurable and capable of facilitating recovery objectives.

A second reason for the lack of ecological consideration may be the expediency with which individuals of a species can be enumerated and assessed, while ecological parameters, such as the impacts of a re-colonizing predator on prey populations, are viewed as too difficult to define and measure, and hence peripheral to the recovery process. However, we believe that studies of predator-prey interactions can illustrate the utility of ecological data for monitoring the extent of carnivore recovery and for assaying predator-induced ecosystem change. Our intent, here, is to offer data within carnivore recovery zones of the Greater Yellowstone area to explore both practical and problematic issues associated with the use of selected non-demographic criteria in gauging ecological recovery of carnivores. We do so by specifically focusing on a case study involving the interactions of moose (*Alces alces*) with grizzly bears and wolves.

We selected moose because it is widely known that moose are affected by large carnivores throughout North America and in Scandinavia (Gasaway et al., 1992; National Academy of Sciences, 1997); annual juvenile mortality may reach 90% (Bowyer et al., 1998; Swenson et al., 1998). Indeed, a priori, moose were expected to be an important prey species for wolves and grizzly bears in the Yellowstone area prior to the reintroduction and/or recolonization of these carnivores (Boyce, 1993; Singer and Mack, 1993), and predation by both species has been subsequently verified (Berger et al., 2001b). Although other prey species such as elk (*Cervus elephas*) and mule deer (*Odocoileous hemionus*) might be equally appropriate choices, only moose allow for application of a robust experimental design. In Alaska, moose exist in areas with complete predator regimes and attendant data on predator–prey dynamics in this system are available (Gasaway et al., 1992; National Academy of Sciences, 1997). Likewise, moose in Wyoming have existed with defunct carnivore assemblages (Berger, 1998), and data on the reproductive and behavioral histories of individuals are available both prior to and after carnivore recolonization in the southern Greater Yellowstone area. Unlike other possible prey species in the Yellowstone area, longitudinal comparisons of moose are available with the advent of carnivores (Berger et al., 2001b). In any event, our study of moose provides a data-driven case study with which we can begin to illustrate the utility of ecological data in the context of carnivore recovery. Our hope is that at the approach used here can serve heuristically to evaluate and discuss progress towards ecosystem restoration.

2. Methods

2.1. Rationale and working hypotheses

As in many predator–prey systems, prey species exhibit a variety of anti-predator actions designed to thwart immediate mortality (Caro, 1998; Byers, 1997), but other effects may be sub-lethal or interactive within the local environment including group formation, habitat shifts, and site abandonment (Lima, 1998). In moose, these vary from simple postures to more evasive, ecological responses (Table 1). Nevertheless, where bears and wolves have been extirpated, so have these responses, often within 10 generations or less (Berger, 1999). It is unclear, however, what intensity of predation must be in place, and for how long, to restore these responses.

Our working hypothesis is this: if wolves and grizzly bears are considered recovered in the Greater Yellowstone area, then moose in carnivore recovery zones should have achieved the normative level observed in more intact ecosystems, as is true of populations experiencing high risk of predation (Table 1). Furthermore, moose in the Yellowstone area should also differ from those populations that lack predators. We assessed whether re-colonizing grizzly bears and wolves have yet re-instilled patterns inherent in intact predator–prey systems by attempting to address four questions: (1) Do predator-detection patterns differ geographically? (2) Does predator-directed aggressiveness vary by population? (3) Is frequency of departure from local feeding sites by moose consistent with patterns in the above two questions? And, (4) Do females that have lost young to predators display greater within-population responses to olfactory cues of carnivores than females that have not? Answers to these questions will help address the broader issue of when carnivores can be considered an integral part of the ecological communities to which they have been putatively restored, irrespective of whether the process involves natural re-colonization or a human re-introduction.

2.2. Study areas, assumptions, and comparisons

Between 1995 and 2000, we studied moose in three types of sites (Fig. 1): (1) Grand Teton National Park (GTNP) where grizzly bears have increased since the 1990s (Bader, 2000; Schwartz et al., in press), and recolonization by wolves began in 1997. Prior to this period, wolves and grizzly bears had been absent for 60–75 years; (2) the Talkeetna Mountains and Denali National Park and Preserve, both located in interior Alaska (USA), where juvenile moose recruitment is low due to high rates of wolf and grizzly bear predation (Gasaway et al., 1992; Bowyer et al., 1998; Testa et al., 2000). We considered our data from the Talkeetnas and Denali as independent, and therefore not pseudo-replicates, because these populations were more than 150 km apart and females typically do not migrate such long distances (Franzmann and Schwartz, 1998); and (3) on the Kenai National Wildlife Refuge where for about 25 years the State of Alaska's Department of Fish and Game has maintained a 2500-acre, fenced research facility within which moose move freely. We categorized the enclosure as "predator-free", although black bears, and to a lesser degree, wolves, infrequently infiltrated the enclosure but had little demographic effect on either adult or juvenile moose prior to or during our study period (Schwartz and Franzmann, 1991). Outside the enclosure, moose are preyed upon by black bears, grizzly bears, and wolves (Franzmann and Schwartz, 1986). To summarize, we assumed that the responses of moose from these

Table 1
Types of anti-predator responses of varying intensity that moose may exhibit in ecosystems with carnivore assemblages that are either intact or defunct

Level of response	Implication	Example of behavior	Behavior shown?	
			Ecologically intact assemblage	Ecologically defunct assemblage
First order	Awareness	Vigilance	Yes	No
Second order	Recognition	Piloerection, ears back	Yes	No
Third order	Avoidance	Site abandonment	Yes	No

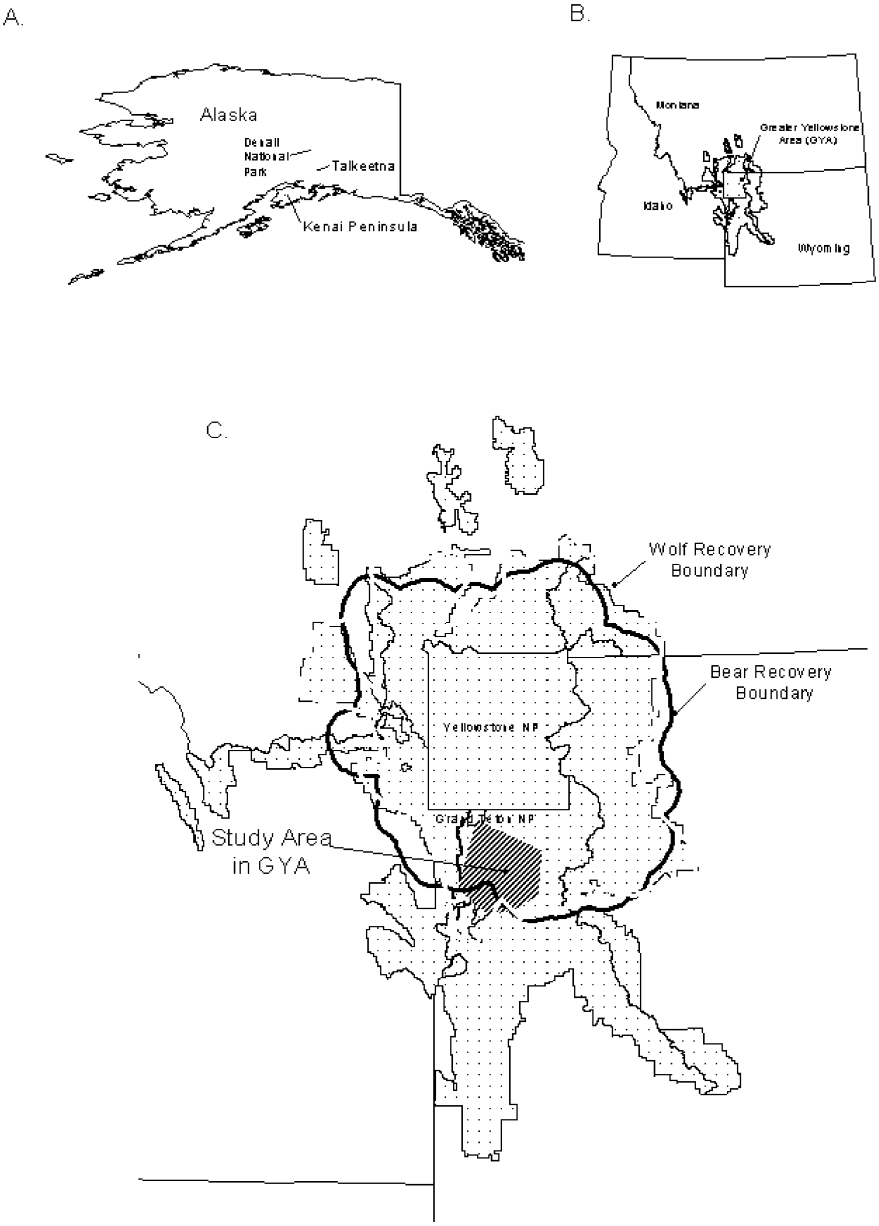

Fig. 1. (A) Study regions of interior Alaska: Denali National Park and Talkeetna, where carnivores present, and the Kenai enclosure, where predators are largely absent; (B) general study areas in the Greater Yellowstone area, where carnivores have been absent until recently; and (C) the specific study area within the southern Greater Yellowstone area, where moose data have been collected within wolf and bear recovery zones.

three discrete areas independently reflected their history of interactions with large carnivores.

We confirmed empirically our assessments of predation status (e.g. predator-free, predator-experienced) using data on survivorship both inside and outside of our mainland Alaska study populations; juvenile mortality was three times as great at sites with grizzly bears and wolves than at those without them (Berger, 1999; Testa et al., 2000). Of equal relevance, of course, is that the predator-free stasis that had existed in Jackson Hole for 60-75 years was recently punctuated due to re-colonizing grizzly bears (in the 1990s) and wolves [that were restored first to Yellowstone Park per se in 1995 (Smith et al., 1999) and then appeared as residents in Jackson Hole in late 1997].

2.3. Sampling and analysis

We focused our sampling on adult female moose because they were minimally harvested in these three study areas whereas adult males were hunted (i.e. outside of National Parks). Baseline data were gathered by establishing the proportion of time that moose spent feeding per 180 second bouts, and then by either allowing the bouts to continue or by inducing a perturbation (Berger, 1999). Control and experimental treatments representing olfactory cues of grizzly bears and wolves were presented to moose in random sequences. Treatments were administered by placement of snowballs immersed in either urine (for wolves) or feces (grizzly bears) to within four body lengths of foraging females (Berger et al., 2001b). Three dependent variables were then recorded, each of which represented levels of behavioral response to novel and familiar cues associated with predators and other species (Table 2). Response data were recorded for two distinct periods: the 30-s period immediately following deposition of the cue, and then until the animal resumed feeding or departed from the local site. All experiments were performed in late winter or early spring during windless conditions and with ambient temperatures between 0 and 5 °C.

Numerous covariates that may have confounded our interpretation of animal responses (Table 2b) include (1) distance between the subject and concealment canopy (Molvar and Bowyer, 1994), (2) snow depth (because animals in deep snow are more vulnerable to predation (Mech et al., 1998), (3) distance to odor (evaluated by body lengths of the subject to the odor deposition site), (4) group size [either because in large groups individual responses are affected by a neighbor's response (Berger, 1998) or less vulnerable to succumbing to an attack (Fitzgibbons and Lazarus 1995)], and (5) presence of a calf. For interactions that we simulated to examine responses to grizzly bears, we used identified females whose calves fates were known whose (e.g. either survived or subsequently disappeared). To evaluate whether calves had been lost, we checked pregnancy status using non-invasive procedures (e.g. contrasts of fecal steroid levels), and then intensively monitored females to document birth and fate of calves (Berger et al., 1999). Thus, it was possible to contrast responses of mothers whose calves died or survived (Berger et al., 2001b).

We controlled for the possible effects of these potential covariates statistically through the use of partial correlation. Our analyses involved a general linear model (SPSS, version 10.0) in which the dependent variable (Y) was transformed according $Y \cong x + 0.5$, where x is the proportion of time spent not feeding. As recommended by Zar (1996), 0.5 was added for variance stabilizing properties. Predation was used as the treatment in a split-plot ANOVA, and multinomial logistic regression was employed for categorically dependent variables (subject stays or departs, calf lives or dies) by site and with calf presence and distance to canopy (cover) as covariates based on Chi-square statistics and −2 log likelihood ratios (Norusis, 2000).

3. Results

(1) *Do predator detection patterns differ geographically?* Levels of vigilance by moose varied both by site and cue (Fig. 2; left side). Neither control (e.g. observations of non-manipulated individuals) nor snow balls with human (hand) scent produced differences

Table 2
Summary of olfactory experiment to evaluate anti-predator responses among Alaskan and Wyoming moose to different odor treatments

a. Independent treatments and experimental justification		b. Covariates	c. Dependent variables measured
(1) Snow ball (control)	Baseline response	(1) Distance to subject	(1) Time vigilant / 30 sec
(2) Human urine	Cue of human predator	(2) Distance to cover	(2) Behavior responsiveness:
(3) Wolf urine	Cue of canid predator	(3) Presence of calf	e.g. Walking approach—curiosity
(4) Grizzly bear feces	Cue of ursid predator	(4) Snow depth	Ears forward—curiosity
		(5) Group size	Sniffing/head lift—passive
			Piloerection—aggressiveness
			Ears retracted—aggressiveness
			(3) Whether local site is abandoned

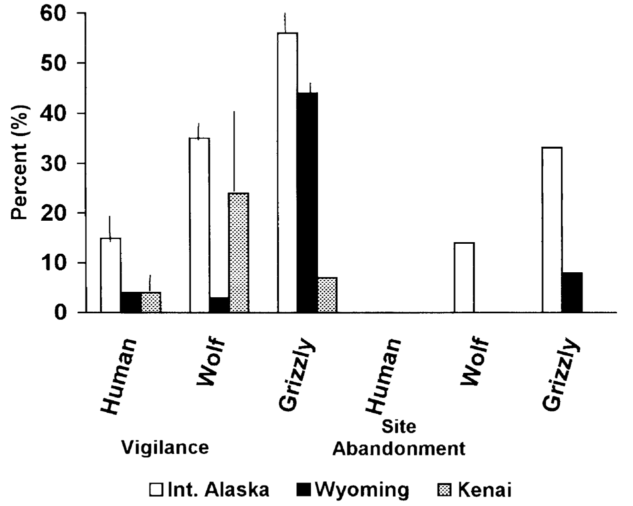

Fig. 2. Comparison of female moose responses (% vigilance per feeding bout and% site abandonment) to different odors among study areas. Control treatments (snowballs) produced no differences among sites for both response types, and thus are not shown. Bars for vigilance data represent standard error. Sample size for vigilance data in Interior Alaska, Wyoming, and the Kenai Peninsula, respectively, are as follows: Human urine (18, 59, 7), Wolf urine (22, 88, 6), and Grizzly bear feces (19, 80, 4). Sample sizes for site abandonment data in Interior Alaska, Wyoming, and the Kenai Peninsula, respectively, are as follows: Human (18,43, 5), Wolf (22, 64, 6), and Grizzly bear (19, 55, 4). (Data modified from Berger et al., 2001b).

among sites. For responses to wolves, however, site effects were striking; female moose from interior Alaska were more vigilant than Wyoming moose irrespective of whether the odor was first deposited or had been on the ground for several minutes ($F=15.843$, df = 4, 114, $P<0.0001$; $F=11.258$, $P<0.0001$, respectively). Responses to grizzly bears also showed variation by site but were not statistically different. Interior Alaskan and Wyoming moose failed to differ at either initial deposition or for subsequent responses to grizzly bear odors ($F=1.428$, df = 4, 91, $P=0.231$; $F=0.648$, $P=0.630$, respectively). Qualitatively, Kenai females were also less responsive but we did not analyze the data due to small samples ($N=4$ trials for grizzly bears, six for wolves).

The presence of human urine affected interior Alaskan moose to a greater degree during both initial and subsequent depositions ($F=3.515$, df = 4, 80, $P=0.011$; and $F=5.481$, df = 4,80, $P=0.011$, respectively) suggesting that unfamiliar smells might also signify possible danger. The only covariate that significantly affected vigilance was the distance of moose to cover at Alaskan sites (F = 4.220, $P=0.042$).

(2) Does predator-directed aggressiveness (i.e. retracted ears or piloerection) vary by population? Moose from interior Alaska were more than three times as likely to respond aggressively than Wyoming moose to any cue associated with a potential predator (Fig. 3; inset). In contrast, Kenai moose never displayed aggression to those same cues. Both the Kenai and Wyoming moose approached odors (44 and 6% of trials, respectively) whereas moose from interior Alaska never did, an indication that predator-naïve moose were insensitive to cues of species that could potentially prey upon them.

(3) Does predation regime affect frequency of departure from feeding sites? More than half the trials in interior Alaska (52%, $n=23$) could not be completed because females departed the experimental area yet only 6% of the trials in GTNP ($n=54$) were not completed (Fig. 2). This result is not a consequence of differences in moose responses to humans, because the deposition of human odors (urine) failed to produce variation between sites (Fig. 2). All 10 trials at the Kenai facility were completed. Only site location exerted a strong effect on the probability of abandonment ($\chi^2=17.580$, $P<0.0001$), whereas distance to cover ($\chi^2=1.519$, $P=0.218$), distance to odor ($\chi^2=1.355$, $P=0.244$) and calf presence ($\chi^2=1.131$, $P=0.288$) did not.

(4) Do females that have lost young to predators display greater within-population responses to olfactory cues of carnivores than females that have not? We restricted our investigation of this question to females in the Grand Teton National Park region because similar data were unavailable for our other regions; calves were lost to predation only rarely at Kenai and/or females were either inaccessible or not sufficiently habituated for olfactory experiments. Wolf odors produced no obvious differences irrespective of calf status and timing of deposition (initial: $F=0.037$; df = 1, 31, $P=0.850$; post-deposition: $F=0.654$; $P=0.468$). For grizzly bear odors, differences in vigilance between mothers that did and did not experience calf deaths at initial deposition were not evident ($F=0.711$, df = 1, 24, $P=0.410$). Subsequently (i.e. at least 30 s later), however, the response

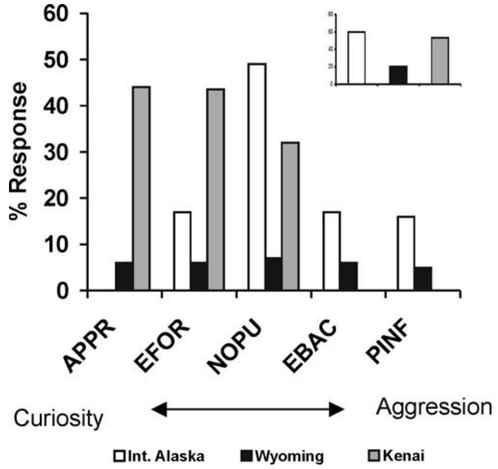

Fig. 3. Comparison of response types by moose to odors of predators among sites. Responses range from curiosity to aggression and were characterized by the following postures: Approach (APPR), Ears Forward (EFOR), Nostrils Pulsate (NOPU), Ears Back (EBAC), Piloerection of Nape Fur (PINF). Inset illustrates overall rates of (any) response. Sample sizes are as follows: Interior Alaska ($n=24$ trials), Wyoming (77), and Kenai Peninsula (9).

was greater for mothers who lost calves ($F = 8.132$, $P = 0.011$; Fig. 4). For neither grizzly bear nor wolf odors did covariates have an effect.

4. Discussion

4.1. Prey in environments with variable predation

Had re-colonizing carnivores in the Greater Yellowstone area re-instilled anti-predator mechanisms into species considered important prey, then moose in these carnivore recovery zones should have reacted similar to or approached levels reflective of conspecifics from interior Alaska. Our evidence from Wyoming, however, shows moose are not yet behaving with resilience to a changing environment with predators. Even the frequency of rudimentary anti-predator behavior was low relative to interior Alaska. The first-order response—vigilance—of Wyoming moose to wolf odors was negligible and surprisingly even less than that of our Kenai (predator-free) population. On the other hand, moose in Wyoming responded to grizzly bear odors at higher rates than those of Kenai females, but still significantly less than those in interior Alaska (Fig. 2). Second-order aggressive responses, retracted ears and piloerection, irrespective of whether cues originated from grizzly bear or wolf, were one-third as frequent among Wyoming moose than interior Alaskan moose, and they were lowest for predator-naïve females on the Kenai (Fig. 3). The third-order response, site abandonment, to grizzly bear odors was almost five times less frequent in Wyoming moose than in interior Alaska, and Wyoming moose never abandoned locales due to wolf odors (Fig. 2). For both second- and third-order cases, moose in Wyoming resembled Kenai individuals. Finally, female moose that lost young in Wyoming show only a delayed response to odors of grizzly bears, and no overt response to odors of wolves (Fig. 4).

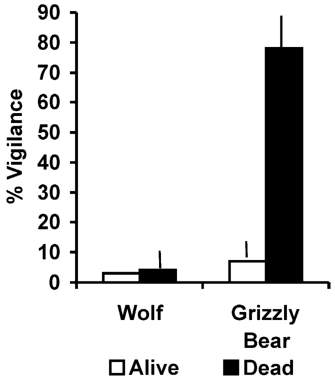

Fig. 4. Comparison of vigilance responses to grizzly bear feces and wolf urine in female moose that did and did not lose young to predators in Jackson Hole, Wyoming. Only post-deposition responses (i.e. 30 s after initial deposition) are shown. Bars represent standard error. Sample sizes for mothers with live and killed calves, respectively, are as follows: Wolf (26,6), Grizzly bear (19, 5).

That major differences still exist between moose in Wyoming and interior Alaska, and that major similarities still exist between moose in Wyoming and a predator-free (Kenai Peninsula) population, suggest that olfactory acuity has not increased appreciably among moose inhabiting these parts of Yellowstone carnivore recovery zones. Thus, although grizzly bear and wolf populations are approaching or may have already exceeded population-level targets for recovery, or even expanded beyond their recovery zones (Bader, 2000), at this point in recovery process , the ecological effect of these carnivores may be incomplete because they are not affecting the behavior of at least one important prey species.

4.2. Half-empty processes and ecosystems

Redford (1992) introduced the idea of the "half-empty forest", suggesting that, even when they look "full", habitats like tropical forests are often depopulated of their mammalian faunas through over-harvest, and thus, are ecologically defunct. Similarly, individual species, even though they are not yet extinct, should be considered ecologically extinct because they have declined to such a critically low level that they rarely interact with other species (Estes et al., 1989; Novaro et al., 1999). While this emphasis on ecological functionality has been advanced to warn about the condition of habitats or species in decline, such ecological thinking should also be applied to instances of species recovery, especially where large carnivores are relevant. Policies and practices that focus strictly on demographic concepts of recovery, and that ignore ecological recovery, may ultimately neglect the resumption of important underlying ecosystem processes (Redford and Feinsinger, 2001; Conner, 1988). That is, recognition of the thresholds at which large carnivores become ecologically recovered, as opposed to strict recognition of demographic viability, will help ensure these large carnivores become truly restored components of their ecosystems.

Nevertheless, a caveat is clearly necessary about truly restored functionality at least within the central or northern Rocky Mountains. The target regions of wolf and grizzly bear recovery contain habitats occupied by seven native ungulates (Berger, 1991), and therefore they differ in community structure and complexity from those subarctic systems where we used moose as a scientific control because of an unbroken stasis in predator–prey relationships. It is possible that moose in the Rocky Mountains system were never as completely "tuned" to grizzly bears and wolves as they are in Alaska because of the presence of a greater diversity of alternate prey in the south. However, the evidence

(Fig. 4) that moose in the Tetons are now becoming savvier to cues associated with grizzly bears suggests that the capability exists for prey to (re-) adapt to predators that affect them in more northern systems. With this being the case, it seems appropriate to initially suggest a loss of functionality because of the fundamental differences in moose responsiveness in systems with and without large carnivores.

Might prey species other than moose have been more apt to assess effectiveness of carnivores with respect to recovery? Elk, clearly, are common targets of Yellowstone wolves, comprising more than 90% of their diet (Mech et al., 2001), and bison have also been noted as occasional victims (Smith et al., 2000, 2001). Although data on anti-predator actions are unavailable for either of these species prior to the re-introduction of wolves, and data are also lacking for responsiveness to grizzly bears, some preliminary data on vigilance have been gathered. Elk apparently were more vigilant inside wolf home ranges than beyond them; for bison, there was no similar effect (Laundre et al., 2001). Despite the possible confounding influence of group size or habitat visibility on vigilance, these results support our notion that wolf effects are immediate, but only in areas of wolves and only for elk. Thus, if the lack of effect on bison vigilance is real, then two of the three species in areas with wolves and grizzly bears show little overt response to these possible carnivores. Elk do, which makes some sense; had they not, or their responses being non-adaptive, extinction would be imminent.

4.3. *A framework to implement ecological recovery of Yellowstone's carnivores*

The use of ecological criteria that are complementary to population-level parameters offers a more conservative approach when evaluating the progress of recovery efforts for influential endangered species. If coordinated ecological data are (or have been) collected concurrently to population monitoring, additional evidence may help support or refute hypotheses about whether recovery has actually occurred. Thus, we offer our data on the grizzly bear–wolf–moose system as an initial step in recognizing the importance of ecological data in consort with demographic data, and as an opportunity to develop a cooperative framework for applying additional ecological information to recovery.

Because there are no formal mechanisms by which ecological criteria can currently be applied to recovery, we have three recommendations. First, if ecological criteria are to be adopted, they should reflect—we would hope—interactions not only involving a single aspect of one prey species but dimensions that incorporate realistic processes throughout the recovery area. Our choice of using moose behavior was perhaps not the best selection for a test of ecological functionality, but was utilized simply to provide a data-driven illustration of the merit of an ecological approach, and, had we promoted moose behavior as an exclusive assay of carnivore status, our approach should rightfully be subject to criticism. But our aim is not to promote moose behavior per se. Perhaps had we selected smaller-bodied ungulates such as elk or mule deer, the results might indeed have shown greater sensitivity to wolves or grizzly bears, as apparently is the case for elk (Laundre et al., 2001). Thus, we recommend that a variety of ecological data, either already available or actively being collected, such as those in Table 3, be applied collectively to corroborate the status of recovery in the Yellowstone area. For instance, existing information is available on several species in addition to moose, both prior to and after wolves reappeared in the Greater Yellowstone area. Such information on demography, distribution, habitat shifts and other variables, will shed light on species- and community-level ecological responses to the progress of recovery efforts.

Second, we recommend utilizing ecological samples that are well distributed throughout recovery zones to most accurately represent the overall status of species. Admittedly, our study focused only on animals primarily along colonizing fronts of carnivores in the southern Greater Yellowstone area. Likewise, we would be hesitant to make conclusions derived from ecological data that are collected solely from the geographic centers of recovery zones, where, for instance, wolves have achieved the highest densities ever recorded not only in Yellowstone history (D. Smith, personal communication) but also in all of North America (see Fuller and Murray, 1998). Such data sets may therefore be subjective and simply not represent the status of the species in recovery zones at-large. Our point is this: to most accurately evaluate the level of concordance between ecological and demographic criteria, ecological assays should extend as far across recovery zones as possible.

Third, should a disparity exists between demographic and ecological conditions, an effort should be made during recovery planning to consider additional actions required to bring about desired ecological conditions. Consideration should be given to understanding the ecological consequences of least two possible actions. One, efforts should be directed to determine not just at what level a population is viable, but what additional population increases may restore ecological functionality. Such assessments will require information about ecologically effective densities and levels of interactions across ecosystems. A logical expectation is that ecological impacts will be evident at a population level higher than that required for viability, and in the Yellowstone predator–prey system, increasing predator densities would most likely increase the probability of predator–prey encounters and therefore levels of ecological response. On the other hand, a second consideration

Table 3
Selected list of information specific to federal recovery areas (Fig. 1) within the Yellowstone area that may be available to evaluate the ecological recovery of wolves and grizzly bears

Type of ecological criteria	Possible example(s)	Possible sources of data
Prey Demography	Elk pop. Size	Singer et al., 1997; Smith and Anderson 1996, 1998; National Park Service, unpublished
	Elk distribution	Schaefer, 2000
	Bison[a]	Smith et al., 2000, 2001
	Moose productivity[a]	Berger et al., 1999, 2001b
	Moose pop. Size	Wyoming Game and Fish, unpublished
	Pronghorn[a]	Caslick, 1998; Byers, unpublished
Prey anti-predator responses	Elk[a]	Laundre, et al. 2001; Berger, unpublished
	Moose	Pyare and Berger, this study
	Bison[a]	Berger, unpublished
	Pronghorn[a]	Byers, unpublished
Mesocarnivore effects	Coyote ecology[a]	Crabtree and Sheldon, 1999a,b
	Black Bear[a]	Holm et al., 1999; Interagency Grizzy Bear Study Team, unpublished; Beecham, unpublished
	Cougars[a]	Murphy, 1998; Ruth, 1999
Lower trophic-level effects	Vegetation structure[a]	Kay 1993; Singer et al., 1994; Dieni et al., 2000; Ripple and Larsen, 2000; Ripple et al., 2001; Berger et al. 2001b
	Scavenging community[a]	D. Smith, unpublished; Berger, 1999; Stahler, 2000
	Avian diversity[a]	Berger et al., 2001a; E. Anderson, unpublished

We propose that such data be collectively applied along with demographic data to support de-listing decisions and/or post-delisting management pratices.

[a] Indicates study ongoing.

should be given to understanding the ecological consequences of maintaining target population levels and protective status for extended periods of time, that is beyond the point in time at which de-listing would normally occur based on demographic criteria alone. Understandably, there may be a time lag associated with the restoration of ecological processes. For instance, in the Yellowstone ecosystem, as a progressively greater proportion of an ungulate population encounters predators, even with negligible increases in predator population levels and expansion trends, one would expect that a greater proportion of these prey populations would exhibit anti-predator responses and be ecologically ‘‘attuned’’. However, because populations simply held at levels targeted for de-listing do not guarantee that ecological processes will be restored, or do future social and political conditions necessitate that ecological criteria be met, a conservative approach to comprehensive recovery would be to verify ecological conditions prior to complete removal of protected status. For either of these two possible solutions, we re-emphasize the importance of considering a multitude of data (such as listed in Table 3) when interpreting the ecological conditions of an ecosystem, for example, restoration of anti-predator behavior does not necessarily imply other ecological processes are prevalent in the ecosystem.

In the Yellowstone case, grizzly bears and wolves will be de-listed from federal protection sometime during the next few years partly because population levels will eclipse demographic criteria. Clearly, de-listing is a conservation victory of sorts because the public benefits as the chances for that species extinction is reduced, and federal expenditures can be directed elsewhere. Nevertheless, because there have been few complementary efforts to evaluate the ecological functionality of these carnivores, the public will inevitably assume that these carnivores have been completely restored to the Yellowstone Ecosystem. We believe that this assumption of recovery is a disservice to the public and, in particular, a misleading (albeit not deliberate) use of the umbrella species concept by which large carnivores initially gained widespread conservation support (Noss et al., 1996; Berger, 1997). It’s unlikely that relevant resource agencies—whether federal or state—will be able to overcome their financial and political strain to include ecological criteria anytime soon. Still, the problem remains that de-listing on the basis of demographic criteria is unlikely to inform decisions about ecologically functional populations. In Wyoming, Idaho, and Montana, some de-listing proponents advocate for regulated harvesting of grizzly bears immediately following reclassification. It should be clear that, even if harvesting has little demographic effect on the viability of bears, processes at the ecosystem level could be attenuated without careful monitoring and taking an ecological perspective of post-delisting impacts. If ecological functionality is not useful as a guide for recovery, efforts may be for naught—what will we have achieved by putting wolves and grizzly bears in the Yellowstone Ecosystem if their ecological roles are not complete in, at least, their recovery areas?

By posing the questions, "When are de-listed species really recovered?", and "What is recovery?", we have hopes that (1) conservation scientists will get involved in efforts that focus on issues larger than demographic criteria alone, and (2) the agencies that assume post-delisting responsibility will begin to support the argument that recovery is truly complete only when viable populations are also ecologically functional.

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