TROPHIC CASCADES

Predators, Prey, and the Changing Dynamics of Nature

CHAPTER 14

Fear-Mediated Food Webs

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Modern humans feel a primordial dread when walking alone through habitat occupied by lions, tigers, or grizzly bears. Many prey species must similarly be gripped with fear in the presence of predators. Even today's megavertebrates—elephants, rhinos, and whales—who some might claim are immune to predation by virtue of their size, alter their movements and patterns of habitat use to reduce predation on neonates (Berger 1993; Reeves et al. 2006). In this chapter I consider the behavioral and ecological consequences of fear as manifested primarily by large mammals and as revealed in comparisons of prey species in contrasting situations of high and low risk of predation.

For behavior in general and fear in particular to affect trophic relationships requires that prey are cognizant of predators, that they adjust their behaviors in relation to predation risk, and that prey responses influence the distribution of herbivory on the landscape. In this chapter, I ask, To what extent does the threat of predation govern prey behavior? How do the indirect effects of predators affect ecological dynamics? And do such indirect effects matter?

I concentrate on large terrestrial mammals because ample evidence already indicates that big carnivores play key (top-down) roles (Terborgh et al. 2001; Smith et al. 2003a), although not all authors agree on this point (Ray et al. 2005). Furthermore, studies of known individuals reveal population-level variability in response to predation and indicate how this variability drives community dynamics.

BACKDROP: LABILE BEHAVIOR AND PREDATION THREAT

Tradeoffs between food acquisition and predator avoidance are widespread in nature and operate in both the terrestrial and aquatic realms (Sih 1992; Bowyer and Kie 2004; Estes et al. 2004; Polis et al. 2004). In marine settings, for example, dolphins, harbor seals, and dugongs use such tradeoffs, as do many fish species (Werner 1991; Wirsing et al. 2007), demonstrating that fear operates across diverse biomes (Kie et al. 2003; Heithaus et al. 2007). Predator-sensitive behaviors are those that differ under situations of high or low risk of predation. When predator-sensitive behavior is pronounced, predators may indirectly regulate food web interactions via shifts in group size, habitat use, or activity period.

To investigate these issues further, I compared a number of Holarctic localities that either did or did not support large carnivores. I then performed field experiments to simulate carnivore presence by exposing prey species to the sounds or odors of predators (Berger et al. 2001b; Berger 2007a). Associated conditions were also explored as covariates, including snow depth and habitat (proximity to dense cover), because each such covariate might either heighten or dampen behavioral responses by altering the perceived vulnerability to predation (Figure 14.1a).

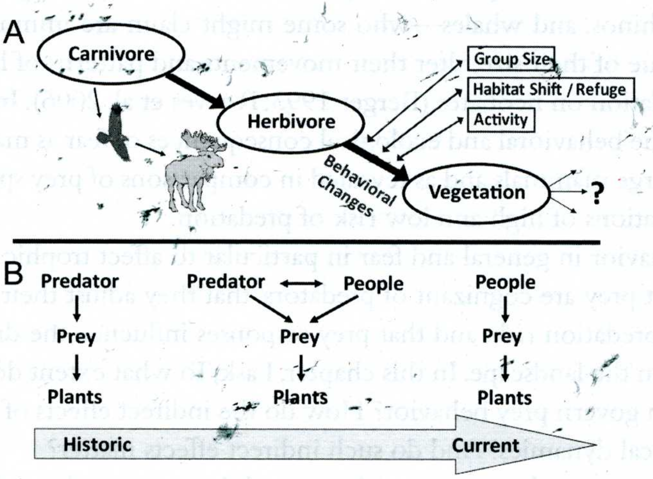

Figure 14.1. **(a)** Depiction of primary pathways by which apex carnivores might be expected to affect indirectly prey behavior and subsequent trophic relationships. **(b)** Depiction of changing temporal dynamics in which historic conditions reflect a simple food web with large apex large mammalian predators in the absence of predator, a transition into a time when people and predators experienced intraguild predation, and, finally, relationships today with people replacing predators.

Conservation Context and Changed Functional Responses

Predator-mediated selection on ungulates has been relaxed over much of the contiguous United States. Only small parts of Washington, Montana, and Wyoming have retained grizzly bears, and wolves survived only in Minnesota and have recently been restored or naturally spread to Michigan, Wisconsin, Montana, Idaho, and Wyoming. However, carnivore presence has been continuous at more northern latitudes, creating opportunities to compare predator-sensitive behavior from behavioral and ecological perspectives.

Fear responses may be general, so that prey such as mule deer or peccaries may still show a full repertoire of predator-sensitive responses in the absence of wolves or cougars, if coyotes or black bears fill the void. Therefore, prey behavior may remain unaltered, even where presumptive top predators are missing. Relationships between prey behavior and carnivore presence were evaluated under three treatments: predators absent (naturally or extirpated by humans); predators present, having coexisted continuously with target prey; and predators reintroduced (Figure 14.2).

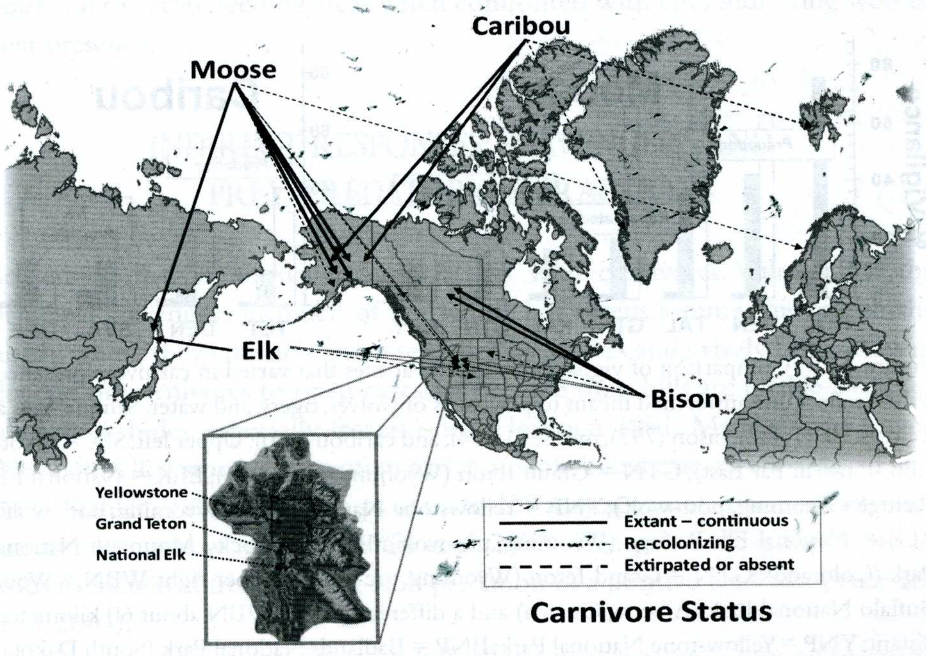

Figure 14.2. Overview of study areas and carnivore status by prey. Extant carnivore distribution is as follows. Russian Far East, tigers, brown bears, and wolves; Alaska, wolves and brown bears except Kalgin island (no carnivores); northern Alberta, wolves; Yellowstone Ecosystem has reintroduced wolves and expanding grizzly bears (see Berger 2007a for further details).

I conducted two types of experiments: exposure to auditory signals (all prey) and olfactory stimuli (moose only). Recordings of running water, wolf howls, tiger roars, and howler monkey hoots were broadcast for 25 seconds at fixed levels (90–100 decibels at 1 meter) under calm conditions. Prey response was gauged as the proportion of time diverted from feeding by vigilance. Additionally, whether the members of a group moved closer together or departed from their feeding sites was noted as responses to wolf playbacks except in the Russian Far East, where tigers were the key predator (Figure 14.3). Covariates

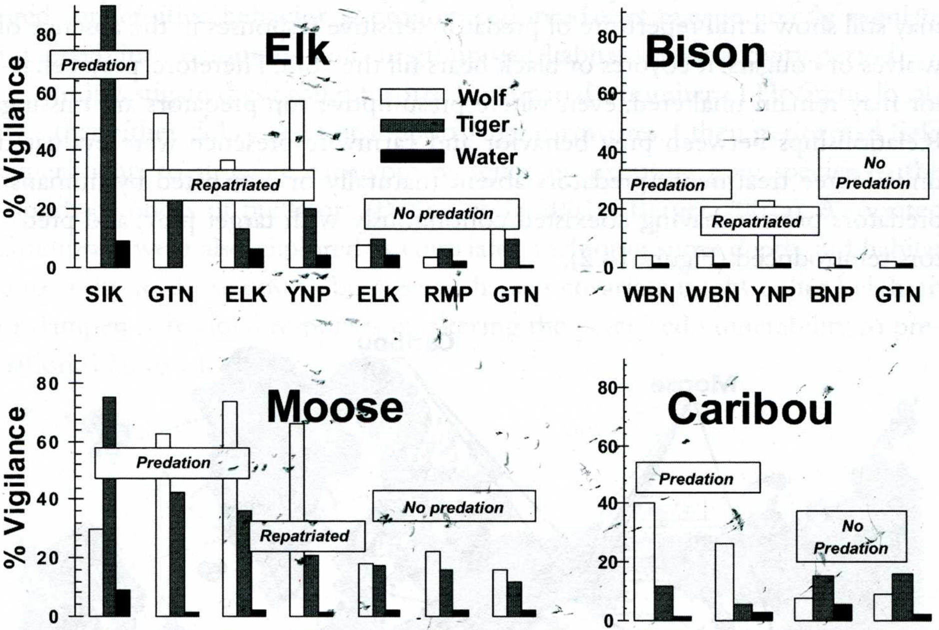

Figure 14.3. Comparison of vigilance by species at sites that varied in carnivore presence. Values reflect untransformed means to playbacks of wolves, tigers, and water. Sample sizes as follows: elk (1,438), bison (797), moose (1,334), and caribou (860). Upper left: SIK = Sikote Alin (Russian Far East); GTN = Grand Teton (Wyoming, post-wolf); ELK = National Elk Refuge (Wyoming, post-wolf); YNP = Yellowstone National Park (Wyoming, post-wolf); ELK = National Elk Refuge (Wyoming, pre-wolf); RMP = Rocky Mountain National Park (Colorado); GTN = Grand Teton (Wyoming, pre-wolf). Upper right: WBN = Wood Buffalo National Park (Alberta, Canada) and a different area of WBN about 60 kilometers distant; YNP = Yellowstone National Park; BNP = Badlands National Park (South Dakota); GTN = Grand Teton (Wyoming). Lower left: KOL = Kolumbe River Basin (Russian Far East); DEN = Denali National Park (Alaska); TAL = Talkeetna Mountains (Alaska); GTN = Grand Teton (Wyoming); KAL = Kalgin Island (Alaska); GRY = Grey's River (Wyoming). Lower right: TET = Tetlin Wildlife Refuge (Alaska); DEN = Denali National Park (Alaska); SVA = Svalbard (Norway); GRE = Greenland.

included distance between an animal and the speaker, distance to potential habitat cover (defined as vegetation sufficient for concealment), snow depth (playbacks were in mid- to late winter), and group size (Berger 1999, 2007a).

Predation-Induced Changes in Prey Behavior

In localities with wolves, elk and caribou responded to playbacks with heightened vigilance, a greater propensity for clustering, and more frequent abandonment of feeding sites than they did in wolf-free areas. Moose responded similarly except, being asocial, they rarely had opportunities to cluster. By contrast, bison were significantly less responsive to wolf howls (Figure 14.3).

Of the covariates, snow depth and distance to suitable vegetation cover significantly influenced vigilance levels in elk and moose but only at sites with wolves. In areas lacking top predators, group sizes were smaller; for caribou on wolf-free Arctic islands, females occurred in associations of two or one between 18 and 29 percent of the time but were never in such small groups in Alaska. In other words, when sympatric with large carnivores, all three species—caribou, elk, and moose—were more vigilant and more likely to cluster (elk and caribou) and to vacate feeding areas when confronted with cues indicating wolf or bear presence.

INDIRECT RESPONSES: SCAVENGERS AND PREY-PREDATOR INTERACTIONS

Scavengers live in mutualistic associations with carnivores. Vultures are the principal scavengers in much of the world, but ravens assume this role in the north, where they consume carcasses killed by wolves and grizzly bears. Ravens depend on carnivores to open carcasses because their bills are unable to penetrate thick hides, especially frozen ones (Heinrich 1991; Marzluff and Angell 2007). In Yellowstone, ravens often arrive at wolf-killed carcasses within 30 seconds (Stahler et al. 2002). Groups of up to 100 may accumulate and remove significant amounts of meat (Wilmers et al. 2003). Usurpation of spoils by ravens leads to increased frequency of wolf predation in a positive feedback (Vucetich et al. 2004).

The association of ravens with kills allows prey species to rely on ravens to assay the presence of predators, using their calls as proxies. Moose retreated from raven calls where they were sympatric with large carnivores in Alaska, but not in Wyoming (Berger 1999). The contrasting effects were not a consequence of geographic variation per se because moose at another Alaskan locality where they had been isolated on a predator-free island for four decades were similar to Wyoming moose in ignoring raven calls. However, once reintroduced wolves began consuming the calves of Wyoming moose, mothers became hypervigilant to wolves, not to ravens (Berger et al. 2001b), an indication that learning in moose proceeds first to the carnivores themselves and secondarily to the scavengers.

As shown by moose living in predator-free environments in Alaska and Wyoming, a widely distributed behavioral response of moose to ravens is readily lost where not reinforced by experience, suggesting that the response is a socially transmitted trait. One must wonder how many other behavioral responses of wild species around the world have been lost as a consequence of the widespread extirpation of large carnivores (Berger 1999).

FEAR-MEDIATED INDIRECT EFFECTS AT LOWER TROPHIC LEVELS

Fear of predators influences prey behavior in several ways. Three of the best-documented behavioral modifications are changes in group size, refuging behavior, and daily activity patterns (Figure 14.1a; Lima 1998; Ripple and Beschta 2004a; Stephens et al. 2007).

Group Size

Per capita predation risk decreases as a function of group size ("safety in numbers"; Hamilton 1971), although larger groups may be more likely to attract the attention of predators (Hebblewhite and Pletscher 2002). Prey aggregations can lead to an increase in the patchiness of the grazing regime, a modification that affects plant growth rates, recruitment, and nutrient cycling (Kie et al. 2003).

Frequent tensions between foraging success and group size can lead to reduced group size under reduced predation risk. For example, long-tailed macaques on leopard-free islands in the Simuele archipelago of Indonesia occur in smaller groups than on Sumatra, where leopards are present (van Schaik and van Noordjwick 1985). Similarly, coloniality of seabirds is often reduced on predator-free islands (Beauchamp 2004). Musk oxen show similar group responses: reductions on predator-free islands and larger groups when wolves are present (Caro 2005).

Movements and Refuge Use

In solitary species, predator-induced adjustments in group size are not an option, but other responses occur at coarse or fine scales. Moose mothers that have lost young to wolves or bears move to new areas immediately upon the detection of fresh predator sign, but those that have not remain more sedentary (Pyare and Berger 2003). By contrast, mothers whose offspring perish for reasons unrelated to predation do not move in response to the same stimuli (Berger et al. 2001b), suggesting that variation in parental experience with predators affects fine-scale movements.

Furthermore, even in the absence of experimental evidence, other changes are also notable. Moose mothers give birth in the same general region annually where calf survival is high but shift birth sites up to 10 kilometers the year after a neonate has perished (Bowyer et al. 1999; Testa et al. 2000). Choice of parturition and nursery sites is therefore governed not simply by evidence of carnivore presence but by carnivore-specific experiences (Berger 2008). Such predator-induced movements and habitat selection affect herbivore density and subsequently food webs (Kie et al. 2003).

Diet may also vary with predation risk and habitat (Chapter 9, this volume), as exemplified by elk use of open grasslands or closed-canopy forests (Winnie and Creel 2007), where grass, sedge, and forb layers are differentially affected (Christianson and Creel 2007).

Activity Patterns

Although predation-sensitive activity patterns are known in rodents and other small mammals (Kotler et al. 1991; Griffin et al. 2005), many of the more striking effects of predation on the activity budgets of larger mammals stem from hunting by humans. Both coyotes and elk become more nocturnal with intensified harvest, adjustments that may lead to diet changes (Berger 2005). The evidence that native predators maintain or govern activity levels is less clear, however.

Somewhat intermediate in this discussion is the endangered endemic island gray fox. Unlike nocturnal mainland foxes, this diurnal insular form has been severely reduced in numbers by golden eagles (Roemer et al. 2001), partly because of its inability to become nocturnal. Despite a few case-specific studies, little attention has focused on relationships between activity patterns, forcing by native predation, and trophic dynamics.

INTRAGUILD PREDATION: THE CONTEXT OF BEHAVIORAL AVOIDANCE

Predators routinely kill and sometimes consume other members of the carnivore guild, a behavior known as intraguild predation (Palomares and Caro

1999; Polis et al. 2004). Where intraguild predation is frequent, lesser carnivores may occur at lower densities than in the absence of larger guild members (e.g., coyotes, wolves, and smaller cats). Altered relative abundances of sympatric carnivores may affect prey species and other components of community structure (Chapters 13 and 20, this volume).

Spatial and Temporal Avoidance

Lesser carnivores may attempt to reduce encounters with larger carnivores by temporal or spatial partitioning of activities. One of the first demonstrations of this was obtained with simultaneously radio-tracked leopards and tigers in Chitwan National Park in Nepal. Leopards systematically avoided neighborhoods that contained tigers (Seidensticker 1976). Whether leopard diet was affected as a consequence is unclear (Woodroffe and Ginsberg 2005). Similarly, cheetahs avoid lions, as demonstrated by movements of targeted cheetahs to areas of lower prey density in response to broadcast lion roars.

Carnivore–carnivore avoidance can be deduced from other forms of spatial evidence. One particularly striking example comes from areas in and around national forests surrounding Yellowstone National Park. Grizzly bears are attracted to gut piles left by hunters outside the park. Cougars move away from these areas, but wolf distribution remains unaffected, suggesting that the presence of bears partially mediates cougar ranging patterns (Ruth et al. 2003; Smith et al. 2003a).

A final example involves coyotes. After wolf reintroduction into Yellowstone, coyotes did not necessarily avoid areas of high wolf density but adjusted their behavior, primarily by resting less and increasing vigilance at carcasses (Gese and Grothe 1995; Gese et al. 1996; Switalski 2003).

Habitat Selection and Diet

Densities of coyotes and wolves in the Yellowstone ecosystem are inversely related (Berger et al. 2008). Solitary coyotes wandering outside their natal territories were killed by wolves at greater rates than pack-living residents (Berger and Gese 2007). Benefiting from this interaction were pronghorn fawns, which experienced four times greater survival in areas with than without wolves, presumably because fawns are not sought by hunting wolves, which prefer larger prey (Berger et al. 2008). Hence, pronghorn recruitment was enhanced by the interaction between a mesopredator and an apex predator.

A similar dynamic has unfolded in the Banff region of Canada, where recolonizing wolves and resident cougars interact. With the recent arrival of wolves, elk have declined about 65 percent, cougars have been killed, and displacement of cougars from carcasses has become more common. As a consequence, the primary prey of cougars has switched from elk to deer. As elk declined, wolves also turned increasingly to deer, a change that lagged 1 year behind the decrease in cougars (Kortello et al. 2007).

INTRAGUILD PREDATION: THE CONTEXT OF HUMAN PERSECUTION

In many areas of the United States, humans have replaced carnivores as the primary hunters of big game. However, nowhere do human hunters play the same functional role in ecological dynamics as do the carnivores they replace (Berger 2005). Next, I present three cases in which prey redistribute themselves in response to humans as predators, and then I draw analogies about how these behavior-mediated changes may affect other trophic levels.

Fear and the Use of Humans as Shields

Given human domination over most terrestrial systems, the strong interaction that once involved only native predators and prey is either nonexistent or modulated by an even more complex, three-way interaction involving people, predators, and prey (Figure 14.1b). In some situations, animals appear to use humans as shields against predators (Terborgh 2000). Conservationist John Muir reported a case of this while traveling in Africa in 1910. "Most of the animals seen today were on the Athi Plains (Kenya) and have learned that the nearer the railroad the safer they are from the attack of either men or lions" (Branch 2001).

However, the presence of animals near humans or their infrastructure can be subject to more than one interpretation. The notion that prey have figured out how to use humans and associated infrastructure to shield against danger is a tricky one. For instance, coyotes may invade suburbs, not because of the danger presented by wolves or varmint hunters on the towns' outskirts but because culinary options such as poodles and unattended food bowls may be attractive. To detect whether distributional patterns change because of buffering against predation requires simultaneous information on both the pace of prey redistribution and the intensity of predation across changing landscapes.

Expanding populations of wolves and grizzly bears in the Greater Yellowstone Ecosystem enable a test of the idea that prey derive protection from predators by using humans as shields. During a 10-year period, grizzly bear numbers increased in and around Grand Teton National Park, whereas adjacent regions with moose remained essentially bear-free. If predation on juveniles was

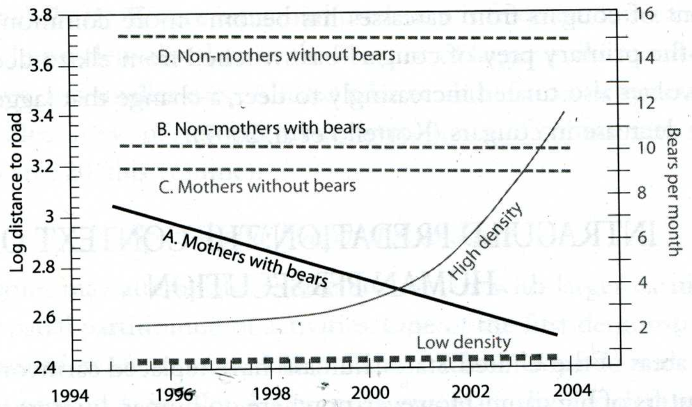

Figure 14.4. Relationships between log median distance to a paved road and expected birthdates by year for adult females at sites differing in bear densities. Dotted lines are not significant: (B) $Y = -0.0126x + 27.259$ ($r^2 = .211; p = .182$); (C) $Y = -0.003x + 9.722$ ($r^2 = .003; p < .894$); (D) $Y = 0.002x - 0.739$ ($r^2 = .02; p = .920$); the low-density site had 3 bears/10 years. (A) $Y = -0.056x + 114.97$ ($r^2 = .875; p < .001$) (details in Berger 2007b). For bears per month and time, $Y = 6E{-}214e^{0.2462}x$ ($r^2 = .614; p < .01$).

a major factor guiding female moose distribution, then females with calves should have been more likely to alter their patterns of distribution than nonparous females.

Over a 10-year period, the locations of birth sites in areas with and without bears were revealing. Moose mothers in bear-free areas showed no consistent patterns in birth sites, but in areas with grizzlies, the median distance between birth sites and paved highways decreased by about 120 meters per year during the 10-year period (Figure 14.4). Because grizzly bears avoid areas within about 500 meters of highways, moose mothers apparently shifted into these areas to avoid bears (Berger 2007b). Hence, grizzly bears appeared to determine the distribution of parous moose. A semianalogous situation occurs with wolves and elk in the Canadian Rockies. Elk congregate around or within towns, areas wolves avoid. As a consequence, high elk densities affected aspen tree growth and willows, as well as beavers and songbirds (Hebblewhite et al. 2005).

Warfare and Game Sinks

As in the preceding example, areas of extraordinary danger tend to be avoided, and prey may fill interstitial zones where the risk of death is diminished. More than 200 years ago Lewis and Clark described wildlife as shy or reclusive near human settlements, but in other areas "the whole face of the country was covered with herds of buffalo, elk and antelopes; deer are also abundant, but keep themselves more concealed in the woodland. The buffalo and elk and antelope are so gentle that we pass near them while feeding, without appearing to excite any alarm among them, and when we attract their attention, they frequently approach us more nearly to discover what we are, and in some instances pursue us a considerable distance" (Moulton 1986–1996: Vol. 4, p. 67). Similarly, boundary zones between mutually hostile wolf packs are places where large mammals are found at greater than expected densities (Mech 1977; Martin and Szuter 1999; Laliberte and Ripple 2003).

Altered Migration Routes and Predation

Mass migrations of mammals constitute another behavioral mechanism of predator avoidance (Fryxell et al. 1988; Hebblewhite and Merrill 2007). However, evidence that migration routes change as a consequence of natural predation is weak. There are only a few studied examples, such as the seasonal movements of elk into and out of Jackson Hole, Wyoming, in which data support the idea that predation (in this case by humans) modulates the temporal and spatial distribution of migration (Connor 2001; Smith et al. 2003a).

CONSIDERATIONS FOR THE FUTURE

I have explored some of the links between behavior and food web interactions by exploiting instances of loss, retention, or restoration of native large carnivores to gauge effects on sentient prey. Predation-sensitive changes in foraging, grouping, movement, and refuge use reveal a powerful mechanism that modifies the operation of top-down effects.

Human interventions into natural landscapes can disrupt historical predator–prey relationships. Intense forestry practices offer a case in point. In the northern Rocky Mountains, clear-cutting has created habitat where white-tailed deer populations are irruptive. Cougars have increased in response and have now reached a level at which they are jeopardizing the persistence of endangered woodland caribou (Kinley and Apps 2001). All three species are native, but the fact of human-altered predator–prey dynamics raises a more general issue: Is the behavior of prey species sufficiently resilient to ensure demographic viability as conditions change?

As humans transform our world from the Holocene to the Anthropocene, the context of behaviorally mediated food webs will become increasingly distorted, given the ceaseless tension between large carnivores and humans (Berger 2005). One consequence is mesopredator release, which impairs biological diversity and is likely to lead to other unforeseen impacts (Crooks and Soulé 1999; Chapter 13, this volume). Another is the invasion of alien carnivores, although our understanding of how or whether behavior contributes to conservation in these transformed ecosystems is limited. Native prey often are poorly equipped to avoid alien carnivores, behavioral deficiencies that may arise because behavior is canalized so prey do not maintain appropriate predator avoidance responses or behavior is insufficiently responsive in the short run to adjust effectively to novel pressures (Blumstein 2006; Berger 2008).

In our world of dizzying change, understandable confusion exists about what is natural and what is not (Chapter 5, this volume). Habitat changes induced by livestock in the Great Basin Desert 130 years ago facilitated colonization by mule deer, and subsequently by cougars, which now prey on naive bighorn sheep and porcupines. Grizzly bears and wolves are currently colonizing Alaska's Seward Peninsula, although effects on food webs are not yet clear. Are these colonizers native or exotic?

What of the humans who entered the New World some 13,000 years ago or the dingoes introduced into Australia 4,000–5,000 years ago by seafaring Asians? What sense do we make of the consequent loss of thylacines and Tasmanian devils from the mainland? And to what extent did these losses leave niches to be filled by other species? Similar thorny concerns about ecological function arise from recent and historic losses of mammoths, bison, and native horses from North America (Donlan et al. 2006). The past is past, but we still have opportunities to implement conservation now and in the future.

Large terrestrial carnivores can be keystones of natural ecological function, but apart from high northern latitudes, the proportion of the earth's terrestrial realm in which they can continue to live is greatly reduced, perhaps to only a few percent of what it once was. Knowledge about the importance of carnivores and their effects on other species will be important as we argue for their survival, whether on ecological, ethical, or economic grounds. Understanding how behavioral responses to predation help to structure food webs is one additional way to appreciate the diversity and complexity of nature.

CONCLUSIONS

Fear is a powerful motivator, perhaps the most powerful of all motivators, and is felt by animals as well as humans. Animals thus modify their behavior in a variety of ways when they know or sense that they are at risk of being preyed upon. This chapter explores the behavioral responses of prey species, primarily ungulates, to three experimental conditions: large carnivores present currently and historically, carnivores at greatly reduced abundance or absent, and carnivores restored after a period of absence. Some prey responses are apparently learned, such as associating ravens with recent kills and hence predator presence. Other responses may be instinctive, such as prey aggregation under increased risk of predation and avoidance of foraging areas exposed to predator ambush. These fear-mediated behaviors can generate indirect effects at both higher and lower trophic levels. Effects at higher levels will emerge in the altered habitat use and perhaps hunting strategies of predators in response to fear-mediated behavior of prey. At lower trophic levels, prey behavior can affect spatial and temporal aspects of habitat use and foraging impacts. Complicated dynamics can arise when carnivores interact among themselves in a hierarchical fashion, sometimes through intraguild predation, so as to affect the survival of particular prey species. In the modern world humans have become a major factor in this scenario by persecuting predators and hunting prey species. Predators and prey may react in distinct ways to the presence of humans, even in parks, thereby adding a layer of complexity to normal trophic interactions. There remains much to learn about the three-way interaction between humans, predators, and prey as each seeks to optimize its advantage in a spatially and temporally complex environment.