CHAPTER 16

Hunting by Carnivores and Humans: Does Functional Redundancy Occur and Does It Matter?

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Throughout history some 50 billion people have inhabited the earth; 10,000 years ago most societies were involved in the harvest of meat. Five hundred years ago, 1% were; by 1900 less than 0.001% were (Lee and Devore 1968). A propensity to eat game meat has changed inversely with human population size and, predictably, so has the abundance of native large mammalian carnivores (Weber and Rabinowitz 1996; Woodroffe 2000). With the replacement of carnivores by human hunters it would be surprising if the ecological effects of native carnivores and humans did not differ in the modern world. One oft-cited ecological rationale for encouraging human hunting is that it substitutes for the role once played by native carnivores. To evaluate this issue, I ask a deceptively simple question: Are human hunters functionally equivalent to large mammalian carnivores?

Under ideal conditions, functional redundancy occurs when one species replaces another with no change in community structure. For the purposes of this chapter, I consider humans as functionally redundant to large carnivores when either individually or combined their presence (or absence) does not markedly change the bounds of a given system. In reality, any proof of functional redundancy is challenging since conditions across broad temporal and spatial scales are rarely constant. Time frames, densities of hunters (human or otherwise), dissimilarities in prey species and their abundance, variation in plant communities and productivity, historic conditions, environmental and demographic stochasticity, and other factors all contribute noise that muddies contrasts between systems with and without human exploitation (Ludwig 2001; Robinson 2001).

Nevertheless, it seems possible to make sense of how humans and carnivores affect biodiversity. In the following text, I (1) test predictions about functional redundancy, and (2) suggest criteria by which humans may replicate the roles of native carnivores. I also offer both a general framework for what is known about how hunting by both modern humans and native carnivores structures ecological communities and make a broader point about how little we know about the subsequent effects of predation by humans on biodiversity.

The issue of functional redundancy is relevant for conservation planning and policy for at least three reasons. First, in many areas where large carnivores have been lost they will never be restored even if sufficient prey is available. For instance, large carnivores will never be tolerated in and around most large cities. Second, where biological conservation is a goal, its potential achievement will be strengthened by knowing the extent to which humans are capable of fulfilling the role(s) once played by carnivores (Holsman 2000). Finally, given that hunting by humans is a pervasive global activity (in the United States, approximately one of every seven males between the ages of 16 and 65 hunts; Enck et al. 2000) and areas designated for hunting include some largely intact ecosystems with extant large carnivores, the possibility of competition for the same prey is high. By understanding the relative contribution of each of these two types of predators to ecological communities, it may be possible to disentangle expectations about how carnivore and human hunting contribute to the conservation of biological processes and attendant diversity.

Limitations of Approach

There are limitations to this analysis. I have not categorized the immense variety of methods used by human hunters nor their often differing harvest goals. Among the former will be cables, snares, leghold and pitfall traps, bows and arrows, spears, muzzle-loading rifles, pistols, and high-powered rifles. Among types of hunters will be those seeking trophies, high-quality meat, and any and all meat. Some will hunt year round (legally and illegally), and others only during a prescribed season. Given that human hunting styles also vary by culture as well as weaponry (Robinson and Redford 1992; Alvard 1998; Robinson and Bennett 2000), both factors must be accounted for when attempting to understand putative effects on the structure of food webs and biological diversity. Therefore, what I lay out here is focused on trying to understand whether and how generally "Westernized" hunters fulfill the role played by nonhuman carnivores. I refer to biodiversity in its broadest sense—populations, species, communities, and ecosystems as well as its attributes (processes, structure, and function; Redford and Richter 1999).

Current Overlap between Hunting Humans and Carnivores

For humans and carnivores to be ecologically equivalent as hunters, several prerequisites must be met, although not necessarily simultaneously. Both must (1) be strongly concordant in species selection, (2) overlap spatially in off-take, and (3) yield mortality that is compensatory rather than additive (Jorgenson and Redford 1993; Ginsberg and Milner-Gulland 1994; Murphy 1998). Although these conditions are in and of themselves insufficient to demonstrate functional redundancy, they represent a necessary first step. For example, it is not sufficient for carnivores and hunters to exhibit high dietary overlap. Rather, similarity in prey functional response is better evidence of functional redundancy. Where the strength of interaction(s) between prey and predator is tightly linked, prey responses may converge in antipredator behavior, activity patterns, or habitat use, irrespective of whether sources of mortality are carnivores or humans.

Evidence in support of the preceding three general prerequisites for ecological equivalency is diverse, spanning all continents where native carnivores and human hunters overlap (Table 16.1). Therefore, an a priori expectation of functional redundancy between carnivores and humans seems not unreasonable. The concept of functional redundancy however requires more than interactions at a single ecological level such as predator and prey. As elaborated in the following text, the nature of hunting styles, densities of humans and carnivores, variance in the strength and timing of predation, environmental heterogeneity, gender-specific harvest, and history are all salient to testing predictions about functional redundancy.

Table 16.1
Selective summary of prerequisite conditions (see text) to be met prior to reasonably assuming a functionally redundant relationship exists between carnivore and human hunting

	Prey Species in Common	Spatial Overlap	Mortality Compensatory	Reference
Europe	Red deer	Yes and no	Yes and no	1
	Roe deer	Yes and no	Yes and no	2
South America	Brocket deer	No[a]	Not likely	3
	Capuchin	No[a]	Unclear	4
	Paca	No[a]	Unclear	3
	Peccary	No[a]	Unclear	3
	White-tailed deer	No[a]	Not likely	3
North America	Bison	Yes	No	5
	Caribou	Yes	No	6
	Elk	Yes	No	7–9
	Moose	Yes	No	7, 8, 10
Asia	Sika deer	Yes	Not likely	11
	Chital	Yes	Not likely	12–14
	Muntjac	Yes	Not likely	14
	Red deer	Yes	Not likely	15, 16
Africa	Buffalo	Yes	Not likely	17
	Impala	Yes	Not likely	18
	Giraffe	Yes	Not likely	19
	Wildebeest	Yes	Not likely	19, 20
	Zebra	Yes	Not likely	19, 20
	duiker	Yes	Not likely	21, 22

[a] Large carnivores may be locally extinct in these specific study regions.

1. Clutton-Brock et al. (1982); 2. Aanes and Anderson (1996); 3. Jorgenson and Redford (1993); 4. Hill et al. (1997); 5. Carbyn et al. (1998); 6. Mech et al. (1998); 7. Kunkel et al. (1999); 8. Kunkel and Pletscher (1999); 9. Boyd et al. (1994); 10. Berger et al. (2001a); 11. Makovkin (1999); 12. Karanth and Sunquist (1992); 13. Karanth and Sunquist (1995); 14. Madhusudan and Karanth (2002); 15. Miquelle (1998); 16. Miquelle et al. (1999); 17. Sinclair (1977a); 18. Creel and Creel (2002); 19. Caro (1999); 20. Arcese and Sinclair (1997); 21. Noss (1998); 22. Ray (2001)

Predictions: Concordance in Effects of Human and Carnivore Hunting

Central to testing predictions about functional redundancy is an understanding of the level of possible effect. "Indirect effects" refer to the strength and direction of interaction between two species that may change as a consequence of a third one (Strauss 1991; Wootton 1994). "Subtle effects," on the other hand, generally apply to systems dominated by humans and denote an array of changes, some of which trickle down because of our nondeliberate actions (McDonnell and Pickett 1993). A distinction between "indirect" and "subtle" is not always clean, but typically the latter involves two species, and the former only one other than humans.

In addition to specific effects, functional redundancy can occur at different tiers of biological organization. I focus here on three general tiers where humans have replaced carnivores: (1) predator–prey interactions, (2) prey–ecological dynamics, and (3) biological diversity (Table 16.2). What I shall not consider are effects of types of predation on prey populations per se, which are considered extensively elsewhere (e.g., age and gender selection [Ginsberg and Milner-Gulland 1994; Berger and Gommper 1999], as well as possible evolutionary change [Harris et al. 2002; Coltman et al. 2003]).

The following three sections and associated subheadings develop the framework to address the overarching question: Are humans functionally redundant to native carnivores? It is important to note that from the perspective of an optimal research design, four general conditions are possible: (1) humans and carnivores present, (2) humans and carnivores absent, (3) humans present–carnivores absent, and (4) humans absent–carnivores present (see Fig. 16.1). In reality, very few areas have empirical results available for each of these four conditions where the strength of predation is known.

Despite this, available data from a variety of sites allow evaluation of the possibility of functional redundancy. For example, both brown bears (*Ursus arctos*) and wolves (*Canis lupus*) exert strong effects on moose (*Alces alces*) population size, particularly through their influences on juvenile recruitment (Gasaway et al. 1983, 1992; NRC 1997). In Grand Teton National Park, at the core of the Greater Yellowstone Ecosystem, moose populations irrupted during a 60- to 75-year period after predation was removed as a selective force. High densities of moose and

Table 16.2

Summary of predictions and outcomes for functional redundancy with human replacing carnivore hunting given the assumption that other factors are equal[a]

		Outcome for Functional Redundancy			
Tier	Prediction	Similar	Dissimilar	Uncertain	Comment
I	Timing and biomass of mortality		xx		Temporal differences large
	Consequent mortality		xx		Wounding loss differs
	Prey densities	xx			Congruent effects possible
	Sexual segregation			xx	Overall role of predation unclear
II	Herbivore–vegetation				
	Behavior	xx			Congruent effects possible
	Foraging rates			xx	Perhaps species dependent
	Habitat shifts			xx	Data on strength of predation lacking
	Activity patterns			xx	Relevance to ecological events unclear
	Carrion–scavenger		xx		Temporal differences
	Intraguild predation		xx	xx	Exploitation and interference may vary
	Subtle				
	Roads, horses, ATVs, camps		xx		
	Dangerous prey and human safety			xx	Differences anticipated but data lacking
III	Biological Diversity	xx	xx	xx	All may apply but paths become increasingly muddled

[a] Generalized relationships (from text) can be similar, dissimilar, or uncertain.

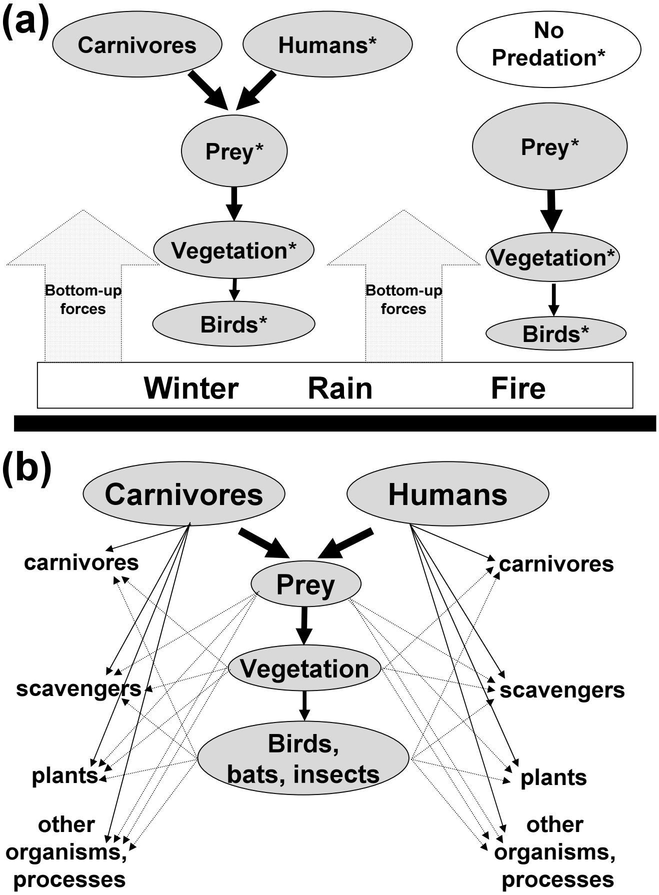

Figure 16.1
Summary of putative apex role of predators. (a) Scenarios with hunting by carnivores, humans, and no predation. Asterisks reflect empirical support derived from systems with moose, humans, riparian willows, and migratory Neotropical birds (after Berger et al. 2001a). Size of circles reflects changes in relative abundance. Possible bottom-up forces as shown. (b) Depiction of predicted outcomes if hunting by humans and by carnivores yield similar effects across various tiers of biological organization. Multiple simple and interactive pathways are illustrated by solid and dotted finer lines, respectively.

associated levels of herbivory decreased riparian willow vegetation and concomitantly avian species diversity (Berger et al. 2001a; Berger and Smith, this volume). In adjacent but nonprotected regions also lacking in brown bears and wolves for a similar period, human hunting reduced moose densities by a factor of 4½; coincident willow riparian biomass and avian species diversity were higher. In this particular case, human predation replaced that by carnivores and enhanced the abundance of neotropical migrants. Because moose in the arid intermountain West tend to be riparian dependent, it is also possible that other elements linked to riverine vegetation may also be affected. This example reinforces the idea that human hunters can affect biological diversity by suppressing prey abundance in the absence of native predators. Table 16.2 outlines predictions and tests for functional redundancy involving humans and carnivores.

Tier 1: Predator–Prey Interactions

An obvious truism is that, where predators are absent, interactions with prey cannot occur. However, from a biodiversity perspective, it is critical to know not only about the form but about the magnitude of prey responses to systems with and devoid of predators.

Timing of Predation and Distribution of Meat

If predation by carnivores and humans is functionally equivalent, then meat consumption schedules should be similar. This is not the case, as illustrated in three examples: (1) three species of nonhuman carnivore predation (Fig. 16.2a–c), (2) a total cessation of predation (Fig. 16.2d), and (3) the distribution of prey biomass as a function of predation by sympatric carnivores and humans (Fig. 16.2e). Although predation by wolves, brown bears, and cougars (*Puma concolor*) produces some similarities in the timing and inflection of curves (Fig. 16.2a–c), the total mortality by carnivores differs from reality in two important ways, one biological and one methodological. First, the respective carnivore–prey system represented in Figure 16.2 is that of a single predator only, whereas each of the study regions portrayed has multicarnivore assemblages. Second, the extent of predation is underestimated because: (a) neonates (except in the moose studies) were not specifically studied, and (b) summer mortality in adult deer is difficult to de-

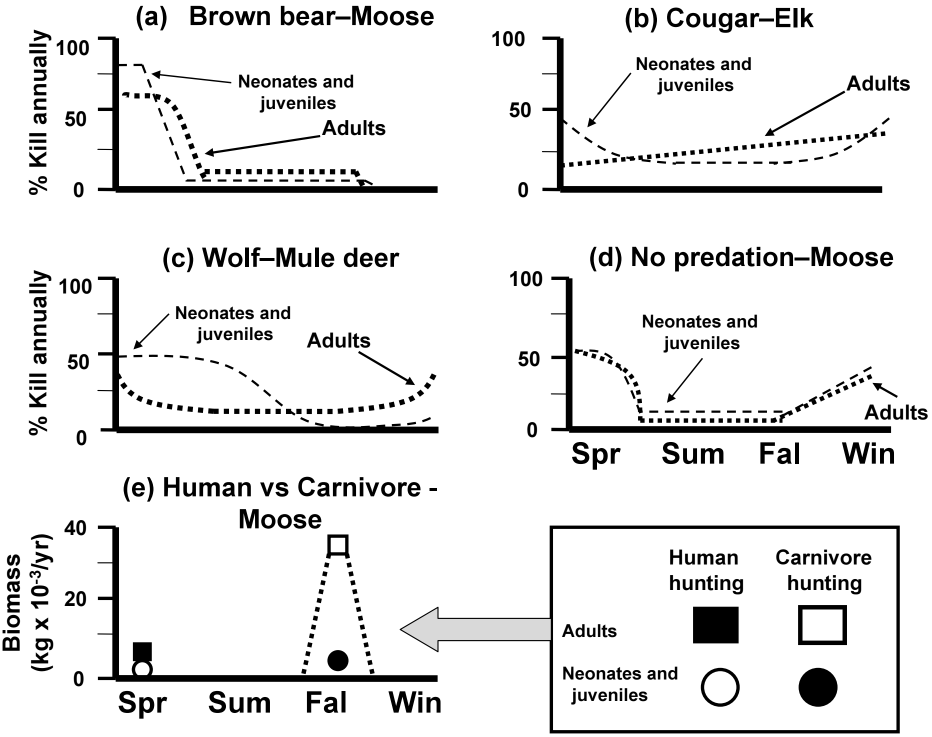

Figure 16.2

Summary of patterns in timing of predation, involving three scenarios: (1) carnivore-specific (brown bear, cougar, and wolf) predation on identified prey (a–c); (2) lack of human and carnivore predation (d); and (3) annual biomass off-take by both carnivores and humans in a moose population. (d) (assumes a population of 1500) and (e) are from the Grand Teton–Jackson Hole region of Wyoming. Depictions from the following: (a) composite of south- and east-central Alaska (Boerjte et al. 1996; Bowyer et al. 1999; Gasaway et al. 1983, 1992); (b) Yellowstone (Murphy 1998); (c) mule deer in northern Rocky Mountains, Montana (Boyd et al. 1994; Kunkel and Pletscher 1999; Kunkel et al. 1999); (d) mortality (*N* = 85) reflects starvation and other sources but not predation, which has been trivial; see (e) (Berger et al. 2001a, unpubl. data); and (e) is the mean for years 2000 and 2001; human off-take values based on hunter success from Wyoming Game and Fish (unpubl. data). The following values used: calf mass @ birth = 20 kg, at 6 months of age125 kg; adult female = 225 kg, adult male = 350 kg, adult female pregnancy rate = 74% (Berger et al. 1999).

tect because monitoring tends to be less intense (Boyd et al. 1994; Kunkel et al. 1999). The preceding caveats aside, the distribution of kills of juveniles or adults as a consequence of hunter type (human vs. carnivore) is striking. If the measure is not total proportion of kills but biomass removal by season, differences become more accentuated, with a fivefold difference in total yield between humans and carnivores (see Fig. 16.2).

From a study design perspective, the condition of "no predation" is portrayed (see Fig. 16.2d), but predator-free areas are unlikely to be realistic as controls since the historic condition across most systems was one that involved predation rather than one without. Predation-free anomalies can, however, characterize nonmanipulated wild ungulates. Native reindeer (*Rangifer tarandus platyrhynchus*) of the Svalbard Archipelago (Norway; Aanes et al. 2003) and caribou (*Rangifer tarandus*) of southwestern Greenland (Denmark) south of the permanent Melville Bulge (icefields) have apparently lived in the absence of native predators until recent human occupation (Melgaard 1988; Marquard-Petersen 1995). Despite such rare exceptions, the overall point is that functional redundancy does not appear to characterize many of the systems with carnivore and human hunting despite variation that inevitably depends on hunter densities.

Wounding Losses and Additional Mortality

Not all human hunters are good shots. As a result some animals are wounded and die later from hunter-related injuries. This proportion is referred to as wounding or crippling loss and varies by weapon type, but the losses can be as high as 21% for rifle hunters in the United States (Smith and Anderson 1998; Carpenter 2000). A similar rate of injury occurred for individuals snared by cable in central Africa (Noss 1998). Animals that die from wounds represent food that becomes available to scavengers and other organisms.

In contrast to humans, data on wounding loss by carnivores is even rarer, although values must be much lower than that for human hunters given the remarkable scarcity of injured prey in areas of Africa with large predators. At sites where large carnivores have been extirpated, such as areas occupied by red deer (*Cervus elaphus*) and bison (*Bison bison*), animals injured in intraspecific combat survive at comparably high rates (Clutton-Brock et al. 1982; Berger and Cunningham 1994). The variation in deaths due to wounding losses as a consequence of effectiveness in carnivore and human predation is suggestive of a lack of concordance in the distribution of death.

Prey Densities through Time

Since neither animal population size nor density remains constant in time, any expectation of congruent effects between carnivores and humans may not be realistic without accounting for temporal variability. If study of multiple systems with carnivores or with humans were possible over many generations, and if amplitudes of fluctuation in density were similar (with other factors equal), one might reasonably argue that human hunters fulfill an ecologically redundant role. But such broad contrasts are rarely possible due to the range of variation and change that characterizes systems (Sinclair and Arcese 1995b; Clark et al. 1999) as well as the degree of environmental perturbation and hunting pressures outside protected areas.

Much work has focused on the potential for predator-limitation of mammalian prey (reviews in Boutin 1992; Sinclair and Krebs 2001; Krebs 2002). That prey densities differ spatially is clear from a geographical snapshot of elk/red deer across 17 systems (Fig. 16.3) with variation from more than 30 animals/km^2 to as few as < 1 km^2. Although elk populations have been manipulated for generations on three continents and have not occurred in many regions with predation by wolves being unabated over time, there remains great interest in relationships between elk abundance and factors that influence population size. In contrast to elk, species that have interacted with predators for at least half a century, and where data on such interactions exist, include wildebeest (*Connochaetes* spp.), buffalo, caribou, and moose; where these have been monitored for decades, fivefold differences in density can occur (Messier 1994; Sinclair and Arcese 1995b; Peterson et al. 1998; Crête 1999). In essence, prey densities can vary widely in both the presence and the absence of predation by large carnivores.

That humans can limit prey density is clear because in the absence of this predation populations irrupt when carnivores are missing (McCullough 2001), although this can also occur when carnivores are present (Sinclair 1989, 1997). However, the question is not whether human predation plays a role in "controlling" runaway ungulate populations but whether it can partially or wholly substitute for carnivores. In systems with carnivores, multiple stable states with both high and low levels of predator and prey are achievable (Walters et al. 1975; Ludwig et al.

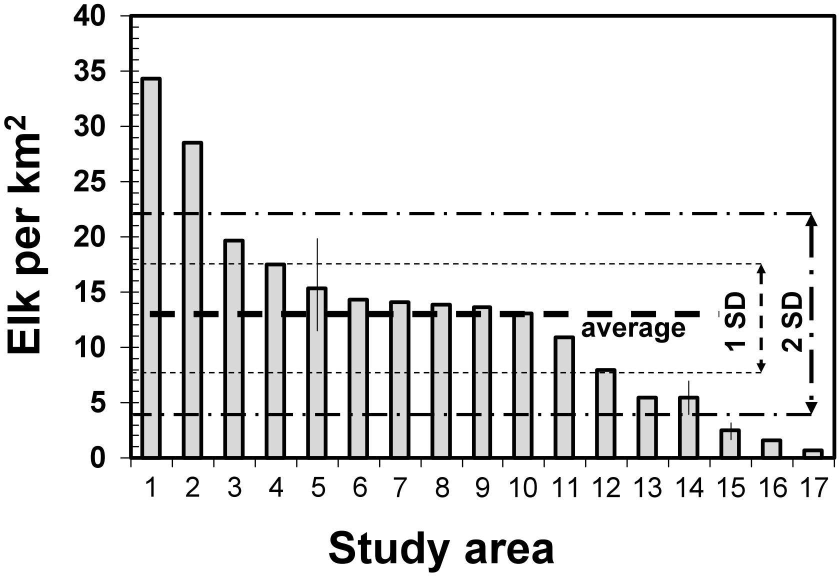

Figure 16.3
Mean densities of red deer–elk populations during winter or year-round. For populations where density estimates spanned multiple years, only the last of a given decade was used. Bars indicate ranges spanning multiple decades. Sites and references as follows: 1–Scarba (United Kingdom), 2–Estes Park, CO (USA; Singer et al. 2002), 3–Rocky Mountain Park, CO (USA; Singer et al. 2002), 4–Yellowstone Park, WY (USA; Houston 1982; Singer and Mack 1999; Smith et al. 2003), 5–Invermark (United Kingdom), 6– Białowieża National Park (Jędrzejewska et al. 1994), 7–Jasper (Dekker et al. 1995), 8–Rhum, 9–lands adjacent to number 4 (Houston 1982), 10–Glenfeshie (United Kingdom), 11–Banff Park–central, AB (Canada; Hebblewhite et al. 2002), 12–Glen Fiddich (United Kingdom), 13–lands adjacent to Starkey in Oregon (Rowland et al. 2000), 14–Białowieża Primeval Forest (Jędrzejewska et al. 1994), 15–Wind Cave Park, SD (USA; Lovaas 1973), 16–Banff–other, AB (Canada; Hebblewhite et al. 2002), 17–Glen Dye (United Kingdom). (UK sources for numers 1, 5, 8, 10, 12, 16 from Clutton-Brock et al. 1982).

1978). Agencies tasked with input from the hunting public understandably prefer the higher state, which enables a higher yield. In these situations humans serves as a de facto substitute for carnivores, and densities can be far lower than where hunting is absent (Berger et al. 2001a). In areas with carnivores, the extent to which consequent prey densities exceed, approximate, or fall below those with human hunters will depend of course on the density of predators and their effectiveness.

An assumption held by some is that large mammal predators control their prey and that humans can functionally replace carnivores (NRC 1997). This assumption can be frail, especially for systems with deer both because weather (e.g., drought or winter) has strong effects on deer densities and because carnivore densities may be highly variable, particularly when alternate prey are available (Fuller and Keith 1980; Fuller and Sievert 2001; Krebs et al. 2001a). Hence, even, if human hunting pressure is more constant than that by carnivores, any effects on prey densities may arise due to a combination of other factors. Still, if prey density was used as a sole criterion by which to measure functional redundancy, then it would appear that human predation has the capacity to perform well as a surrogate for carnivores.

Tier 2: Prey Ecological Dynamics

Although studies have examined relationships between ungulate densities and community-level effects, only a few have extended the analysis to examine the role predators (human or nonhuman) might play in modifying these relationships (see Fig. 16.1). Nevertheless, since both humans and carnivores can modulate prey densities, direct, indirect, and subtle effects can be summarized with respect to the potential for functional redundancy (see Table 16.2).

Ungulate Densities and Herbivory

Predation can affect herbivore densities and therefore plant communities. Growth in balsam fir is modified by wolf abundance through moderating influences of moose (McLaren and Peterson 1994). Where wolves were extirpated and in the absence of heavy human hunting, elk densities were high and they exerted strong influences on plant canopies (Jędrzejewski and Jędrzejewska 1998; Singer et al. 2002). As with the Tier 1 predictions, when herbivore densities are the sole criterion, then humans may perform well as a surrogate for carnivores (Terborgh and Wright 1994; Berger et al. 2001a; Wright and Duber 2001).

Behavior

Prey species are not necessarily automatons. Even though many do not break the scale on intelligence or conscious decision making, some species learn about and react to the threat of predation. Both mongooses (*Helogale* spp.) and moose learn to key on birds that alert them to potential predators (Rasa 1983; Berger 1999; Berger et al. 2003). And, as noted by Georg Stellar some 250 years ago, sea otters (*Enhydra lutris*) apparently altered their habitat use in response to human hunting (Frost 1988). So how might an appreciation of behavior contribute to understanding the relative effects of human and carnivore predation on ecological dynamics? Some promising behaviors for investigation include: (1) foraging rates and grouping, (2) habitat shifts and refuge use, and (3) activity patterns.

Foraging Rates and Predator Detection Individuals stop feeding to scan for predators (Lima 1998), a behavior that affects use of the landscape. This becomes relevant for assessing whether prey movements and habitat use are similar when prey are hunted by humans and by carnivores. The evidence is mixed.

Elk under pressure from reintroduced wolves apparently foraged less efficiently than when wolves were absent (Laundré et al. 2001) and have become less concentrated at local food patches (Ripple et al. 2001). Not surprisingly, elk also become highly alarmed when targeted by rifles (Bender et al. 1999). However, bison in Canada under predation threat from wolves and those from South Dakota living in the absence of all predation did not vary in their vigilance (Berger and Cunningham 1994). Similarly, Alaskan moose in areas with native carnivores did not vary in vigilance from Wyoming moose, the latter living in areas where either humans were the only predators or predation was lacking. Once predator cues were detected, however, differences in foraging rates and subsequent movements did occur (Berger et al. 2001b). Among African ungulates, behavioral differentiation by predator (carnivores vs. humans) may occur, although relative differences in predation intensity by type of predator remain unknown (Caro 1999). Finally, at several Neotropical sites where human predation occurs in the absence of large carnivores (see Table 16.1), densities of nine-banded armadillo (*Dasypus novemcinctus*), capuchin (*Cebus apella*), tapir (*Tapirus terrestris*), and brocket deer (*Mazama* spp.) were reduced; how much prey wariness contributed to lower detection rates by ecologists (and hence densities via redistribution across the landscape) was uncertain (Wright et al. 1994; Hill et al. 1997). Overall, a lack of evidence showing differing effects of carnivores and humans on foraging and predator detection can stem from many sources of variation. With respect to testing the prediction of functional redundancy, the appropriate series of experiments have not yet been conducted.

Habitat Shifts and Refuge Use It is not clear what differences exist between humans and carnivores in inducing habitat shifts and changes in refuge use by prey. Although not strictly comparable, independent effects of both humans and carnivores can be inferred. In the absence of human predation, many prey species shift to or use as refuges areas with humans that are avoided by native carnivores. Such species include chital (*Axis axis*), wildebeest, moose, and vervet monkeys (*Cercopithecus* spp.) (Berger 1998). Perhaps the best example of broad-scale redistribution across a landscape in response to predation is the movement and migration of ungulates when hunted by humans to private lands or national parks where harvest is limited or prohibited.

For carnivores there is also evidence of refuge use when they may be prey. Coyotes (*Canis latrans*) and cheetahs (*Acinonyx jubatus*), each of which are killed by larger predators (Palomeres and Caro 1999), use refuges that may include roads or habitats low in prey density where encounters with larger carnivores are diminished (Thurber et al. 1992; Durant 2000). White-tailed deer are more frequent at territorial boundaries of wolves (Mech 1977). Parturient moose, after the expansion of brown bears into Grand Teton Park, increased their use of habitats within 500 m of paved roads (Berger, unpubl. data); such regions tend to be avoided by brown bears (Mattson et al. 1992). Overall, prey appear to use parallel approaches to decrease chances of being killed or eaten. The possibility clearly exists that predation both by carnivores and by humans may yield concordance in prey habitat use, but without well-designed comparative experiments that account for predation pressure current analyses are inconclusive.

Activity Patterns A good deal of information indicates prey modification of activity in response to predation. Coyotes and elk both become more nocturnal in areas where hunted by humans (Kitchen et al. 2000; Rowland et al. 2000; McClennen et al. 2001). Whether a similar pattern characterizes prey when hunted by carnivores is not clear. However, carnivores themselves may partition their own activities to avoid competition with or predation by other carnivores. Whether such change is relevant to ecological or community dynamics is another issue. For coyotes (or elk), influences might be large; for example, consumption of ground squirrels (*Spermophilus* spp.) versus nocturnal mice or moles, but subsequent effects of variation in activity are mostly unknown. At this point, the relevance of activity patterns to functional redundancy is inconclusive.

3. Scavenging

Relationships involving scavengers, prey, and carnivores can be both direct and indirect. Ravens (*Corvus corax*) follow wolves and may locate potential prey before they are killed (Stahler et al. 2002). And both native folklore and naturalists report similarly; ravens follow and signal humans about the location of potential prey (Heinrich 1989). Just as the timing and distribution of meat that results from human hunters differs from that by carnivores (see Fig. 16.2), so too does the availability of carrion for scavengers (Selva et al. 2003; Wilmers et al. 2003a,b). However, differences in the timing of kills by humans and carnivores mean that magpies (*Pica* spp.), ravens, and other nesting scavengers can provision young with carrion from carnivores but not from humans since human predation typically occurs during the nonnesting season. Finally, high densities of ravens may be sustained in some systems by carrion from hunters. At the center of the Greater Yellowstone Ecosystem ungulate biomass may be the highest in North America (Berger, unpubl. data), and raven densities have increased over a 40-year span (Dunk et al. 1997).

Does carrion produced through carnivore and human predation yield similar effects among mammalian scavengers? An interesting case involves potential changes in the distribution of three sympatric large carnivores—wolves, brown bears, and cougars—each of which occurs inside Yellowstone National Park (where hunting by humans is prohibited) and outside (where hunting by humans is permitted). In response to the shooting and subsequent gut piles of elk, brown bears shifted to areas outside the park; the distribution of wolves was unchanged, and cougars moved away from areas with carrion-feeding bears (Ruth et al. 2003). In sum, there are both similarities and differences in the extent to which the pulse-phase availability of carrion resulting from hunting by humans and by carnivores may affect other levels of biological diversity.

4. Intraguild Predation and Mesocarnivore Release

Intraguild predation is relevant to understanding the potential for functional redundancy not because carnivores kill carnivores but because human removal of carnivores ultimately affects biodiversity. Here I briefly consider linkages among specific carnivores and how they relate to biodiversity.

Interference Competition Among the best examples of mammalian intraguild predation (Polis et al. 1989; Polis and Holt 1992) are those involving canids where interactions and population level consequences are well documented (White and Garrott 1997, 1999; Crabtree and Sheldon 1999). Numerous cases are illustrative of the possibility of functional redundancy with respect to interference competition. Both humans and wolves kill coyotes, although all three species may coexist. Historically, coyotes were more restricted in distribution than wolves in North America, a relationship that today is the converse as coyotes have spread throughout the continent (Peterson 1995). Although habitat change may account for some expansion, the killing of wolves by humans released coyotes from one source of predation (e.g., carnivores). Still, the predation pressure exerted by wolves on coyotes has not been equivalent to that by humans, and the two forms of intraguild predation have not resulted in similar densities of coyotes. Such differences are relevant to an understanding of potential functional redundancy; variation in coyote abundance produces strong community effects that include an abundance and diversity of other carnivores, birds, and rodents (Crooks and Soulé 1999a; Henke and Bryant 1999), but just how humans and wolves modulate coyote densities has received little scrutiny. On the other hand, functional redundancy may be achievable at small scales. Both carnivores and humans have the capability of reducing coyote densities, although the adult harvests must regularly approximate 75% to be effective (Knowlton et al. 1999). Where coyotes tend to be abundant and are sympatric with pronghorn antelope (*Antilocapra americana*), fawn survival is generally low (Byers 1997). If a density reduction of coyotes (irrespective of source) yields similar levels of fawn survival in the absence of other mitigating factors, then functional equivalency is possible.

Exploitation Competition Prey removal by human hunters will alter densities or biomass available to other carnivores. This scenario should more appropriately be considered an indirect food web interaction of human hunting and has real-world relevance, particularly where concern about competition between carnivores and humans for prey exists (Phillips and Smith 1996; Creel and Creel 2002). Exploitation competition is critically important for conservation because the densities and ranges of carnivores such as tigers (*Panthera tigris*) or bears are reduced where they cannot harvest prey at the same rates of hunting humans (Mattson et al. 1992; Karanth and Stith 1999).

Indirect and Key Subtle Effects

A consideration of functional redundancy involving humans and carnivores might be restricted to possible effects of human hunting alone, but hunting by humans (at least in Western society) usually relies on an infrastructure that is far different from that of native carnivores. This creates a range of indirect and subtle effects that are not usually acknowledged.

Roads and the Hunting Season in Western North America Effects associated with roads are usually considered as large-scale disturbance (Trombulak and Frissell 2000; Havlick 2002). During the autumn hunting season these effects may include both direct and subtle ones, where hiking by tourists is replaced by all-terrain vehicles (ATVs), horses, and hunt camps. The situation is the opposite of summer when hordes of nonarmed hikers and mountain bikers visit montane regions. Although effects of recreation can be large (Knight and Landres 1998), I ignore these here, given this chapter's focus on potential for functional redundancy between human hunters and carnivores.

The pulse of activity on lands outside protected regions changes during the autumn. Roads, both gravel and paved (Fig. 16.4), are often extensive, but dirt two-tracks enable entry into regions that otherwise would be too far for many on-foot hunters. Access is thereby available to virtually all but legally designated wilderness (e.g., nonroaded) and some national park areas in the 60,000 km^2 Greater Yellowstone area (GYA). ATVs (not all associated with human hunters) have the potential to displace wildlife, and they compact soils, alter hydrological regimes, increase erosion, destroy meadows, crush plants, and increase noise, air, and water pollution (Havlich 2002). These effects are unique to human predators.

Firearms also produce outcomes that differ from those of carnivores beyond those of wounding loss discussed previously. A not infrequent occurrence in the GYA is the unintentional harvest of moose that were incorrectly identified as elk, a mix-up in species identity that also occurs between black (*Ursus americanus*) and brown bears (the former can be harvested legally, and the latter are an endangered species in the contiguous United States [Mattson and Craighead 1994]). Additionally, during the fall hunting season, competition for hunter-killed carcasses may occur, often resulting in bears being killed by hunters while attempting to appropriate the meat (Mattson et al. 1994).

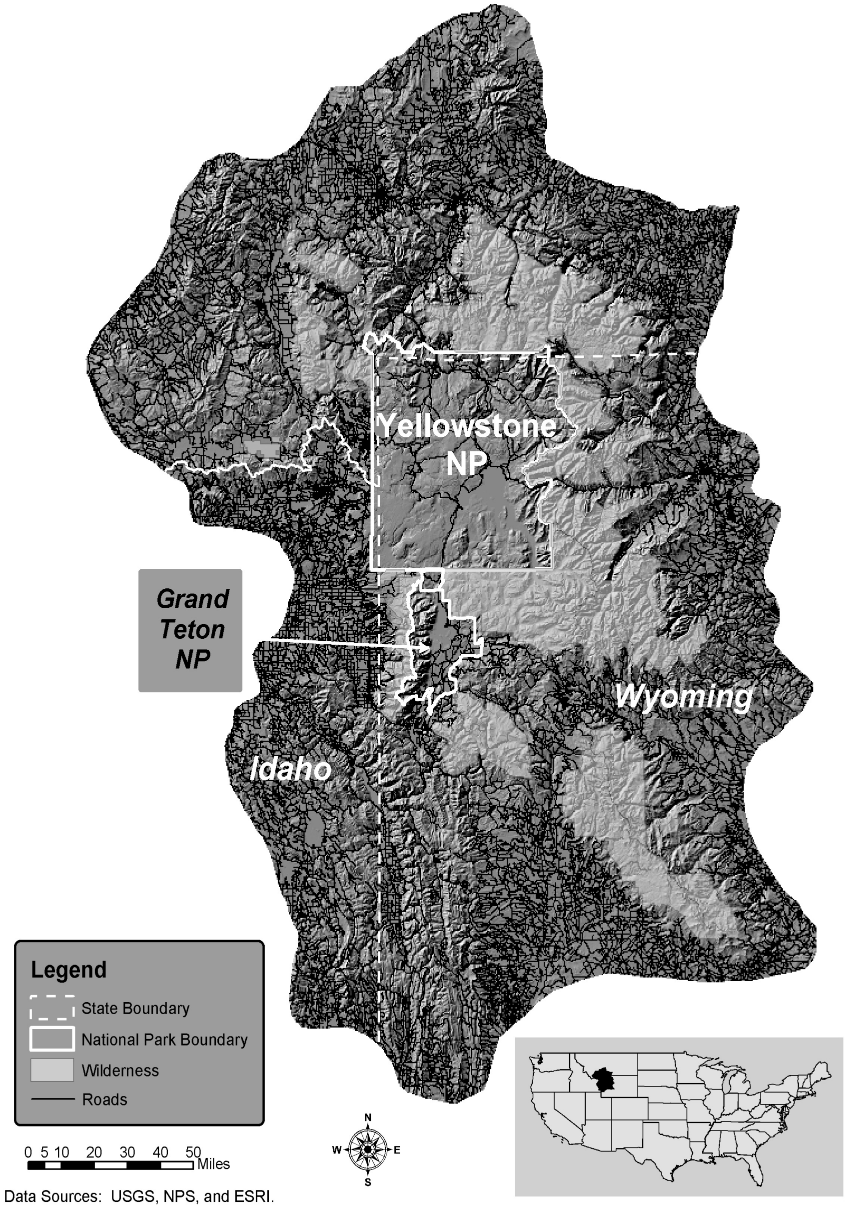

Figure 16.4

The road network in the southern Greater Yellowstone Ecosystem (GYE). Roads (paved roads, secondary, gravel, two-track) shown in black and the wilderness areas (that all lack roads) are highlighted in light gray. Map: sources are USGS, NPS, ESRI; map prepared by Jon Rieck, Wildlife Conservation Society).{AQ: please spell out acronyms here.}

A less direct but important broad-scale effect stems from the loss of available habitat. Both deer and elk move further from roads during the hunting season, often become more nocturnal, and decrease use of open habitats (Kilgo et al., 1998; Rowland et al. 2000). Some carnivores are similarly displaced (Maehr 1997b; Ruth et al. 2003). Finally, numerous and uncounted species are killed as incidental off-take; porcupines (*Erethizon dorsatum*), skunks, snakes, coyotes, rabbits, and squirrels are designated as "varmints" in some western states. Effects of guns beyond those of targeted prey can therefore include either indirect or subtle effects on inadvertent prey, carnivores, and scavengers (Fig. 16.5).

A different effect derives from horses that offer access to remote wilderness areas. Some horse and mule trains contain up to 30 animals and may remain for 10 days or longer. When salt is placed for horses, it often attracts other wildlife including elk. Food for both horses as well as humans can attract bears. Conversely, some wildlife is displaced due to avoidance of humans. So, as indicated in the previous section on scavenging, the potential influx of human hunters may leave different-sized footprints. Most have yet to be measured but they must extend well beyond those of guns as they affect plants, other organisms, and processes (see Fig. 16.5). Finally, in seasonally cold environments camps involve trailers, mobile homes, and other forms of recreational vehicles. These may or may not have effects similar to those already described, but they will be far different from those incurred by carnivores hunting prey (see Fig. 16.5). To be fair, the millions of people that recreate on lands with wildlife also have very serious effects.

Tier 3: Effects on Biodiversity at Other Trophic Levels

The third and final set of predictions relates to the cascading effects on trophic levels beyond prey that emanate from predation.

A Few Clear Linkages

Because some prey are dependent on vegetation and other habitat components, animal and plant biodiversity may be modified through predation by carnivores (Terborgh et al. 1999, 2001). This is clear from studies in four protected areas of western North America (Yellowstone, Banff, and Rocky Mountain national parks, and the National Elk Refuge) where humans reduced large carnivores, and high

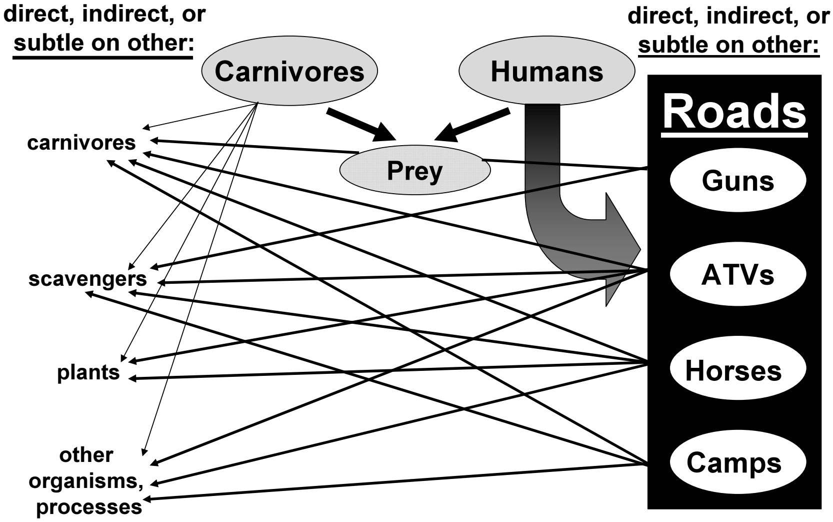

Figure 16.5
Interactive food web illustrating direct, indirect, and subtle effects of human hunting that differ in strength and direction from those of carnivore hunters.

elk densities compromised the productivity of aspen communities or coincident songbird diversity (White et al. 1998; Dieni et al. 2000; Soulé et al. 2003). Ungulate densities beyond the borders of these regions are regularly reduced by human hunting, and associated plant communities and avian diversity may be greater in such areas (see Berger et al. 2001a; Singer et al. 2002).

Although other work concentrates on effects of native ungulates at levels beyond those of herbivory alone (Frank et al. 1994; Frank and Groffman 1998; Singer et al. 2002), a general absence of direct contrasts between systems with predation by carnivores and by humans precludes strict assessments of functionality. On the other hand, before and after studies have been conducted in systems where carnivores were once extirpated and have now returned (e.g., wolves in Yellowstone Park) or in systems with great temporal variation in carnivore densities (Isle Royale Park). In these analyses both top-down and bottom-up forces have been shown to operate on biological diversity via carnivore–prey–vegetation dynamics (Pastor et al. 1993; Ripple et al. 2001). Cascading effects beyond these two trophic levels become less directly tied to carnivores per se, although density limitation of ungulates seems widely tied to enhanced biodiversity (Michelli et al. 2000).

Vegetation change and community processes linked to ecosystem function and biological diversity via herbivory by ungulates include nutrient cycling, fire, and decomposition (McNaughton et al. 1988; Hobbs 1996). Although high densities of grazers have the capacity to modify systems (Frank et al. 1994; Singer et al. 2002), understanding whether effects are positive or negative, are within reasonable bounds of natural variation, and/or attain points where predation dampens fluctuations is difficult and contentious (Kay 1994; Keigley 2000; Singer et al. 2000; Yochim 2001).

The difficulty lies not in understanding effects of prey densities on ecosystems but in interpreting relative roles of carnivores and humans in affecting those densities. Where wolves and moose have interacted for half a century in the absence of human predation (Peterson 1995; Jordan et al. 2000), high levels of herbivory change communities from deciduous to coniferous (Pastor et al. 1993). In Sweden, moose herbivory also affected forest leaf litter, which is associated with the diversity of ground-living invertebrates (Suominen et al. 1999a). However, making sense of change over time and understanding its relationships (if any) to the intensity of predation can be bewildering due to potentially confounding effects of fire regime, logging, and direct and indirect human effects. Linnaeus apparently never saw a moose in Scandinavia (how hard he tried is unclear) but more than 300,000 occurred there 10 years ago (Clutton-Brock and Albon 1992).

Fuzzier Pathways

How reasonably can effects of carnivore and human predation be extended to additional ecological components? In addition to indirect influences on vegetation, nutrient cycling, macroinvertebrates, and neotropical migrants (see preceding text and Figs. 16.1, 16.2), it is also possible that the loss of carnivores can change dynamics of predator–prey interactions to affect lower trophic levels. In the arid American West riparian zones contain as much as 90% of the species diversity (Stacey 1995; Fleishman et al. 1999, 2001). Because populations not limited by predation but by food alter vegetation structure (Schmitz et al. 2000; Berger et al. 2001a), and some insects, including midges and mosquitoes, show a strong preference for mesic vegetation (Darsie and Ward 1981), an interaction beyond that of mosquitoes feeding on moose may be involved. Insectivorous bats, for example, are more abundant and feed preferentially in and adjacent to mesic habitats where aquatic insects, midges, and mosquito abundance is greater than in less mesic habitats (Brigham et al. 1992; Seidman and Zabel 2001). If predation on ungulates by either large mammalian carnivores or humans alters insect-dependent vegetation, then the predators will also affect the strength and direction of bat–insect interactions. A similar speculation can be created for butterflies given the proclivity of some species toward riparian sites (Fleishman et al. 1999, 2001).

A particularly interesting case involves a link between elk browsing and the abundance of leaf-galling sawflies (*Phyllocolpa bozemanii*), which subsequently affect arthropod foraging and the diversity of insectivorous birds (Bailey and Whitham 2003). However, the extent to which carnivores have affected elk densities relative to that of humans has been less certain. One of the crucial challenges will be to unravel just how these likely pathways operate, and another challenge will be to develop rigorous tests to assay the role of factors alternative to predator and prey densities.

Conservation Recommendations: Functionality in Systems with Carnivores and Humans

Is knowledge of ecosystem structure and processes sufficient to assure that inferences about functional redundancy among types of predators are on target? The answer is likely to be yes in Westernized countries where there has been a history of exploitation, science, and conservation. For developing countries with far fewer resources, answers are generally less clear. Although predation by humans may or may not mimic that by carnivores (see summary in Table 16.2), it is possible to shape human hunting to simulate effects of carnivores. I focus here on biological attributes only, given the suite of social, political, cultural, and ethical challenges that otherwise will affect true implementation. It is important to note that, even where functional redundancy between humans and carnivores is a goal, some systems may never respond in the intended fashion simply because of vagaries associated with environmental variance and bottom-up forces that may have little to do with hunting per se.

How to Make Human and Carnivore Hunting Equivalent

To replicate predation by carnivores, humans should hunt year-round, kill a high proportion of neonates, remove young-of-the-year, and in some instances take a higher proportion of adult females. The kill by humans would have to be measured against the predicted off-take, site-specific densities, and nutritional needs of carnivores (were native predators present) while to some extent balancing prey dynamics in a very general way. For modern humans to mimic predation by carnivores, hunts must be at close (rather than a distant) range since native carnivores ambush or chase prey to make their kills. Modern arsenals that include rifles, ATVs, bikes, and other "contemporary" products obviously did not evolve with prey. So, the best way to mirror carnivore hunting *might* be as an effective archer. The issue, to be sure, is not whether our human ancestral effects should be duplicated today (a controversial proposition; Redford 1992; Kay 1994; Redford and Feinsinger 2001; Yochim 2001) nor even a goal; instead, merely how to equilibrate effects of modern human hunters and carnivores on biological diversity at different levels.

Even if carefully designed experiments were conducted there are practical issues: how best will functional redundancy be evaluated with respect to biological diversity? Spatial considerations become an imposing issue. At least two areas of Alaska that exceed in size the state of Idaho are available for hunting by indigenous subsistence users, but what of smaller and more populated regions, whether in Europe, Asia, or the contiguous United States? Do we measure vegetation or behavior, butterflies or bats, soil microorganisms or macroinvertebrates? These are not trivial questions, because to truly understand whether hunting by humans and by carnivores can ever be semi-equal, follow-up monitoring will be necessary, yet the selection of appropriate measures is uncertain.

Why Care If Functional Redundancy Occurs?

Although large dangerous carnivores might have shaped human behavior and subsequent patterns of colonization when humans were unarmed thousands of years ago, today, the opposite is true—it is rare that the presence of carnivores controls human destiny. Moreover, hunting by humans is held up by many as a de facto replacement of predation by carnivores. That is, human hunting is regarded as necessary because carnivores have disappeared or become ecologically irrelevant in many places (Pyare and Berger 2003). If the top-down influence of predation is an important structural feature of ecosystems, then the putatively replacement function of humans has a great deal of relevance for the conservation of biodiversity. If, however, a great deal of scrutiny is not focused on how this replacement occurs, then either we risk further ecosystem erosion or we just do not care. An understanding of the manner in which human hunting can serve the same role as that served by carnivores will affect management decisions.

To understand whether human and carnivore effects can ever be equal, appropriate areas must be available to evaluate ecological change (Dassman 1972). Otherwise the relative roles played by so many factors, both within and beyond reserves, will remain conjectural (Arcese and Sinclair 1997). The restoration or elimination of carnivore populations represents experimental opportunities to test hypotheses related to the ecological role of carnivores. This currently is occurring in the Greater Yellowstone Ecosystem where wolves have been reintroduced and brown bears are expanding their geographical range (Smith et al. 2003; Pyare et al. 2004). In reality, however, the question for practical on-the-ground management has little to do with ecological dynamics of wolf recovery or even biodiversity. Instead, local state game boards and appointed wildlife commissioners are interested in the degree of resultant interference and exploitation competition between humans and carnivores. Although the quantity of prey acquired by carnivores and people has bearings on biodiversity, rarely at such local levels are concerns voiced beyond that of prey abundance.

Beyond the interest of local hunters, ecologists, wildlife biologists, environmental advocates, ranchers, business councils, and politicians, the public from afar may hold notions of existence value and healthy ecosystems. This is particularly true in places where large carnivore populations are in a state of recovery. But do these carnivores then exert some type of "normative" ecological role (Pyare and Berger 2003; Soulé et al. 2003)? The individual states of Montana, Idaho, and Wyoming have either introduced or discussed legislation to begin harvesting both bears and wolves once they are removed from federal protected status. Such action not only underscores competition between humans and carnivores for prey but for some highlights the expectation of functional redundancy between these two sorts of hunters.

In Yellowstone, Alaska, and most corners of the planet, human hunting does not and will not replicate effects of carnivores that resonate across tiers of biological organization (see Table 16.2). The potential to do so may exist. Indeed, in some carefully manicured areas human predation may already mirror the temporal variability in predation by native carnivores. But, where intact functioning systems with carnivores can never be achieved, perhaps the best we can do is recognize differences imposed by our own human culture and our hunting, and attempt to maintain places that are good for our souls.

Summary

This chapter asks whether hunting by humans is functionally redundant to that by carnivores. Systems with and without humans and carnivores are contrasted with respect to multiple tiers of biological organization, including prey dynamics (and behavior), vegetation, and species dependent upon plant mosaics. The evidence that humans can replace carnivores in an ecologically functional way is not strong, although few studies have been designed a priori to examine these issues. Despite much site-specific variability, primary similarities between hunting by carnivores and by humans include density-reduction in prey and consequent change in herbivory. As such, one way in which human hunting affects biodiversity is through a chain of events in which the reduction of prey results in reduced herbivory and consequent enhancement of native species diversity. Nevertheless, major differences between human and carnivore hunting include (1) alteration of the intensity and timing of predation, (2) removal of different prey age and sex classes, (3) off-take of species other than harvestable prey, (4) modulation of mesopredator densities, (5) infrastructure to support human hunting with consequent effects on vegetation and plant-dependent species, (6) manipulation of carrion–scavenger relationships, and (7) modification of patterns of intraguild predation. In an ideal world, if modern humans were to replicate predation by carnivores, humans must kill at close range, remove a disproportionate number of neonates, harvest year-round, approximate in a general way biomass removal by carnivores, and reduce reliance on "Westernized" hunting styles that rely upon elaborate modern infrastructure. Because the world is not ideal and neither carnivore repatriation nor hunting may be invoked in many regions, perhaps the best that can be achieved for biodiversity conservation is to recognize its local loss while reaffirming its existence value in areas where it remains.

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