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Designing and Managing Protected Areas for Grizzly Bears: How Much Is Enough?

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Grizzly bears (*Ursus arctos*) have survived in the southern part of their current North American range only because of stringent protection and the availability of habitat inaccessible to humans. Hunting regulations and the U.S. Endangered Species Act have contributed substantially to grizzly bear survival, along with de facto protection by roadless areas and the organic acts of provincial and national parks (Keiter, 1991; U.S. Fish and Wildlife Service, 1993; Keiter & Locke, 1996). However, as much as nearly all involved concede these points, there is major disagreement over the protection grizzlies will need for long-term survival in parts of their range that are more heavily impacted by humans (Shaffer, 1992; Primm, 1993; Mattson & Craighead, 1994).

The debate has focused on the size and distribution of populations, the level and effectiveness of protection accorded bears within their occupied range, and the associated need for connectivity among populations (see Wilcove et al., 1986). In other words, how many bears, distributed over how large an area, with what level of interchange among "populations," and exhibiting what level of long-term fluctuations in growth, do humans want? At one level, this discussion is about the degree to which short-term human prerogatives are curtailed and the areas where these restrictions occur. Therefore, part of the debate could

be resolved by identifying factors clearly relevant to answering questions about the size, juxtaposition, and protection of bear ranges; at the very least, it would provide a common framework for discussion.

Much of protected-area design is predicated on existing or potentially induced heterogeneity in the vital rates of target species (see Howe et al., 1991). In theory, species densities vary with the rates of births, deaths, immigration, and emigration, depending largely on habitat productivity and the densities of predators. Prior to the arrival of Europeans, the distribution of North American grizzlies reflected broad-scale patterns of climate and vegetation, possibly modified by competition with black bears (*Ursus americanus*) and low rates of mortality caused by indigenous humans (Storer & Tevis, 1955; Herrero, 1978; Brown, 1985). Grizzlies otherwise had no known major predators.

There is little doubt that the current persistence of grizzly bears at lower latitudes is largely determined by human predation, modified by the effects of food abundance on recruitment (Bunnell & Tait, 1981; Servheen, 1990; Stringham, 1990; McLellan, 1994). The decline of grizzly bear populations is clearly linked to human-caused mortality, which continues to account for virtually all deaths of grizzly bears older than 1 year in the southern Canadian Rockies and in the contiguous United States. Out of 174 grizzlies that were radio-marked and died in this area between 1974 and 1996 (Russell et al., 1979; Dood et al., 1986; Craighead et al., 1988; Aune & Kasworm, 1989; McLellan, 1989a; Nagy & Gunson, 1990; Raine, 1991; Wakkinen & Zager, 1991; Mace & Manley, 1993; Kasworm & Thier, 1994; Wielgus & Bunnell, 1994; Montana Department of Fish, Wildlife, and Parks, unpublished data), 85 to 94 percent were killed by humans (the range in percentages depends on whether unknown causes of death were included and whether the calculation was pooled or averaged over studies). The few demographic studies from this area have also concluded that survivorship, especially of females, outweighs the effects of fecundity on population growth and density (Knight & Eberhardt, 1985; McLellan, 1989b; Eberhardt et al., 1994).

Protection of grizzlies thus needs to reflect the importance of human-grizzly bear interactions. In particular, good management and reserve designs depend on a robust understanding of factors that control the frequency and lethality of contact between humans and grizzly bears (Mattson et al., 1996) and especially the spatial characteristics of this contact. Ideally, we would know what attributes of grizzly bear habitat increase the likelihood of human-grizzly bear contact and which classes of bear are most affected; equally important, we would know why. We would also know how human behavior affects human-bear interactions and their outcome, and how human behavior is modified by the presence of facilities such as roads, trails, and residences.

Having said this, human values are clearly of overriding importance in the design of protected areas for grizzly bears (Mattson et al., 1996). We decide how much we value grizzlies relative to resources that would otherwise be available from their habitat. In other words, humans inescapably define the benefits and opportunity costs of saving grizzly bears and, thus, the risk we are willing to take with this species (Shrader-Frechette, 1991; Kellert, 1994a). This human-centered accounting generates the policies that guide choices governing what, where, and when human activities occur, and are defined for our purposes in terms of spatially explicit modifications of human behavior (if any) intended to conserve grizzly bears (see Clark & Kellert, 1988).

For these reasons, this chapter is devoted to two major topics: (1) the spatial dimensions of human–grizzly bear relationships and factors that influence their dynamics, and (2) a conceptual model for protected-area design that does not just reflect grizzly bear behavior and related features of the biophysical environment but also considers human behavior and the constraints imposed by human values. We hope that this information will establish useful points of reference and thus promote more fruitful discussions about protected-area design, not only for grizzly bears but also for other medium- to large-size carnivores. To this end, we conclude the chapter by generalizing some points to the management of other carnivores as well as some guidelines for the design of carnivore protection in areas with substantial foreseeable or existing human impacts.

The Spatial Dimensions of Human–Grizzly Bear Relationships

Much of the research on grizzly bear habitat relationships has been motivated by concerns over human impacts and safety. How much is bear habitat use affected by the presence of humans or their facilities? Or, how do other human-induced habitat modifications affect grizzly bear cover, security, and food? Regardless of the specific question, these studies have typically relied on the relative spatial distribution of locations from radio-marked bears for their answers and have registered human presence in terms of physical surrogates such as roads, trails, campsites, and towns (Mattson, 1990; McLellan, 1990); it is too difficult or has been deemed less important to track individual humans. Less often, the research design has employed transects that provided absolute estimates of sign density. In either case, the behavior and distribution of live bears have been emphasized.

Perhaps more to the point, spatially explicit mortality risk has also been investigated. What is the probability of a given bear dying as a function of habitat attributes, most importantly, those related to human presence? For various

reasons, relatively little research on this topic has been done for bears despite its obvious relevance; interestingly, elk researchers have vigorously pursued the issue because of its tie to hunter success and behavior (Christensen et al., 1991). However, whether we consider behavior or survival to be the primary mediator of human–grizzly bear interactions, both are important parts of the equation. In the following sections, we consider behavior and survival separately but then integrate these factors for a more holistic consideration of habitat–human–grizzly bear interactions, using the Yellowstone ecosystem as an example.

Behavior as a Spatial Phenomenon

There is a relative wealth of information concerning the spatial responses of grizzlies to humans or human facilities. At the population level, a number of studies have shown that grizzlies typically underused areas within 100 to 500 meters of roads, but in one study avoided areas as far away as 914 meters (Archibald et al., 1987; Mattson et al., 1987; McLellan & Shackleton, 1988; Aune & Kasworm, 1989; Kasworm & Manley, 1990). Construed a different way, Mace and Manley (1993) found that grizzlies in their Montana study area underused habitat where road densities exceeded 1.6 kilometers per square kilometer. Interestingly, this underuse by bears did not vary appreciably with use by humans or road design and was exhibited at very low levels of traffic (0.5–1.9 vehicles per hour) (Archibald et al., 1987; McLellan & Shackleton, 1988).

Underuse of areas near campgrounds and town-sites was even more extreme. Use of habitat within 400 to 2000 meters of campsites or cabins by grizzlies and brown bears was 40 to 67 percent less than expected by the available area (Elgmork, 1983; Gunther, 1990). In Yellowstone National Park, underuse of habitat near major recreational developments was typically evident out to 4–5 km (but in spring only out to 1 km) and was 46 to 94 percent less than expected by area and food abundance, depending on the season, food (e.g., ungulates or cutthroat trout [*Onchorhynchus clarki*]), and site (Mattson et al., 1987; Reinhart & Mattson, 1990; Mattson & Knight, 1992).

All of these studies were compromised potentially by uncontrolled biases. Most important was the possible “avoidance” of human facilities as an artifact of bears underusing inherently less attractive habitats that were fortuitously correlated with roads and town-sites. Human-influenced habitat may also receive full, but undocumented, use at night (Schleyer, 1983; Harting, 1985; McLellan & Shackleton, 1988; Nadeau, 1989). These biases most likely affect studies based strictly on daytime sampling of radio-marked bears, coupled with analyses that do not control for the spatial abundance of foods. Transect-based

studies of grizzlies using ungulate carcasses (Mattson & Knight, 1992) and spawning cutthroat trout (Reinhart & Mattson, 1990) in Yellowstone National Park avoided both pitfalls and suggested relatively strong avoidance of roads and other human developments. Consistency of results among studies from diverse study areas, coupled with the nonexistence of studies showing bear use greater than or equal to that expected at random near humans, increase our confidence that, wherever killed by humans, grizzlies will not fully use habitat near human facilities.

A HYPOTHESIS. These behavioral results could imply that grizzly bears exhibit an irreducible avoidance of humans. Yet, there are numerous observations of grizzlies foraging within a few meters of humans during daylight hours (i.e., habituating to the human presence) (Herrero, 1985). Bears are clearly able to tolerate humans, presumably as a means of accessing food or finding security from other potentially threatening bears (McCullough, 1982; Herrero, 1985; Mattson et al., 1987, 1992; McLellan & Shackleton, 1988). Habituation therefore seems to affect disproportionately subadult males and females with young, who are plausibly at risk from older males (Tracy, 1977; Warner, 1987; Dau, 1989; Mattson et al., 1992; Fagen & Fagen, 1994).

We know or have good reason to believe that habituated bears are more likely than wary bears to be killed by humans (Meagher & Fowler, 1989; Mattson et al., 1992). Habituated bears are more vulnerable to poaching, more often in conflict with humans, or simply viewed as more of a threat to human safety (Herrero, 1985). Yet, because habituated bears tend to concentrate nearer to humans (within 2–4 km of human facilities in Yellowstone National Park), they are also candidates for making fullest use of human-influenced habitats (Mattson et al., 1992).

Taken together, these results suggest that the behavioral responses of grizzly bears to humans at the population level are largely artifacts of the rate at which humans kill bears and the degree to which this mortality is selective against habituated animals. In other words, we expect greater “avoidance” of human facilities if bears able to use this human-influenced niche are killed faster than they are recruited or simply at a higher rate than wary bears. This type of selective mortality would provide surviving bears more foraging opportunities in remote areas because of reduced overall bear densities. In summary, this hypothesis predicts that habitat “impairment” and the related need for grizzly bear habitat secure from humans devolve to the rate at which we kill bears and to the degree of our tolerance for bears that tolerate humans. In any case, the focus is on human-caused mortality rather than some presumed fundamental inability of grizzlies to use habitat near humans.

Mortality as a Spatial Phenomenon

In the relatively few instances when researchers have examined the joint distributions of human facilities (for lack of records from humans themselves) and known grizzly bear mortalities, there has been a positive association. Nagy et al. (1989) found that 75 percent of bear mortalities occurred within 1 kilometer of all-weather roads in their Alberta study area; Aune and Kasworm (1989) and Dood et al. (1986) found similar concentrations within 1.0 kilometer (63%) and 1.6 kilometers (48%), respectively, of roads in central and north-western Montana. Unfortunately, none of these studies treated the analyses in terms of how the observed pattern departed from patterns expected at random, and other researchers have merely commented that most grizzly bears killed by humans were shot from or near roads (McLellan & Shackleton, 1988). One of the strongest associations between human access and, in this case, brown bear mortality comes from Chichagof Island, Alaska, where deaths of legally hunted bears were annually highly correlated ($r^2 = 0.86$) with miles of road during a period of road expansion (Titus & Beier, 1992).

Despite these convergent results, it could be argued that there is a bias toward detecting grizzly bear deaths nearer roads, regardless of their frequency, simply because, at a road, it is more likely humans will discover a bear if it dies. Presumably, this bias would be stronger for illegal mortality, which predictably goes unreported by the perpetrator, and for observations of unmarked dead bears. By these standards, the results from Alberta, Montana, and Alaska, based largely on reports of legal hunting kills, would be relatively robust. However, we still do not know how much illegal, unreported poaching goes on and to what extent this mortality is dissociated from access. Clearly, this topic warrants further inquiry.

Although most of these studies are potentially biased or statistically inconclusive, and none has benefited from comprehensive analyses of the several variables likely to influence grizzly bear mortality, they are consistent with history, theory, and more numerous and conclusive observations of the human-grizzly bear conflict. That is, observations of bear mortality concentrated near roads do not contradict some well-supported expectations. A number of studies at several locations in Alaska, Montana, and Wyoming have shown that human-grizzly bear conflict is positively correlated with annual or seasonal changes in human activity or frequency of human and bear contact, especially in areas where human activity is largely unregulated (i.e., excluding areas such as McNeil River Falls, Alaska) or where the bear population is protected from hunting (e.g., most national parks) (Martinka, 1982; Kendall, 1983; Keating, 1986; Dalle-Molle & Van Horn, 1989; Smith et al., 1989; Albert & Bowyer, 1991; Mattson et al., 1992; Fagen & Fagen, 1994). History also has

Table 8.1 The proportion of total area and recorded grizzly bear mortalities, and numbers of these mortalities prorated to the affected area, for strata defined by the level and nature of human impacts and the control of firearms (i.e., park versus nonpark lands), for the Yellowstone National Park ecosystem, 1975–1994

Strata	Proportion of Yellowstone ecosystem ^a	Proportion of recorded mortalities ^b ($n = 179$)	Mortalities per 1000 km ²
Town-sites and park developments ^c	0.09	< 0.30 ^d	28.4
Primary (paved) roads ^e	0.12	= 0.13	9.0
Secondary roads ^f	0.12	< 0.25	17.2
U.S. Forest Service roadless areas	0.38	> 0.09	4.9
Yellowstone backcountry	0.29	> 0.23	2.6

^aDefined by the most peripheral recorded grizzly bear mortalities (see Fig. 8.1).

^bIncluding known, probable, and possible (see Craighead et al., 1988).

^cMajor human facilities where food services and overnight accommodations are provided (see Fig. 8.1), including areas within 4 km (the zone of influence on bear behavior [Mattson et al., 1992]).

^dIndicates the relationship of proportional mortality to proportional area; protected ($df = 4$, $G = 121.8$, $P < .001$) multiple comparisons (Bonferroni confidence intervals) at $\alpha = 0.05$.

^ePaved all-weather roads, open during the bears' active season, including areas within 2 km (Mattson et al., 1992).

^fGravel roads passable to most vehicles during the bears' active season, including areas with 1 km.

clearly shown that most grizzly bears that died between 1850 and the mid-1980s were killed by humans (Storer & Tevis, 1955; Brown, 1985) who we know or suspect did not range far from roads and trails (see Thomas et al., 1976; Lucas, 1980, 1985).

Results from the Yellowstone ecosystem suggest that mortality has varied substantially depending on agency jurisdiction and nearness to human facilities. Roughly 33 percent of the total habitat available to grizzlies is impacted substantially by humans; this is evidenced most graphically by the disproportionate 68 percent of recorded grizzly mortality from 1975 through 1994, for which humans are responsible (taken from Craighead et al. [1988] and Montana Department of Fish, Wildlife, and Parks, unpublished data). When prorated to zones of influence defined by behavioral responses of grizzlies to town-sites and roads, unit-area mortality was greatest near town-sites, and 5.8 to 11.0 times greater than the lowest rates in U.S. Forest Service roadless areas and U.S. Park Service backcountry, respectively (Table 8.1). Mortality in front-country areas was more often due to agency control of a "hazardous" bear, while mortality in the National Forests, in roadless areas and near secondary roads, was largely due to conflict with hunters and livestock, respectively (Table 8.2). Mortality in Yellowstone's backcountry was further distinguished from all other strata by a high proportion of "natural" cub mortality (Table 8.3).

Table 8.2 Proportional distribution of recorded grizzly bear mortality among causes, by strata (see Table 8.1 for definitions), for the Yellowstone National Park ecosystem, 1975–1994

Cause	Developments (n = 53)	Primary roads (n = 24)	Secondary roads (n = 45)	Yellowstone backcountry (n = 16)	U.S. Forest Service roadless areas (n = 41)
Poaching ^a	0.208a ^b	0.125ab	0.133ab	0.000b	0.073ab
Hunter/outfitter-related ^c	0.076bc	0.167bc	0.244b	0.000c	0.683a
Management ^d	0.528a	0.125b	0.089b	0.000b	0.000b
Livestock-related ^e	0.000b	0.000b	0.400a	0.000b	0.049b
Natural	0.076b	0.333b	0.089b	0.812a	0.171b
Other human-caused ^f	0.113a	0.250a	0.044a	0.188a	0.024a

^aIllegal mortality not directly associated with hunting or livestock.

^bProportions followed by the same letter in rows are not different at $\alpha = 0.05$, based on Bonferroni confidence intervals calculated on both proportional distributions, pairwise, by strata. Multiple comparisons were protected ($df = 20$, $G = 172.8$, $P < .001$), and all strata differed from each other in aggregate.

^cMortality resulting from chance encounters with hunters, mistaken identity, conflict over hunter kills, or conflict at camps of outfitters that catered to hunters.

^dBears removed by managers because of concern for human safety or for "humane" reasons.

^eMortality resulting from conflict over livestock, primarily sheep.

^fIncludes accidental deaths due to research captures, collision with motor vehicles, etc.

These results illustrate why it makes sense to describe grizzly bear habitat fragmentation in terms of the increased mortality risk associated with human facilities and differences in jurisdictions (Mattson & Reid, 1991). By this reckoning, fragmentation is an increasing threat to grizzly bear populations in their southernmost ranges. The Yellowstone ecosystem is already substantially fragmented (Fig. 8.1), while most grizzly bear ranges in southern British Columbia and Alberta are at risk (see Horejsi, 1989; McCrory et al., 1990)—situations exacerbated by the common juxtaposition of human facilities with primary grizzly bear habitat concentrated in narrow transverse valleys (Purves et al., 1992).

SOURCES AND SINKS. There is a strong spatial component to grizzly bear mortality that is closely associated with human access and the unregulated presence of firearms. This spatial heterogeneity is perhaps most usefully described as a source-sink structure, with areas near human facilities constituting the sinks (Knight et al., 1988; Doak, 1995). As an obvious consequence, grizzly population growth rate will decline as the ratio of sink (human-impacted) habitat to source (remote) habitat increases. More importantly, depending on the rate of movement by bears between source and sink habitats, the decline in averaged population growth rate may accelerate relative to the increase in areas impacted by humans (Wilcox & Murphy, 1985; Doak, 1995).

Parks are commonly perceived as grizzly bear population sources. This structure has been postulated for southern Alberta, associated with the Rocky Mountain parks complex (Nagy & Gunson, 1990), and is also thought to exist along some boundaries of Glacier (eastern) and Yellowstone (western) National Park in the United States. As has been shown, backcountry areas of Yellowstone National Park do seem to have the lowest unit-area mortality rates in the ecosystem, approximately half being recorded in roadless areas under the jurisdiction of the U.S. Forest Service. By contrast, town-sites or other major human developments on private and public lands are the most lethal to bears, followed by areas affected by secondary roads. Relative to proportional area, there was also a pronounced difference (2.3 times) between recorded grizzly bear mortality inside and outside Yellowstone National Park (i.e., 23% of total mortality and 41% of total area in the park [log-likelihood test, $G = 26.6$, $P < .001$]). This was despite the application of stringent protections to all federal lands under the U.S. Endangered Species Act, in contrast to an even greater dichotomy of protection between park and nonpark lands in Canada (Keiter & Locke, 1996).

Several researchers have observed that large ranges render grizzlies extremely vulnerable to *population sinks*, whether these are defined as settled areas outside park boundaries or simply as areas impacted by major human

Table 8.3 Proportional distribution of recorded grizzly bear mortality among bear sex-age cohorts, by strata (see Table 8.1 for definitions), for the Yellowstone National Park ecosystem, 1975–1994

Grizzly bear sex-age cohort	Developments (n = 53)	Primary roads (n = 24)	Secondary roads (n = 45)	Yellowstone backcountry (n = 16)	U.S. Forest Service roadless areas (n = 41)
Subadult male ^b	a ^a 0.315a ^c	ab 0.250ab	ac 0.136ab	b 0.062b	c 0.146ab
Subadult female ^b	0.111a	0.167a	0.114a	0.062a	0.000a
Adult male	0.167ab	0.125b	0.250ab	0.062ab	0.293a
Adult female	0.241a	0.208a	0.227a	0.188a	0.293a
Cubs ^d	0.148b	0.208ab	0.114b	0.625a	0.122b
Other ^e	0.018ab	0.042ab	0.159a	0.000b	0.146a

^aStrata identified by the same letter did not differ in aggregate by protected (df = 20, G = 46.7, P = .001) multiple comparisons at $\alpha = 0.05$.

^bAnimals < 5 years old, unless accompanied by dependent young.

^cProportions followed by the same letter in rows are not different at $\alpha = 0.05$, based on Bonferroni confidence intervals calculated on both proportional distributions, pairwise, by strata.

^dDependent young, typically $\leq 1\frac{1}{2}$ years old.

^eAnimals not identified to cohort.

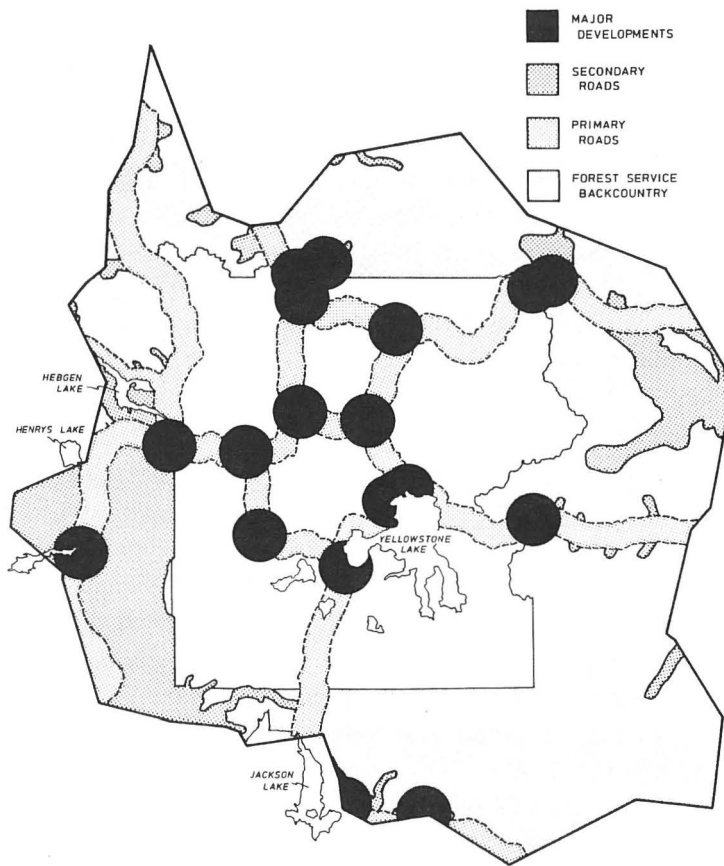


Figure 8.1 Stratification of the Yellowstone National Park ecosystem by the nature of road access and the legal presence of assembled firearms, configured by zones of influence on grizzly bear behavior (see Table 8.1 for definition of strata). Unshaded areas in the core coincide with Yellowstone National Park backcountry.

development (Bunnell & Tait, 1980; Knight et al. 1988; McCrory et al., 1990). For example, bears that spent relatively little time outside of Yoho and Kootenay National Parks in British Columbia were nonetheless quite vulnerable to legal bear hunters (Raine, 1991). In effect, the rate of bear movement between source and sink habitat is often quite high. While mitigating against unpredictable nonlinear responses in population growth rate, this exchange between source and sink habitats could make populations sensitive to each incremental increase in the area of human impacts (Doak, 1995). By implication, heterogeneity in vital rates sufficient to maintain a stable source-sink structure

may require very large areas free of substantial human-caused mortality, depending on overall population growth rate (Doak, 1995; see Schonewald-Cox & Bayless, 1986).

An Integrated View: Yellowstone National Park as an Example

Grizzly bear research from the Yellowstone ecosystem gives us the opportunity to construct an integrated view of relationships among grizzly bears, their foods, and humans that may have general application to southern portions of the grizzly bear range. The Yellowstone data set is of sufficient duration and breadth to provide some room for inference, albeit with a dose of speculation. Radio-marked grizzlies relevant to this discussion have been tracked since 1975, and their relocations analyzed relative to a map of habitat types and human features. The abundance of key foods was also monitored for much of this period, and attention has been given to the consequences of bear behavior.

During this study, the survivorship of bears habituated to humans or conditioned to human foods was much lower than bears judged to be wary. Proportionally, 3.1 times as many radio-marked habituated bears were killed from 1975 to 1990 compared to their wary counterparts (Mattson et al., 1992). Because these habituated bears accounted for most habitat use within 2 kilometers of roads and 4 kilometers of major recreational developments, it is likely that the higher mortality of these bears also accounted for the population-level under-use of habitat in these corresponding zones (Mattson et al., 1987; see above).

Not all bear sex and age classes were equally prone to habituation. Adult males, on average, were the wariest of all bears, while subadult males and adult females with dependent young tended to range closest to human facilities and were as likely as subadult females to be habituated (Mattson et al., 1992). Humans were exceptionally intolerant of habituated subadult males and killed most of these animals as they were recognized. Thus, apparently few habituated subadult males survived to be habituated adults. At the same time, subadult males and females with young seemed to avoid the surviving wary males distributed in typically remote areas, presumably because these males posed a threat to them or to their dependent young (Mattson et al., 1987, 1992).

Thus, the human tendency not just to kill habituated bears but virtually eliminate habituated subadult males had several plausible consequences. Remote foraging sites were apparently preempted by the surviving wary adult males, who displaced other bears into chronically underused human-influenced habitats, where these bears habituated to humans as a means of accessing otherwise unavailable resources. The common availability of foods at

human facilities no doubt increased the frequency and intensity of habituation, as these bears also conditioned to human foods (Herrero, 1985).

This situation arguably placed adult females in increased jeopardy by effectively reducing the availability of habitat remote from humans. From the perspective of fitness strategies, they were in a catch-22 between what may have been for them the palpable, evolutionarily potent risk of losing offspring to other adults (Bunnell & Tait, 1981), and the latent, evolutionarily recent risk of losing their own lives to humans. Although not yet conclusively demonstrated, the demographic consequences were probably significant, given the sensitivity of population growth rate to survivorship of adult females (Knight & Eberhardt, 1985).

Apparently, these conditions were aggravated by the juxtaposition of human facilities and key bear habitats. Not surprisingly, roads, recreational developments, and town-sites were concentrated in lower-elevation valley bottoms as was prime grizzly bear spring range (Mattson et al., 1987). Adult females also happened to make disproportionately intense use of spring habitats (Mattson et al., 1987), likely increasing the probability that they would lose their fear of humans as they sought out and used ungulate carcasses on elk and bison winter ranges. Although human-caused mortality occurred primarily during late summer and early fall, it is reasonable to expect that potentially fatal patterns of behavior could be initiated or reinforced at any time during the nondenning season.

In contrast, human facilities typically were far removed from the richest fall habitats (Mattson et al., 1987), where, during some years, bears foraged on seeds in high-elevation whitebark pine stands (*Pinus albicaulis*) (Mattson & Reinhart, 1994). While this disposition was ostensibly favorable to grizzlies, bears still died in their greatest numbers during the fall foraging season. However, this mortality occurred largely during years when whitebark pine seeds were unavailable and bears sought out alternate foods that typically occurred at lower elevations, nearer to, if not closely associated with, human facilities (Mattson et al., 1992). Thus, it was not sufficient for humans to be remote from the richest habitats when food crops produced in these areas failed. Perhaps as important, grizzly bear mortality was dependent on the presence of humans in habitats containing various alternate foods. Because predicting these alternate foods is fraught with uncertainty (Mattson et al., 1991a) and because they are often astride park boundaries, resolution of this problem is inherently difficult.

The choice of bears to kill and the placement of human facilities thus appear to be central parts of grizzly bear management, although likely secondary to decisions regarding the overall level of bear mortality and human activity. Killing "problem" habituated bears probably enhances human safety (Herrero,

1985; Herrero & Fleck, 1990), but it very likely reduces a population's ability to fully use available habitat and could indirectly increase the vulnerability of adult females to human-caused mortality. It probably is also insufficient to merely judge the impacts of human activities in terms of habitats that are, on average, most heavily used by bears during hyperphagia. Spring habitat and infrequently productive fall habitats are of equal importance to an assessment.

Designing Protected Areas

So far, we have emphasized the effects of human facilities on grizzly bear mortality and distribution, and the extent to which these effects might vary depending on the site and bear behavior. We have not addressed questions of larger import related to the size, security, and connectivity of protected areas. Although we cannot provide answers, in this section we identify some relevant considerations and relate them to existing protected area strategies.

Given an interest in grizzly bear conservation, protected areas are relevant usually where the bears' range has been or is becoming fragmented by human settlement. In areas typical of Alaska and northern Canada, there are few resident humans, and currently conservation is primarily a function of managing legal hunts and apprehending poachers. The design and establishment of protected areas is thus most immediately relevant to conservation of grizzly bears in Alberta and British Columbia and in the few areas of the contiguous United States where grizzlies survive (McCrory et al., 1990; U.S. Fish and Wildlife Service, 1993); it will become more important in the North as resource development continues.

A Conceptualization

Protected-area size is theoretically a function of population goals, range sizes and range overlap, impairment by human activity and behavior (Schonewald-Cox & Buechner, 1991), lethality of the surrounding matrix (Schonewald-Cox & Bayless, 1986; Franklin, 1993), habitat variability (Goodman, 1987; Thomas, 1994), and the shape of the protected area (Schonewald-Cox & Bayless, 1986). In other words, protected areas need to be larger if the desired population is large, composed of wide-ranging animals that occupy highly variable habitat impacted by substantial human use, and if the protected area is surrounded by a deadly matrix from which the bears need to be buffered. Conversely, protected areas theoretically can be smaller where range sizes and population goals are smaller, the habitat better protected and less variable, and the surrounding ma-

trix more benign. As illustrated by Kootenay and Yoho National Parks in southeastern British Columbia (McCrary et al., 1990; Raine, 1991), all else being equal, linear protected areas leave bears more vulnerable than areas with a lower edge-to-interior ratio.

SOME PRIMARY DETERMINANTS. It could be argued that population goals, more than anything else, determine the size and design of protected areas for grizzly bears (Fig. 8.2). Protected areas would vary substantially depending, for example, on whether 50 or 2000 bears were deemed sufficient. In the same way, societal decisions regarding acceptable risks to populations and relevant time frames have major theoretical implications to protected area design. Managing at a very small risk of extinction within 1000 years obviously entails substantially greater levels of protection than managing for a moderate risk of extinction within 100 years (compare Shaffer, 1992, and U.S. Fish and Wildlife Service, 1993). Despite assertions to the contrary, these decisions are fundamentally expressions of human values, possibly influenced by a cost-benefit analysis that considers biological information (Kellert, 1994a).

Carrying capacity is another important variable in protected area design (see Fig. 8.2). Lower unit-area carrying capacity obviously engenders the need for greater space, all else being equal. However, the usefulness of this concept is compromised by its ambiguity and the fact that it has a frequently ignored temporal dimension (McNab, 1985). Carrying capacity could be described in primal terms; i.e., given the existing vegetation, how many grizzlies would have lived in an area prior to the arrival of Europeans? Inevitably, however, this type of construct needs to be translated as "habitat effectiveness" or "habitat capability," by accounting for diminishments attributable to humans. Sidestepping these semantics, the area required to support a given number of bears will depend on both habitat productivity and the human presence (Weaver et al., 1986). Less productive habitat and a chronically lethal human presence will dictate a need for greater space as a means of providing more inherently lower-density feeding opportunities in areas secure from human impacts.

Humans, therefore, are perhaps best characterized as a habitat feature. Like vegetation types, human presence will vary temporally and spatially. However, unlike vegetation, which is understood primarily as a surrogate for population productivity, the human presence is most fruitfully understood as a surrogate for mortality, as described earlier. In simple terms, habitat variation is gainfully understood as fecundity varying with food abundance and mortality varying with the numbers and behavior of humans. Although not explicit in current grizzly bear cumulative-effects models, this conceptualization is implicit to the way habitat effectiveness is calculated and to the acknowledgment that separate

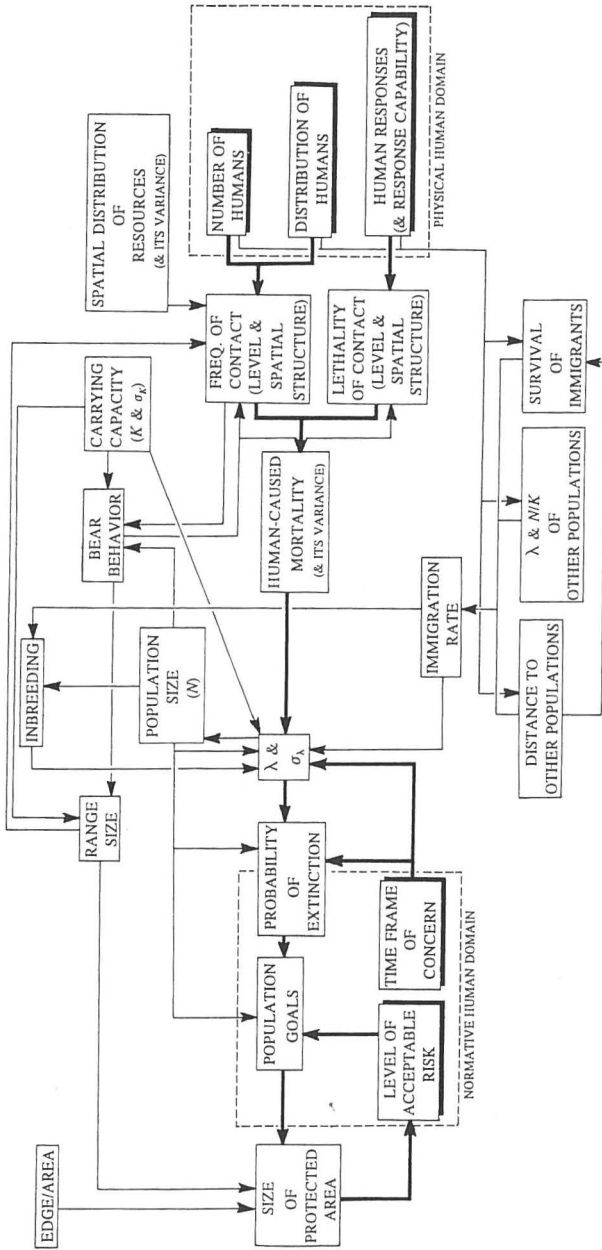


Figure 8.2 A simplified conceptual model of the relationship between attributes of grizzly bear protected areas and influential factors related primarily to human and grizzly bear behavior. Key manipulable factors are denoted by broken boxes and major relationships by heavier lines. Human-related factors are segregated as physical and normative (related to values or cultural norms) elements. Population growth rate is denoted by λ and variance, in places, by σ .

calculations of mortality risk as a function of the human presence are needed (Weaver et al., 1986).

While information on the spatial distributions of humans and foods is important, it is not sufficient for deciding how much protection a bear population needs to achieve specified goals. The abundance and quality of food may vary dramatically, not only from one year to the next but among decades or centuries (Hamer & Herrero, 1987a; Mattson et al., 1991a; Mattson & Reid, 1991). Similarly, both the numbers and behavior of humans may vary so that the frequency and lethality of contact between bears and humans changes (see Fig. 8.2). In theory, bear populations in areas subject to greater variation in human and biophysical domains need greater protection as well as prerogative on a larger area to ensure longer-term survival (Goodman, 1987; Thomas, 1994).

These considerations are graphically illustrated by historical changes in the Yellowstone National Park ecosystem and the Canadian ecosystem containing the four Rocky Mountain National Parks (i.e., Banff, Jasper, Yoho, and Kootenay). Habitat conditions are dynamic and relatively unpredictable in both areas. For example, in the Yellowstone ecosystem, fires recently burned a substantial part of available grizzly bear habitat (Schullery, 1989) during the same period that bears were beginning to use an entirely new (at least in recent history) grizzly bear food (army cutworm moths [*Euxoa auxiliaris*]) (Mattson et al., 1991b). Fire control along the east front of the southern Canadian Rockies has similarly led to the widespread diminishment of a key bear food (buffalo-berry [*Shepherdia canadensis*]) that is dependent on periodic stand-replacement fires (Russell et al., 1979; Hamer & Herrero, 1987b). Considerable annual variation in abundance of key foods is further nested within these longer-term changes. More to the point, this environmental variation has affected bears and, in the Yellowstone ecosystem, has led not only to possible changes in grizzly bear fecundity (Mattson & Reinhart, 1994) but also dramatic variation in conflict with humans (Mattson et al., 1992).

Recent theoretical work suggests that catastrophes and endemic environmental variation are important in defining extinction risks for currently stable populations (e.g., Lande, 1993). Parenthetically, it is worth noting that both types of variation are probably secondary in importance to the deterministic effects of increasing numbers of humans in grizzly bear habitat (Mattson et al., 1996). Nonetheless, annual human-caused mortality in or near protected areas is quite varied, and, prorated to the number of humans, has no doubt changed with time. While recognizing the importance of deterministic grizzly bear-population declines, it makes sense to recognize variance in the human-related causes and design, accordingly. If other buffers are absent, it seems logical to buffer grizzlies from variations in habitat conditions that lead to variation in risk of human-caused mortality. It also makes sense to at least

anticipate the possible consequences of catastrophes, most logically defined in terms of dramatic adverse changes in either the numbers or behavior of humans. Although grizzlies may be physically able to accommodate most annual variation in the distribution and abundance of foods (Herrero, 1978; Stirling & Derocher, 1990), they are exceptionally ill-equipped to buffer themselves from temporal and spatial variations in risk posed by humans.

THE HUMAN DIMENSION. It is evident from these considerations that the key variables in designing protected areas for fragmented grizzly bear populations are the numbers, distribution, and behaviors of humans, both in and around reserves, and management time frames and levels of acceptable risk (see Fig. 8.2). While important, it would be difficult to argue that variation in habitat productivity, aside from effects on the frequency of encounters between humans and bears, equals the effects of those factors more directly tied to the rate at which humans kill grizzlies. In part, this follows from the apparent greater sensitivity of grizzly bear–population growth to survivorship rather than fecundity (Knight & Eberhardt, 1985; McLellan, 1989a; Eberhardt et al., 1994), and the demonstrated ability of humans to eliminate grizzlies, regardless of their reproductive potential (Storer & Tevis, 1955; Brown, 1985).

The size and characteristics of protected areas, therefore, will largely be a function of human values and behavior, although the role of “carrying capacity” as well as the need to understand how human numbers and behavior affect grizzly bear vital rates should not be trivialized. In this light, protection is ultimately defined in terms of frequency and lethality of contact with humans (see Fig. 8.2) (Mattson et al., 1996). Thus, the need to control humans varies with the number of humans in bear habitat, their distribution, and their behavior. More specifically, it is relevant whether humans are dispersed or aggregated, near or far from important bear habitat, armed or not, and prone to intolerance and fear of grizzlies.

Theoretically, grizzlies could coexist with relatively large numbers of humans if the humans were unarmed, tolerant of injury and competition for common resources, and aggregated in the poorest grizzly bear habitat. If this scenario were pervasive, the issue of providing grizzly bears with areas secure from humans might be moot. We do not know the theoretical or practical limits of human tolerance, but we do know that grizzlies can become highly habituated to humans and that unarmed humans do not pose much immediate risk to a grizzly bear. Clearly, many issues—and limitations—of grizzly bear conservation are rooted in human values and behavior.

There is contradictory evidence and some dispute over the extent to which human values can be changed in a short-term tactical sense (Clark & Reading, 1994; Kellert, 1994a). Additional information often is used to justify or ratio-

nalize set values and opinions (Reading & Kellert, 1993). On the other hand, education can modify the expressed values of students (Caro et al., 1994). Regardless, we know of no situation when, as a consequence of education programs by advocacy groups or government agencies, base values have changed toward the management of grizzly bears and their habitat. At best, such efforts might serve to mobilize interested people and reduce unintended conflicts between bears and humans by providing people with the information needed to produce an already desired outcome.

Although it may not be possible to change human values, human behavior can be influenced by the extent to which people are involved in decision-making processes. Greater acknowledgement of individual concerns often serves to alleviate conflict and can lead to more successful management (Gregory & Keeney, 1994; Wondolleck et al., 1994). In the case of grizzly bears, antagonism toward protective measures and, possibly, the proclivity to kill bears illegally might be reduced by recruiting acceptance, if not goodwill, through collaborative development of management strategies (Kellert 1994b). Although this type of endeavor would have to be bounded at some level by broad policy objectives, there is good reason to believe that a consensus-building approach may have the greatest short-term impacts on human behavior (see Cohn, 1988; Nowak, 1995). Unfortunately, there has been little impetus from policymakers for this kind of approach to grizzly bear management, and interaction between managers and stakeholders has largely consisted of a formal exchange of "information" and "concerns."

These reasons, as well as limited authority to change public values, have led to a management style that emphasizes modification of human behavior through coercion (i.e., laws, regulations, and their enforcement), access restriction, and control of firearms (as in most parks) (Dood et al., 1986; Nagy & Gunson, 1990; U.S. Fish and Wildlife Service, 1993). In a proximal sense, this management style has focused on sanitizing human facilities to reduce their attractiveness to bears and regulating direct human-caused mortality. Very little attention, if any, has been given to limiting the overall number of people in grizzly bear habitat or to the major capital investments, such as roads and accommodations, that often facilitate human presence. In the final analysis, because education seems to have limited tactical use—especially when confronted by millions of transient tourists—because regulation of human numbers seems to be challenging politically, and because disarming humans is feasible politically only in a few areas, "protection" of grizzly bears has come to be defined in terms of coercion and access restriction. Protected areas for grizzly bears are correspondingly defined primarily in terms of prohibitive regulations and few roads.

Corridors and Connectivity

Connectivity among populations is generally thought to enhance long-term survival. Relatively high levels of exchange, in theory, allow for "risk averaging," characterized by periodic rescue of declining populations (see Brown & Kodric-Brown, 1977) by emigration from growing populations and prevention of inbreeding by maintenance of genetic heterozygosity. Conversely, Simberloff and Cox (1987) point out that interchange among populations might transmit catastrophic diseases and dilute local genetic adaptations in species, which tend to maintain fragmented ranges under natural conditions. Therefore, as a bottom line, these authors contend that connectivity is not always a good thing.

But how does connectivity affect bears? There is no evidence that grizzly bear populations were characteristically fragmented or exhibited anything resembling a classic metapopulation structure prior to European settlement. There is no evidence that grizzlies exhibit major local genetic adaptations, as would be expected by their more-or-less continuous distribution, large ranges, phenotypic plasticity, and flexible behavior (F. Allendorf, personal communication). Unlike some other carnivores (see Young, 1994), brown bears are not threatened by any known virulent diseases anywhere in the world. In short, there are no obvious biological reasons why connectivity would be bad for grizzlies and numerous reasons to think it would be good (Shaffer, 1992; U.S. Fish and Wildlife Service, 1993). Theoretically, it would be especially beneficial to increase exchange among small, otherwise vulnerable, populations, especially if connections were made to larger populations (Harrison, 1991).

Corridors are commonly conceived as strips of connecting habitat that not only are attractive to a species but also are sufficiently secure to allow for safe transit. In this sense, corridors provide a means for individuals to travel among populations. However, this conception is useful only when populations are within a range of lifetime movements (Fahrig & Merriam, 1994). There is limited information about how far grizzlies will disperse. In the Yellowstone area, juvenile males have been known to relocate 45 to 105 kilometers from maternal ranges through relatively friendly habitat (Blanchard & Knight, 1991). Populations isolated by greater distances of hostile habitat, like Yellowstone's and possibly the bears in Washington State's North Cascades, would not benefit from traditionally conceived corridors. Successful movement to these more isolated populations instead would depend, in particular, on the establishment and survival of adult females in intervening habitat, which would function as a sequence of demographic stepping stones. In these cases, connectivity becomes a matter of creating conditions where females can survive and reproduce; the exact demographic requirements logically depend on the distance

between "populations." In essence, separate populations would be united (Shaffer, 1992).

Conclusions and Implications

Hopefully this discussion clarifies that there is no single size, configuration, or suite of attributes for areas designed to protect grizzly bears. The primary determinants of size seem to be (1) specified or operational time frames and levels of acceptable risk; (2) rates of human-caused mortality and the extent to which they are selective against habituated bears; (3) unit-area carrying capacity, in the loose sense that it has been defined here; and (4) net exchange with other bear populations. Of these key factors, only one falls largely within the biological domain, while the others are determined primarily by human values, behavior, densities, and distribution within protected areas and the intervening "hostile" matrix. It therefore is logical that the design of protected areas for grizzlies should consider pertinent information about humans and the attributes of human-grizzly bear interactions that lead to bear deaths (Mattson et al., 1996). By this reckoning, bear biology is secondary to human biology.

Compartmentalization: A Key Strategy

A key strategy has been implicit to this entire discussion, assuming that there is some level of irreducible conflict between grizzlies and humans and related demonstrable risks to human safety. This scheme, which we call compartmentalization, follows from our analyses and is a more formalized approach, convergent with the fragmented evolution of grizzly bear management during the last two decades. Simply put, compartmentalization seeks to segregate a given number of humans and grizzlies, as a means of minimizing contact between the two species. Implementation of this strategy depends on (1) minimizing the attractiveness to bears of areas occupied by humans, whether this attractiveness derives from human activity or native foods (Herrero, 1985; Herrero & Fleck, 1990); (2) aggregating as much human use as possible within areas that are inherently unattractive to bears (Herrero et al., 1986; McCrory et al., 1986); (3) coercing bears that enter these human aggregations to leave as soon as they are detected (Greene, 1982; McCullough, 1982); and (4) excluding humans from high-value grizzly bear habitat during the seasons when bears are most active (Martinka, 1982). When implemented in concert with firearms control, this strategy promises to maximize short-term compatibility between grizzlies and humans.

National parks in Canada and the United States have come closest to implementing this strategy. Thus, we see grizzlies surviving during their active season in areas visited by several million people. Virtually all visitors remain aggregated in relatively few areas, sanitation is usually stringent, and areas of frequent bear use or known high-quality habitat are closed as needed or by a regular schedule, which allows for areas permanently allocated to high levels of human use, regardless of attractiveness to bears. Extremes of this strategy are evident at places like McNeil River Falls, Alaska, where the number and temporal and spatial distributions of humans are tightly controlled, albeit in extremely attractive bear habitat, but with minimal apparent impacts on bear behavior or survival (Aumiller & Schoen, 1991).

However, conflicts continue to plague the national parks, partly because many human developments were placed in attractive bear habitat at a time when minimizing conflict with grizzlies was not a priority. This is especially true of places such as Lake and Grant Villages in Yellowstone National Park, located on top of cutthroat trout spawning streams (Reinhart & Mattson, 1990); Old Faithful and Mammoth Villages, located in prime ungulate winter ranges (Mattson & Knight, 1992); and the Town of Banff and the Trans-Canada Hiway in Banff National Park, located in the middle of a travel corridor and otherwise productive habitat (Purves et al., 1992). In addition, the mere presence of such human multitudes seems to precipitate unavoidable conflict.

There are thus obvious limits to compartmentalization, even in parks. However, predictably, these limits are reached sooner in nonpark areas, where humans are freely armed and many are engaged in activities inherently prone to disperse them on the landscape, i.e., hunting, backcountry recreation, ranching, and most industrial activities. In these cases, we are confronted with somehow limiting the numbers of people or modifying their behavior to such an extent that their presence poses little threat to grizzlies. For reasons discussed previously and in other sources (Mattson & Craighead, 1994; Mattson et al., 1996), these tactics are exceptionally difficult to implement. Parks will therefore likely remain cornerstones of grizzly bear conservation (Martinka, 1982; McCrory et al., 1990), especially in areas with high densities of resident humans or where grizzlies still are hunted legally (Herrero, 1994).

Possible Improvements

HUMAN DIMENSIONS. It is vital for people involved in grizzly bear conservation, and especially the biologists and scientists, to understand that population goals and acceptable risks and time frames are societal choices that reflect the

relative value placed on grizzlies by humans. None of these issues is inherently "biological," although biological information may be germane to human deliberations, especially as it elucidates the consequences of different choices (Kellert, 1994a). Biological information commonly is used to support a given position by highlighting specific implications, but this information still does not equate to the advocated values. Thus, the single most important variable in protected-area design is likely social and not biological. The process of designing protected areas for grizzlies therefore may rely as much on the efficiency and utility with which we garner consensus or specify guidance in law as on our ability to generate and use information about grizzly bears (Mattson et al., 1996).

Protected-area design and grizzly bear management, in particular, would therefore benefit from more systematic elucidation of relevant norms, either as a useful protocol for involving local stakeholders in the specification of goals or as a useful direct specification in high-level policy documents (Mattson & Craighead, 1994; Mattson et al., 1996). Some have contended that grizzly bear management already accounts for local social considerations. However, we believe that it is important not to confuse the minimization of risk to individual managers with the optimal expression of human values at the local and national levels. It could be argued that grizzly bear management has too often expressed more of the former and less of the latter, this rationalized as being attentive to "social realities" (Primm, 1993; Mattson & Craighead, 1994).

Moreover, managers would have more options and could be more effective if they had greater knowledge of socially acceptable techniques for modifying human behavior (Clark & Reading, 1994), with the intent of harmonizing humans and grizzly bears. Although other means may exist, one promising approach integrates stakeholders more closely in the development of management objectives and strategies (see earlier discussion; Gregory & Keeney, 1994) and even the design and implementation of research (Mattson et al., 1996). This not only increases the positive investment of people most likely to directly or indirectly affect bear survival, but also increases the likelihood that their concerns will be addressed in a constructive preventive manner (Wondolleck et al., 1994). Most important, this type of process holds the promise of increasing local acceptance of grizzly bears and the related necessary restrictions on human activity (Kellert, 1994b). Ironically, unless legislation in the United States is revised so that citizens can be more directly involved in management of federal lands, this potential reconciling tactic may be unavailable to managers.

BIOLOGICAL DIMENSIONS. Our understanding of spatial variation in grizzly bear mortality is not yet very robust. For example, no one has explicitly accounted for either movement between sources and sinks or the effects of ancillary variables. Existing information also does not clarify whether park boundaries or human-impacted areas, regardless of jurisdiction, better distinguish sinks and sources; the utility of either stratification will likely depend on jurisdictional dichotomies in legal protection. By implication, further analysis and modeling would simultaneously consider both stratifications of the landscape. Conservation efforts would benefit substantially from a more detailed understanding of how specific human activities affect grizzly bear survival and, taken together, ultimately how they affect population growth (Mattson et al., 1996). As a bottom line, ideally planners would be able to predict the demographic consequences of changing the types, numbers, and locations of human facilities, or changing management regimes associated with jurisdictional lines.

The existing empirical research for grizzly bears is a weak base for developing the spatially explicit models and predictions that most scientists and managers consider central to applying scientific results. Doak (1995) modeled the Yellowstone population as a fairly simplistic source-sink structure, yet elucidated some important management implications. However, to go beyond this type of first approximation, the available data must be subjected to more rigorous and comprehensive spatial analyses, and, perhaps, we will need to design additional field studies around explicit hypotheses concerning the spatial component of grizzly bear mortality. All of this research is inherently limited, however, by relatively small numbers of grizzly bears and the correspondingly small numbers of dead animals on which we can base any model or statistical test. So while this is a vital issue, we will have continuing difficulty generating relevant but reliable information (Mattson et al., 1996).

Furthermore, designers and managers of protected areas would benefit from being able to express biophysical landscapes in terms of grizzly bear fecundity. Together with an understanding of how grizzly bear mortality varies with the human presence, we would then be able to anticipate grizzly bear population dynamics as a function of dynamic landscapes. The difficulties of such an undertaking are obvious. There first needs to be some common currency for describing landscapes of the composition and productivity of varied plant species. We then need to relate this currency to observed fecundity, presumably through some analysis of ecological energetics. Finally, if there are density-dependent responses in reproduction at the landscape level, we need at least to comprehend the magnitude and nature of this effect. At best, researchers have made some small uncoordinated steps in this direction, but there is a long way yet to go.

Implications to Other Carnivores

We conclude this chapter with some observations on whether or how considerations in the design and management of protected areas for grizzly bears extrapolate to other medium- to large-sized carnivores such as black bears, American martens (*Martes americana*), fishers (*M. pennanti*), lynx (*Lynx canadensis*), cougars (*Felis concolor*), wolverines (*Gulo gulo*), and wolves (*Lupus canis*). Commonalities logically follow from (1) the extent to which humans cause mortality; (2) the extent to which densities are affected by variations in prey induced by humans either directly or through modification of habitat structure; (3) the extent to which there are economic incentives for humans to kill the carnivore; and (4) the extent to which the carnivore threatens human safety or assets such as livestock and crops.

By these standards, cougars probably pose nearly as much threat to human safety as do grizzlies. Wolves and cougars (Dixon, 1982; Paradiso & Nowak, 1982), along with grizzlies and black bears (Mattson, 1990), are sometimes a threat to livestock. Together with wolverines (Banci, 1994), these four large carnivores seem to die largely because humans kill them, at least under the same types of conditions where protected areas are important to conservation of grizzlies (Dixon, 1982; Paradiso & Nowak, 1982; Brown, 1983). Although humans may have additional substantive impacts on cougars and wolves through management of ungulates, it is likely that direct interactions with humans, and associated human behavior, are of great importance to the design of protected areas for all four larger carnivores. Many of the considerations regarding human-grizzly bear interactions are therefore relevant to black bears, wolves, cougars, and wolverines, although habituation to humans may not be of as much importance to mortality of the nonbear species.

Lynx, American martens, and fishers pose virtually no direct threat to human safety or assets. All are potentially subject to heavy trapping because of the sometimes high economic value of their pelts, and all can be dramatically affected by changes in the structure of their habitat, which are manifested primarily through changes in prey tied closely to older, typically closed-canopy, forests (see Powell, 1993; Buskirk et al., 1994; Ruggiero et al., 1994). Because of these dissimilarities to grizzly bears, the considerations in this chapter probably have minimal or, at most, only very general relevance to conservation of these species. A different model would better tend to the importance of habitat-prey dynamics and the economics of trapping and timber harvest.

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