
Conservation of the Yellowstone Grizzly Bear

DAVID J. MATTSON

Interagency Grizzly Bear Study Team
Forestry Sciences Lab
Montana State University
Bozeman, MT 59717, U.S.A.

MATTHEW M. REID

Department of Biology
Montana State University
Bozeman, MT 59717, U.S.A.

Abstract: *We review literature relevant to the conservation of Yellowstone's grizzly bear population and appraise the bear's long-term viability. We conclude that the population is isolated and vulnerable to epidemic perturbation and that the carrying capacity of the habitat is likely to shift downward under conditions of climate change. Viability analyses based on the assumption that future habitats will closely resemble those existing at present have limited applicability; more information is needed on the autecology of important bear foods and on the implications of landscape-scale changes for bear population dynamics. Optimism over prospects of long-term persistence for Yellowstone's grizzly bears does not seem to be warranted, and management of this population should be conservative and not unduly swayed on short-term positive trends.*

Resumen: *Revisamos la literatura relevante a la conservación de la población del oso gris (*Ursus arctos horribilis*) en Yellowstone y presentamos una evaluación de su viabilidad a largo plazo. Concluimos que la población está aislada y es vulnerable a la perturbación epidémica y que la capacidad de carga del hábitat es probable que vaya declinando bajo las condiciones de cambios climáticos. Los análisis de viabilidad basados en la asunción de que habitats en el futuro se parecerán a los que existen en el presente, tienen una aplicación limitada; se necesita más información sobre la autoecología de las fuentes alimenticias importantes para los osos y sobre las implicaciones de los cambios de paisaje en la dinámica de las poblaciones de osos. El optimismo sobre el prospecto a largo plazo para las poblaciones de osos en Yellowstone no parece estar garantizado y el manejo de esta población debe de ser conservado y no se debe de dejar llevar por tendencias positivas a corto plazo.*

Introduction

The Yellowstone grizzly bear (*Ursus arctos horribilis*) has been at the center of controversy since the closure of garbage dumps within and adjacent to Yellowstone National Park in the early 1970s. The dumps were arguably an important food source for the bears (Craighead & Craighead 1972; Mattson et al. 1991). Their closure ultimately contributed to a dramatic decline in

the Yellowstone grizzly bear population (Craighead et al. 1974) as well as the 1975 listing of grizzly bears in the lower 48 states as threatened under the Endangered Species Act.

In the last decade, long- and short-term viabilities of the Yellowstone grizzly bear population have been evaluated by mathematical population modeling (e.g., McCullough 1981; Shaffer 1983; Suchy et al. 1985; Knight & Eberhardt 1984, 1985, 1987; Dennis et al. 1989). In all of these analyses, environmental and behavioral factors have been treated primarily as indeterminate stochastic input. In recent years, however, the complex

Paper submitted July 1, 1990; revised manuscript accepted January 23, 1991.

relationships between habitat and bears and between bears and humans in Yellowstone have become increasingly clear. We contend that an adequate assessment of viability for Yellowstone's grizzly bears and the development of effective conservation strategies requires looking simultaneously at all parts of the bears' environments.

In this paper we have marshaled information relevant to a more holistic appraisal of long-term viability for the Yellowstone grizzly bear population and identified deficiencies in our current knowledge. We do not intend to provide a philosophical or functional argument for preserving the Yellowstone grizzly but rather to synthesize the components relevant to grizzly bear conservation.

The Current Situation

The Habitat

In the Greater Yellowstone Ecosystem (GYE) 23,300 km² of habitat is available for occupancy by grizzly bears (USFWS 1990). This is roughly 6 times the size of the average male lifetime home range and 26 times the size of the average female lifetime range (cf. Blanchard & Knight 1991). Within this area ungulates (Cervidae, Bovidae) and whitebark pine (*Pinus albicaulis*) seeds are the principal high-quality foods available to bears. Unlike most occupied bear habitat, berries are relatively scarce in this region (Mattson et al. 1991). Another prominent feature of Yellowstone's bear habitat is its considerable variation in time and space (Knight et al. 1984; Mattson & Knight 1989). Food habits vary concordantly to the extent that singularly new patterns are observed even after 11 years of habitat data collection (Mattson et al. 1991).

Bear habitat in the GYE has undergone and will continue to undergo long-term changes in productivity. From the early 1970s until the present there has been a dramatic increase in the amounts of proteinaceous foods available to bears due to changes in human management of Yellowstone National Park's ungulate and cutthroat trout (*Oncorhynchus clarki*) populations (Servheen et al. 1986). Competition and indirect risks posed to bears by domestic sheep have also been reduced by the elimination of sheep from most occupied grizzly bear habitat. However, the GYE and its bear foods appear to be vulnerable to global climatic warming (Picton et al. 1986). Two very important grizzly bear foods that are distributed only at high elevations (whitebark pine at >2500 m [Mattson & Jonkel 1990] and army cutworm moth [*Euxoa auxiliaris*] aggregations at >3100 m [Mattson et al., in prep.]), may disappear altogether with worst-case scenarios of climatic warming (cf. Dickenson & Cicerone 1986; Kerr 1986).

High-quality foods that might replace the ones lost are unknown. Although fish and ungulate populations are more abundant now than in the past, these high-protein foods are primarily available during the spring and early summer, when bear ingestion rates are inherently low (Mattson et al. 1991). These foods contribute less to body fat accumulation than the high-fat whitebark pine seeds and army cutworm moths. Although the trend in productivity of Yellowstone's grizzly bear habitat has been positive over the last 20 years, it is not likely to remain so and may deteriorate over the next century.

Although not conclusively demonstrated, several phenomena suggest that the Yellowstone grizzly bear population is at or near carrying capacity (K) over much of its core range, which is centered in Yellowstone National Park. This is indicated by the sensitivity of several parameters to variation in habitat conditions, including mortality (Picton et al. 1986; Knight et al. 1988b; Mattson & Knight 1989), natality (Picton et al. 1986; Picton & Knight 1986), weights (Blanchard 1987), and movements (Picton et al. 1986; Blanchard 1990; Blanchard & Knight 1991). Although McDonald et al. (1989) have suggested that populations are expanding, the reliability of their long-term data are questionable, and analysis of more comparable data sets has shown only minor range expansion by Yellowstone's grizzly bears in the last 10 years (Basile 1982; Blanchard et al., in prep.). It is therefore likely that under current habitat conditions relatively little room remains for additional grizzlies in the GYE.

The Population

The Yellowstone grizzly bear population constitutes a significant portion of the estimated 700–900 grizzly bears remaining in the conterminous United States (cf. Servheen 1989b). There is probably a minimum of 170–180 grizzly bears (Knight et al. 1988a) occupying as little as 8300 km² of habitat in the GYE, although Blanchard and Knight (1980) allowed for the possibility of 350 bears distributed over 20,000 km². Verified distribution of the Yellowstone grizzly population was documented by Basile (1982) and, more recently, by Blanchard et al. (in prep.).

The dynamics of the Yellowstone grizzly bear population were studied from 1959 to 1970 by the Craighead research team and since 1974 by the Interagency Grizzly Bear Study Team (IGBST). Craighead et al. (1974) suggested a 45 percent decline in population from an estimated peak of 245 grizzlies in 1967, attributable to human-caused mortality in the wake of dump closures. A total of 127 grizzlies were known to have been killed over a 3-year period during and immediately after closure of the major open-pit dumps (Craighead et al. 1988). Known annual mortality subsequently dropped to an average of nine bears over each of the next 5 years.

A series of analyses by Knight and Eberhardt (1985, 1987) and Knight et al. (1988a) showed a grizzly bear population that was first slightly decreasing, then stabilized, and most recently slightly increasing during the 1970s and 1980s. These more recent analyses suggest that the Yellowstone grizzly bear population is not likely to go extinct in the next 30 years, but it has more uncertain prospects beyond that time. It is possible that the population went through a critical bottleneck following closure of the dumps and has only recently started to recover. The IGBST is currently monitoring survivorship and distribution of adult females, with special attention to sightings of females with cubs of the year. The Recovery Plan for Yellowstone's grizzly bear population is in the process of revision, with recovery estimated for all grizzlies in the conterminous United States by the year 2010 (USFWS 1990).

Human-Bear Conflict

Chronic under-use of available habitat by bears has been documented in numerous areas of Yellowstone's occupied habitat (Gunther 1984, 1990; Mattson et al. 1987; Mattson & Henry 1987; Henry & Mattson 1988; Green & Mattson 1988; Reinhart & Mattson 1990) as a consequence of bears avoiding humans (Mattson et al. 1987; Mattson 1990). This underuse of habitat is mediated through the consistent harvest of human-habituated bears that would otherwise be able to use habitat near humans more fully (Mattson et al. 1987; Mattson 1990). Mortality of nonhabituated bears has also taken its toll (cf. Craighead et al. 1988) but has not contributed as much to probable declines in access-mediated carrying capacity (Mattson 1990).

The intensity of human-bear conflict in the Yellowstone ecosystem is aggravated by bear-bear interactions and the distribution of human activities in seasonally productive bear habitat. In Yellowstone, adult males apparently have prerogative on habitat that is not only more productive but also more secure from humans. Other bear classes appear to avoid the adult males and use the remaining habitat as best they can (Mattson et al. 1987; Mattson 1990). Because of their more stressful

energetic predicaments, adult females and subadult males are probably more likely to tolerate humans in their pursuit of food and are thus more likely to become human-habituated and food-conditioned (Mattson et al. 1987; Mattson 1990). This scenario is corroborated by the tendency for adult females and subadult males to experience a higher mortality and management trapping rate than other bear classes, especially in Yellowstone National Park (Table 1).

During good food years these bear-bear interactions have few consequences. However, the number of adult female deaths and bear management actions escalates substantially during poor food years (Knight et al. 1988b; Blanchard 1990) when there are fewer rich feeding opportunities and subordinate or security-conscious bears are displaced by adult males to less secure low-elevation areas near human facilities (Mattson & Knight 1989). These relationships suggest that under deteriorating habitat conditions mortality will increase disproportionately for adult females, the class of animals most critical to viability of the Yellowstone grizzly bear population (Knight & Eberhardt 1985).

Management

Federal and state agencies have designated a large portion of the GYE for recovery of the grizzly bear population. This area has been further stratified by priority given to grizzly bears with respect to human activities and other resources (cf. USFWS 1990). Ostensibly the recovery area was delineated to reflect bear distribution and to be large enough to support a viable population (USFWS 1990). However, the adequacy of the recovery zone to support a viable population has never been evaluated, and bears occupy and, in places, intensively use habitat well outside the recovery zone (Reid & Gehman 1986).

There have been virtually no intentional efforts to manipulate the abundance and quality of native foods for the benefit of grizzly bears in Yellowstone, although management of proteinaceous foods for other objectives has been beneficial. It is likely that most overt

Table 1. Human-caused grizzly bear mortalities in Yellowstone National Park (YNP) and on national forest and private lands (NF&PR), and total management actions against grizzly bears, by sex and age class for the Yellowstone area, 1975–1988.

	Observed ^a mortalities		Expected ^b mortalities		Mgt. actions ^c per bear year	Mgt. actions ^c per managed bear	
	YNP	NF&PR	YNP	NF&PR		\bar{X}	SD
Adult female	7	23	4.2	18.4	0.17	2.0	1.3
Adult male	1	24	2.7	11.9	0.13	1.5	1.1
Subadult female	2	7	4.6	20.0	0.14	1.6	0.8
Subadult male	6	16	4.5	19.7	0.18	1.8	1.1

^a From Craighead et al. (1988).

^b From Knight et al. (1988a), for a population with a stable age structure, 3-year reproductive cycle, and 51:49 (M:F) ratio for litters.

^c From unpublished IGBST data.

manipulation of vegetation, for example, through timber harvest, is detrimental to Yellowstone grizzlies. This is due to their reliance on older timber stands for high-quality foods (Knight et al. 1984; Mattson & Knight 1989; Mattson & Jonkel 1990; Mattson et al. 1991) and because of problems associated with increased access. However, because most research data have been collected from bears using wilderness areas, direct extrapolation of results to managed forests and forests cut by roads is problematical.

Grizzly bear habitat has probably been most enhanced by the creation of Bear Management Areas in Yellowstone Park, where humans are seasonally or permanently excluded. These areas provide refuge where bears can live without incurring the risks of human habituation that predictably increase with increased frequency of human contact (McArthur-Jope 1983; Meagher & Fowler 1989). Creation of similar areas in the national forests could add significantly to the quality of grizzly bear habitat in the GYE.

Since closure of open-pit garbage dumps in the early 1970s, management of grizzly bears in Yellowstone has focused primarily on making human foods unavailable to bears. This is because food-conditioned bears are dangerous to humans (Herrero 1985) and as a consequence are much more likely to be killed by humans (Meagher & Fowler 1989). Although management to decrease food conditioning has been fairly successful (Servheen 1989a), bears habituated to humans while using native foods are still common (IGBST unpubl. data). Habituation has been more difficult to manage than food conditioning, because habituation involves less manipulable factors such as bear-bear interactions and distribution of native foods, rather than simply controlling access to foods of human origin (Mattson 1990).

Some efforts (brochures, signs, and visitor center programs) have been made to educate people to minimize and accept the risks of being around bears. However, these efforts appear to be inadequate. There is still a large gap between real and perceived risks from grizzly bears, and both the public and managers show a general unwillingness to accept any legitimate risks. People can live near and in frequent contact with bears provided they know bear habitat and behavior well enough to act appropriately (cf. Jonkel & Demarchi 1984; Jope & Shelby 1984; Herrero 1985). However, there are major problems in reaching the millions of people who use the Yellowstone area each year.

Some efforts have been made to educate bears to fear and avoid humans by the use of aversive conditioning. However, this technique has been expensive and logistically demanding, and the few results have been inconclusive (Hunt et al. 1988). Although the approach is conceptually sound (McCullough 1982), the fact that most bears in chronic conflict with humans are energetically stressed and have few options for habitat else-

where (Mattson et al. 1987; Mattson 1990) does not bode well for the success of the technique.

Conservation Considerations

Habitat

Occupied grizzly bear habitat in the GYE constitutes a habitat island and is a small fragment of the species' historical range (cf. Wilcove et al. 1986). The distance to other known occupied grizzly bear habitat in Northwest Montana is approximately 240 km, and movement between the Yellowstone Ecosystem and these areas, although possible (Picton 1986), has not been documented in 31 years of research.

Wilcove et al. (1986) argued that fragmentation remains the principal threat to most temperate-zone species because individual fragments may lack the full range of habitat found in the original block and hence are not sufficiently diverse to allow risk averaging in the face of habitat perturbations (Goodman 1987). Although grizzlies occupy relatively large areas of diverse habitat in the Yellowstone ecosystem, other large areas exist where lack of high-quality habitat during some season substantially limits local bear densities (Knight et al. 1984). In addition, perturbations tend to occur on a very large scale in the Yellowstone ecosystem (Romme 1982), as evidenced by the 567,000 hectares that burned during the 1988 wildfires (Mills 1989). Although grizzly bears are adapted by their large body size and large home ranges to surviving major within-generation habitat variation (Stirling & Derocher 1990), their low densities may have made them vulnerable to large-scale, transgenerational disturbances (Mattson 1990). Consequently, Yellowstone's grizzlies may have been periodically reliant on natural augmentation from contiguous populations to survive such disturbances (Mattson 1990). This potential for natural augmentation no longer exists, and the GYE may be only marginally sufficient in size to average out large-scale perturbations.

Fragmentation also renders a population vulnerable to long-term climate- or pathogen-induced changes in carrying capacity. In North America there is a history of major diseases affecting important bear foods, especially the chestnut (*Castanea dentata*) and whitebark pine (Mattson 1990). Although white pine blister rust (*Cronartium rubicola*) has so far affected whitebark pine only in wetter regions, it is a potential threat in the Yellowstone area as well (Kendall & Arno 1990). Further, high-fat-content foods available during the critical late-summer and fall fattening period, that is, whitebark pine seeds (Romme & Turner, 1991) and alpine aggregations of cutworm moths, are likely to decrease with most scenarios of global warming. Thus, despite the possible increase of ungulates during the less critical spring

and early summer period (Romme & Turner 1991), habitat conditions will probably deteriorate with global warming.

Species normally survive long-term habitat changes by migration and dispersal; thus, they are dependent on travel corridors or contiguous suitable habitat (Graham 1988). This option is no longer available to the Yellowstone grizzly bear population because of habitat fragmentation and a circumscribed static range. The distinct possibility of major change in carrying capacity makes this consideration extremely relevant to assessing long-term prospects of the Yellowstone grizzly bear population.

Edge effects are also relevant to the Yellowstone grizzly bear population, but in a slightly unorthodox way. Traditionally, edge has been viewed as an ecotonal phenomenon (Wilcove et al. 1986). But for the grizzly bear, "edge" must be considered within a human context. Knight et al. (1988b) and the summary by Craighead et al. (1988) have clearly demonstrated that concentrations of humans, whether in the front- or back-country, are lethal to bears and act as spatially defined population sinks. Thus, any interface between grizzly bears and human concentrations may correspond to a mortality gradient. Inherently large grizzly bear ranges guarantee encounters with severe potential population sinks during any bear's lifetime. As Knight et al. (1988b) stated, "there are no true refuges for Yellowstone grizzly bears." This is especially relevant given that 81% of all known mortalities (Craighead et al. 1988) and 88% of all radio-instrumented bear mortalities (Knight et al. 1988c; Knight et al. 1989) between 1975 and 1988 were human-caused. It is also relevant because history demonstrates a general intolerance by humans of appreciable competition or risk from grizzly bears (Mattson 1990).

Population and Genetic Factors

Recently Dennis et al. (1989) evaluated long-term growth and extinction probabilities for the Yellowstone grizzly bear population and concluded that "the Yellowstone grizzly population is doomed to extinction, though not in our lifetimes." This conclusion was derived from the population's small size and high variances in birth and death rates (Dennis et al. 1989) and from life history attributes grizzlies share with most other large-bodied mammals, such as delayed sexual maturity and low reproductive rate. These attributes are particularly sensitive to further constraints imposed by unfavorable habitat or demographic conditions (Eberhardt 1990). Invariably, bear population models show low thresholds between decline and increase of a population and precipitous declines once a minimum threshold has been passed (e.g., McCullough 1981; Suchy et al. 1985; Yodzis & Kolenosky 1986). These models highlight the

vulnerability of small populations of bears to even low levels of increased mortality. This is especially true for the Yellowstone grizzly bear population, in which the difference between an average of two and three known adult female mortalities per year may mean the difference between an increasing and decreasing population (Knight & Eberhardt 1985; USFWS 1990).

Assessments of bear population viability by population modeling are based on the assumption that the nature and range of future variation in population processes will remain roughly the same as in the past. However, conditions are likely to deteriorate in the Yellowstone area. Pimm (1986) has suggested that some species losses may not be readily predictable by extrapolating previous population or habitat trends, and those losses can occur rapidly following superficially healthy population levels. Taking the conservative view, we think that existing models for the Yellowstone grizzly bear population generate optimistic long-term scenarios and that extinction over the next 100 years may be even more likely than suggested by Dennis et al. (1989).

Theoretically, populations have demographic and genetic thresholds below which nonadaptive random forces prevail over adaptive deterministic ones (Gilpin & Soulé 1986). The status of the Yellowstone grizzly bear population with respect to these thresholds is unknown. However, studies by Picton et al. (1990) analyzing fluctuating asymmetry of skeletal components and by Allendorf et al. (1990) analyzing genetic variation suggest that the Yellowstone grizzly bear population already exhibits genetic impoverishment, which could result in reduced reproductive rates. However, genetic problems could be alleviated by the successful introduction of even a few bears per generation from other populations (Allendorf et al. 1990; USFWS 1990).

Global Perspective

Assessing the Yellowstone situation in the context of other insular brown bear populations is instructive (Table 2). All of the insular populations for which information is available are of the European brown bear (*Ursus arctos arctos*), a subspecies suspected to be more compatible with humans because it tends to be shyer and less aggressive and have smaller home ranges (Table 3) than the grizzly bear. Thus, for equivalent population and range sizes and comparable human attitudes, the grizzly bear may be more vulnerable to extinction than the European brown bear.

Given this perspective, the Yellowstone population falls between European populations that are declining or near extinction and other eastern European populations that appear to be thriving and further emphasizes the marginal nature of the Yellowstone population. It is also instructive to note that none of the eastern European populations are known to have declined at their

Table 2. Status of insular brown bear (*Ursus arctos*) populations in Europe and North America.

Population	Population size (n)	Occupied area (km ²)	Status	Historical population estimates
Trentino, Italy	10–16 ^a	250 ^b	Extinction expected ^a	—
Pyrenees, Spain, and France	19–28 ^a	—	Extinction expected ^a	150–200 (1937) ^c
Western Norway	8–16 ^d	—	Highly vulnerable ^d	—
Apennines, Italy	50 ^g	2770 ^g	Declining ^g	—
Cantabria, Spain	54–142 ^e	5000 ^e	Declining ^{a,e}	—
Yellowstone, United States	200–350	23,300 ^f	Stable	—
Bulgaria	700–750 ^a	11,600 ^a	Increasing ^a	450 (1950s) ^a
Dinara Mtns., Yugoslavia	1600–2000 ^a	66,500 ^b	Increasing ^a	—
Carpathian Mtns.; Romania, Soviet Union, Czechoslovakia, Poland	7500 ^a	90,000 ^a	Increasing ^a	1500 (1950) ^a

^a Serubeen (1988b).^b Verstrael (1988).^c Raffin (1988).^d Sorrensen et al. (1990).^e Clevenger et al. (1987).^f U.S. Fish and Wildlife Service (1990).^g Fabbri et al. (1983).

lowest point to fewer than approximately 450 animals, a number considerably greater than the 200–350 estimated for Yellowstone.

Discussion and Conclusions

We have identified some major population, habitat, and management considerations:

1. The Yellowstone population is isolated, and because of this isolation it is questionable whether the population and available habitat are large enough to accommodate potential long-term habitat changes attributable to epidemic perturbation and long-term climatic changes (cf. Peters & Darling 1985).

2. Relevant research and documents such as the draft Grizzly Bear Recovery Plan (USFWS 1990) have not seriously addressed the implications of isolation and the effects of habitat dynamics on this population.

3. Grizzly bear habitat in the GYE will probably deteriorate with climatic warming as distributions of important high-elevation foods decline. High-quality foods that might replace the ones lost are unknown.

4. If general habitat conditions change, population dynamics will also change. Thus, population models that implicitly project historical population dynamics into the future have limited applicability, unless they are coupled with habitat projections.

5. The Yellowstone population is small and thus vulnerable to variation in population parameters, and existing analyses are not optimistic about long-term prospects for the population. Although not insurmountable, problems related to loss of genetic variation can also be expected.

6. Postnatal mortality is the key parameter associated with population decline; most of it is human-caused. Human-caused mortality is contingent on a complex interaction between bear behavior and human behavior. Thus, human-caused mortality is subject to management action. Successful strategies are needed for future non-lethal management of human-habituated bears and for educating humans to mitigate risks associated with bear encounters.

7. Grizzly bear management in the GYE needs improvement. Expansion of the recovery area, education, and designation of restrictive bear management areas show the greatest promise for the future. However, all strategies need to be further evaluated so that their relative efficacy can be determined and their execution optimized.

8. Optimism about the long-term viability of the Yellowstone grizzly bear population is not warranted.

Thus, conservation of Yellowstone's grizzlies will probably depend on the vigorous implementation of several strategies and not be accomplished by focusing on just one effort. Conceivably, if more land were secured for grizzlies in the Yellowstone area, and both people and bears were educated to live near each other,

Table 3. Range sizes (minimum convex polygon) for insular European and North American brown bear populations, by sex.

Sex	Southern Europe	Sweden	Yellowstone
Female	56–85 ^{a,b}	171–1002 ^d	541–1391 ^e
Male	50–1438 ^{a,b,c}	726–2634 ^d	2106–4599 ^e

^a Roth (1983).^b Huber and Roth (1986).^c Clevenger et al. (1990).^d Bjarvall et al. (1990).^e Blanchard and Knight (1991); adults only.

a pessimistic prognosis could become positive. Certainly the long-term interests of Yellowstone's grizzlies could be irreparably harmed by complacency over what appears to be a relatively secure short-term future. Probably no greater error could be made than to make decisions that have long-term repercussions based on short-term considerations. Taking the Yellowstone grizzly population off the threatened species list is an example of such a potential decision.

Conservation of the Yellowstone grizzly bear population offers insight into conservation of large omnivores and carnivores elsewhere. Despite many years of data collection and population modeling, projecting the population's future remains fraught with difficulties and inherently prone to error. This is due to the substantial consequences of small changes in population parameters and the use of small data sets inherent in sampling a species that exhibits low densities and reproductive rates. These difficulties are compounded by uncertainties over future scenarios. Thus, even with an animal as intensively studied as the Yellowstone grizzly bear, a small population of large-bodied animals will probably always have to be managed with a large degree of uncertainty over its future prospects. A very conservative approach seems appropriate, and optimism over short-term positive trends should be questioned.

In addition, the predicament of Yellowstone's grizzlies demonstrates the need for an ecosystem approach to conservation. Without understanding the connections among human-bear conflict, whitebark pine seed crops, and bear-bear interactions or the implications of habituation and food conditioning, conservation of grizzly bears in Yellowstone would be severely handicapped. In short, research that focuses solely on estimated population parameters and neglects the many facets of behavior will probably offer little for the development of conservation strategies for small populations of large-bodied mammals.

Acknowledgments

We appreciate comments by Harold Picton, Bert Harting, Daniel Reinhart, and Richard Knight on earlier drafts of this paper and suggestions by the anonymous reviewers.

Literature Cited

- Allendorf, F. W., R. B. Harris, and L. H. Metzgar. 1990. Estimation of effective population size of grizzly bears by computer simulation. Proc. 4th Int. Congr. of Syst. and Evol. Biol. Div. Biol. Sci., Coop. Wildl. Res. Unit, Missoula, Mont. In press.
- Basile, J. V. 1982. Grizzly bear distribution in the Yellowstone area, 1973-79. U.S.D.A. For. Serv. Res. Note INT-321. 11 pp.

Bjarvall, A., F. Sandegren, and P. Wabakken. 1990. Large home ranges and possible early sexual maturity in Scandinavian bears. International Conference on Bear Research and Management 8:237-241.

Blanchard, B. M. 1987. Size and growth patterns of the Yellowstone grizzly bear. International Conference on Bear Research and Management 7:99-108.

Blanchard, B. M. 1990. Relationships between whitebark pine cone production and fall grizzly bear movements. Page 362 in W. C. Schmidt and K. J. McDonald, compilers. Proc. symposium on whitebark of a high-mountain resource. U.S. Forest Service General Technical Report INT-270.

Blanchard, B. M., and R. R. Knight. 1980. Status of grizzly bears in the Yellowstone system. Transactions of the North American Wildlife and National Resource Conference 45:263-267.

Blanchard, B. M., and R. R. Knight. 1991. Movements of Yellowstone grizzly bears. Biological Conservation. In press.

Blanchard, B. M., R. R. Knight, and D. J. Mattson. In prep. Distribution of Yellowstone grizzly bears during the 1980's. Submitted to Conservation Biology.

Clevenger, A. P., F. J. Purroy, and M. S. de Burvaga. 1987. Status of the brown bear in the Cantabrian Mountains, Spain. International Conference on Bear Research and Management 7:1-8.

Clevenger, A. P., F. J. Purroy, and M. R. Pelton. 1990. Movement and activity patterns of a European brown bear in the Cantabrian Mountains, Spain. International Conference on Bear Research and Management 8:205-211.

Craighead, J. J., and F. C. Craighead, Jr. 1972. Grizzly bear-man relationships in Yellowstone National Park. International Conference on Bear Research and Management 2:304-332.

Craighead, J. J., K. R. Greer, R. R. Knight, and H. I. Pac. 1988. Grizzly bear mortalities in the Yellowstone ecosystem 1959-1987. Mont. Fish Wildlife and Parks, Interagency Grizzly Bear Study Team, Craighead Wildlife-Wildlands Institute, National Fish and Wildlife Found. 104 pp.

Craighead, J. J., J. R. Varney, and F. C. Craighead, Jr. 1974. A population analysis of the Yellowstone grizzly bear. Montana Forestry and Conservation Experiment Station, School of Forestry, University of Montana, Bulletin 40. 20 pp.

Dennis, B., P. L. Munholland, and J. M. Scott. 1989. Estimation of growth and extinction parameters for endangered species. Montana State University, Statistics Group, Department of Mathematical Sciences, Technical Report 71 pp.

Dickenson, R. E., and R. J. Cicerone. 1986. Future global warming from atmospheric trace gases. Nature (Lond.) 319:109-115.

Eberhardt, L. I. 1990. Survival rates required to sustain bear populations. Journal of Wildlife Management 54(4):587-590.

Elgmork, K. 1976. A remnant brown bear population in southern Norway and problems of its conservation. International Conference on Bear Research and Management 3:281-297.

Fabrizi, M., G. Boscagli, and S. Lovari. 1983. The brown bear population of Abruzzo. Acta Zoologica Fennica 174:163-164.

- Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19–34 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Goodman, D. 1987. How do species persist? Lessons for conservation biology. *Conservation Biology* 1(1):59–62.
- Graham, R. W. 1988. The role of climatic change in the design of biological reserves: the paleoecological perspective for conservation biology. *Conservation Biology* 2(4):391–394.
- Green, G. I., and D. J. Mattson. 1988. Dynamics of ungulate carcass availability and use by bears on the northern winter range: 1987 progress report. Pages 32–50 in Annual report of the Interagency Study Team: 1987. U.S.D.I. National Park Service.
- Gunther, K. 1984. Relationship between angler and bear use in the Clear Creek area of Yellowstone Lake. U.S.D.I. National Park Service, Yellowstone National Park. Information Paper Number 40. 8 pp.
- Gunther, K. 1990. Visitor impact on grizzly bear activity in Pelican Valley, Yellowstone National Park. *International Conference on Bear Research and Management* 8:73–78.
- Henry, J., and D. J. Mattson. 1988. Spring grizzly bear use of ungulate carcasses in the Firehole River drainage: third year progress report. Pages 51–59 in Annual report of the Interagency Study Team: 1987. U.S.D.I. National Park Service.
- Herrero, S. 1985. *Bear attacks: their causes and avoidance*. Nick Lyons Books, New York. 287 pp.
- Huber, D., and H. V. Roth. 1986. Home ranges and movements of brown bears in Plitvice Lakes National Park, Yugoslavia. *International Conference on Bear Research and Management* 6:93–97.
- Hunt, C. L., F. M. Hammond, and C. M. Peterson. 1988. Behavioral responses of Yellowstone grizzly bears to applications of aversive conditioning techniques: 1987 progress report. Wyoming Game and Fish Department, Cody, Wyoming. 68 pp.
- Jonkel, C., and R. Demarchi. 1984. Subdivisions and grizzly bears: a matter of jurisdiction. *Western Wildlands* 10(2):24–27.
- Jope, K. L., and B. Shelby. 1984. Hiker behavior and the outcome of interactions with grizzly bears. *Leisure Science* 6(3):257–270.
- Kendall, K. C., and S. F. Arno. 1990. Whitebark pine—an important but endangered wildlife resource. Pages 264–273 in W. C. Schmidt and K. J. McDonald, compilers. *Proceedings—whitebark pine ecosystems: ecology and management of a high-mountain resource*. U.S. Forest Service General Technical Report INT-270.
- Kerr, R. A. 1986. Greenhouse warming still coming. *Science* 232:573–574.
- Knight, R., J. Beecham, B. Blanchard, et al. 1988a. Report of the Yellowstone grizzly bear population task force: equivalent population size for 45 adult females. Interagency Grizzly Bear Committee. 7 pp.
- Knight, R., B. M. Blanchard, and L. L. Eberhardt. 1988b. Mortality patterns and population sinks for Yellowstone grizzly bears, 1973–1985. *Wildlife Society Bulletin* 16:121–125.
- Knight, R., B. M. Blanchard, and D. J. Mattson. 1988c. Yellowstone grizzly bear investigations: report of the Interagency Study Team 1987. U.S.D.I. National Park Service 80 pp.
- Knight, R., B. M. Blanchard, and D. J. Mattson. 1989. Yellowstone grizzly bear investigations: report of the Interagency Study Team 1988. U.S.D.I. National Park Service 34 pp.
- Knight, R. J., and L. L. Eberhardt. 1984. Projecting the future abundance of the Yellowstone grizzly bear. *Journal of Wildlife Management* 48:1434–1438.
- Knight, R. J., and L. L. Eberhardt. 1984. Population dynamics of Yellowstone grizzly bears. *Ecology* 66(2):323–334.
- Knight, R. J., and L. L. Eberhardt. 1987. Prospects for Yellowstone grizzly bears. *International Conference on Bear Research and Management* 7:45–50.
- Knight, R. J., D. J. Mattson, and B. M. Blanchard. 1984. Movements and habitat use of the Yellowstone grizzly bear. U.S.D.I. Natl. Park Serv., Interagency Grizzly Bear Study Team Report. 177 pp.
- Mattson, D. J. 1990. Human impacts on bear habitat use. *International Conference on Bear Research and Management* 8:33–56.
- Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1991. Food habits of Yellowstone grizzly bears, 1977–87. *Canadian Journal of Zoology*.
- Mattson, D. J., C. M. Gillin, S. A. Benson, and R. R. Knight. In prep. Bear use of alpine insect aggregations in the Yellowstone ecosystem. Submitted to *Canadian Journal of Zoology*.
- Mattson, D. J., and J. Henry. 1987. Spring grizzly bear use of ungulate carcasses in the Firehole River drainage: second year progress report. Pages 63–72 in Annual report of the Interagency Study Team: 1986. U.S.D.I. National Park Service.
- Mattson, D. J., and C. Jonkel. 1990. Stone pines and bears. Pages 223–236 in W. C. Schmidt and K. J. McDonald, compilers. *Proceedings—whitebark pine ecosystems: ecology and management of a high-mountain resource*. U.S.D.A. Forest Service General Technical Report INT-270.
- Mattson, D. J., and R. Knight. 1989. Evaluation of grizzly bear habitat using habitat type and cover type classifications. Pages 135–143 in D. E. Ferguson, P. Morgan, and F. D. Johnson, compilers. *Proceedings—land classifications based on vegetation: applications for resource management*. U.S.D.A. Forest Service General Technical Report INT-257.
- Mattson, D. J., R. Knight, and B. M. Blanchard. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *International Conference on Bear Research and Management* 7:259–273.
- McArthur-Jope, K. L. 1983. Habituation of grizzly bears to people: a hypothesis. *International Conference on Bear Research and Management* 5:322–327.
- McCullough, D. R. 1981. Population dynamics of the Yellowstone grizzly bear. Pages 173–196 in C. W. Fowler and T. D. Smith, editors. *Dynamics of large mammal populations*. John Wiley and Sons, New York.

- McCullough, D. R. 1982. Behavior, bears, and humans. *Wildlife Society Bulletin* 10(1):27–33.
- McDonald, L. L., A. H. Wheeler, and H. B. Harvey. 1989. Progress report: sightings of grizzly bears in the greater Yellowstone ecosystem: results of a mail survey covering 1988. Department of Statistics and Zoology, University of Wyoming, Laramie, Wyoming. 84 pp.
- Meagher, M., and S. Fowler. 1989. The consequences of protecting problem grizzly bears. Pages 141–144 in M. Bromley, editor. *Bear-people conflicts: proceedings of a symposium on management strategies*. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Mills, S. M., editor. 1989. *The greater Yellowstone postfire assessment*. U.S.D.I. National Park Service, U.S.D.A. Forest Service 147 pp.
- Peters, R. L., and J. D. S. Darling. 1985. The greenhouse effect and nature reserves. *Bioscience* 35:707–717.
- Picton, H. D. 1986. A possible link between Yellowstone and Glacier grizzly bear populations. *International Conference on Bear Research and Management* 6:7–10.
- Picton, H. D., and R. R. Knight. 1986. Using climate data to predict grizzly bear litter size. *International Conference on Bear Research and Management* 6:41–44.
- Picton, H. D., D. J. Mattson, B. M. Blanchard, and R. R. Knight. 1986. Climate, carrying capacity, and the Yellowstone grizzly bear. Pages 129–135 in G. P. Contreras and K. E. Evans, compilers. *Proceedings—grizzly bear habitat symposium*. U.S.D.A. Forest Service General Technical Report INT-207.
- Picton, H. D., D. Palmisciano, and G. Nelson. 1990. Fluctuating asymmetry and testing isolation of Montana grizzly bear populations. *International Conference on Bear Research and Management* 8:421–424.
- Pimm, S. L. 1986. Community stability and structure. Pages 309–329 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Association, Sunderland, Massachusetts.
- Raffin, J., editor. 1988. *L'ours, notre patrimoine à tous*. Pages 4–9 in *Textes et documents pour la classe No. 500*. Hebdomadaire. Centre National de documentation pédagogique.
- Reid, M. M., and S. D. Gehman. 1986. Common sense approach to grizzly bear habitat evaluation. Pages 92–98 in G. P. Contreras and K. E. Evans, compilers. *Proc.—grizzly bear habitat symposium*. U.S.D.A. Forest Service General Technical Report INT-207.
- Reinhart, D. P., and D. J. Mattson. 1990. Bear use of cutthroat spawning streams in Yellowstone National Park. *International Conference on Bear Research and Management* 8:343–350.
- Romme, R. W. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monograph* 52(2):199–221.
- Romme, R. W., and M. G. Turner. 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem. *Conservation Biology* 5:373–386.
- Roth, H. V. 1983. Home ranges and movement patterns of European brown bears as revealed by radiotracking. *Acta Zoologica Fennica* 174:143–144.
- Servheen, C. 1989a. The management of the grizzly bear on private lands: some problems and possible solutions. Pages 195–200 in M. Bromley, editor. *Bear-people conflicts: proceedings of a symposium on management strategies*. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories.
- Servheen, C. 1989b. The status and conservation of the bears of the world. *International Conference on Bear Research and Management*. Monograph Series Number 2. 32 pp.
- Servheen, C., R. Knight, D. Mattson, et al. 1986. Report to the IGBC on the availability of foods for grizzly bears in the Yellowstone ecosystem. *Interagency Grizzly Bear Committee*. 22 pp.
- Shaffer, M. L. 1983. Determining minimum viable population sizes for the grizzly bear. *International Conference on Bear Research and Management* 5:133–139.
- Sorensen, O. J., K. Overskaug, and T. Kvam. 1990. Status of the brown bear in Norway 1983–86. *International Conference on Bear Research and Management* 8:17–23.
- Stirling, I., and A. E. Derocher. 1990. Factors affecting the evolution and behavioral ecology of the modern bears. *International Conference on Bear Research and Management* 8:189–204.
- Suchy, W. J., L. L. McDonald, M. D. Strickland, and S. H. Anderson. 1985. New estimates of minimum viable population size for grizzly bears in the Yellowstone ecosystem. *Wildlife Society Bulletin* 13(3):223–228.
- Verstrael, T. J. 1988. De verspreiding van de bruine beer *Ursus arctos* in Europa. *Lutra* (31):44–61.
- U.S. Fish and Wildlife Service. 1990. *Draft grizzly bear recovery plan*. U.S. Fish and Wildlife Service, Denver, Colorado, 190 pp.
- Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Association, Sunderland, Massachusetts.
- Yodzis, P., and G. B. Kolenosky. 1986. A population dynamics model of black bears in east central Ontario. *Journal of Wildlife Management* 50(4):602–612.