YELLOWSTONE GRIZZLY BEAR MORTALITY, HUMAN HABITUATION, AND WHITEBARK PINE SEED CROPS

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Abstract: The Yellowstone grizzly bear (*Ursus arctos horribilis*) population may be extirpated during the next 100–200 years unless mortality rates stabilize and remain at acceptable low levels. Consequently, we analyzed relationships between Yellowstone grizzly bear mortality and frequency of human habituation among bears and size of the whitebark pine (*Pinus albicaulis*) seed crop. During years of large seed crops, bears used areas within 5 km of roads and 8 km of developments half as intensively as during years of small seed crops because whitebark pine's high elevation distribution is typically remote from human facilities. On average, management trappings of bears were 6.2 times higher, mortality of adult females 2.3 times higher, and mortality of subadult males 3.3 times higher during years of small seed crops. We hypothesize that high mortality of adult females and subadult males during small seed crop years was a consequence of their tendency to range closest (of all sex-age cohorts) to human facilities; they also had a higher frequency of human habituation compared with adult males. We also hypothesize that low mortality among subadult females during small seed crop years was a result of fewer energetic stressors compared with adult females and greater familiarity with their range compared with subadult males; mortality was low even though they ranged close to humans and exhibited a high frequency of human habituation. Human-habituated and food-conditioned bears were 2.9 times as likely to range within 4 km of developments and 3.1 times as often killed by humans compared with nonhabituated bears. We argue that destruction of habituated bears that use native foods near humans results in a decline in the overall ability of bears to use available habitat; and that the number and extent of human facilities in occupied grizzly bear habitat needs to be minimized unless habituated bears are preserved and successful ways to manage the associated risks to humans are developed.

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The Yellowstone grizzly bear population will likely survive the next 30 years (Knight and Eberhardt 1985, 1987) but may not survive beyond the next 100–200 years (Dennis et al. 1991, Mattson and Reid 1991). Short- and long-term survival is contingent upon maintaining known average annual mortality at ≤ 2 adult female and 7 total deaths/year (Knight and Eberhardt 1984, 1985). Thus, management of Yellowstone's grizzly bear population has focused on reducing mortality to acceptable levels, which has in turn been dependent on understanding the causes of mortality.

McArthur Jope (1983), Jope (1985), and Herrero (1985) applied the concepts of human habituation and human food conditioning to the behavior and management of bears. They demonstrated that many management problems with bears arose from food conditioning and habituation, which are characterized by less fear of humans and a predilection towards humans or human facilities as a source of food. Subsequently, management of bears has become increasingly phrased in terms of habituation and food conditioning, and some programs have included a direct assessment of these factors as a basis for managing individual bears (Claar et al. 1986, Dalle-Molle and Van Horn 1989, McCrory et al. 1989, and McLean and Pelton 1990). Therefore, we posed hypotheses concerning distributions and mortality of Yellowstone grizzly bears in terms of human habituation and food conditioning, as follows:

H_{a1}: Frequency of human habituation and food conditioning differs among grizzly bear sex-age cohorts.

H_{a2}: Frequency of human-caused mortality differs between human-habituated and wary bears, and among sex-age cohorts.

H_{a3}: Distributions of human-habituated and wary bears differ with respect to human facilities.

While the last hypothesis appears to be circular, given that frequency of human habituation would predictably increase with nearness to humans (Herrero 1985), it is relevant to determining spatial impacts of human facilities that are

mediated through the habituation of bears to humans.

Whitebark pine seeds and ungulates appear to be the 2 most important foods of Yellowstone grizzly bears, whereas berries are relatively unimportant (Mattson et al. 1991). Consequently, food habits of Yellowstone grizzly bears are relatively unique in North America, and most closely resemble those of central Siberian brown bears (*Ursus arctos jeniseensis*) (Mattson et al. 1991). Whitebark pine seeds are predictably important because of their high fat content and potential abundance during pre-hibernation hyperphagia (Mattson and Jonkel 1990), and when available, Yellowstone grizzly bears consume the seeds almost exclusively, typically by raiding red squirrel (*Tamiasciurus hudsonicus*) middens (Kendall 1983, Mattson and Jonkel 1990). For these reasons we postulated that availability of whitebark pine seeds has the greatest potential of any single food-related factor to impact behavior and demography of the Yellowstone grizzly bear population.

Little specific information is available describing the effects of variation in food supplies on bear mortality, although poor food conditions often result in greater bear movements and mortality (Slobodyan 1976, Garshelis and Pelton 1981, Grenfell and Brody 1983, Garshelis 1989). In Siberia, brown bears apparently range farther, kill domestic livestock more frequently, and are in turn killed more frequently by humans when stone pine (*Pinus sibirica* and *P. pumila*) seed crops are small (Ustinov 1976). Yellowstone grizzly bears also exhibit greater movements and use lower elevations during years of small whitebark pine seed crops (Mattson and Knight 1989, Blanchard and Knight 1991). However, relationships among variation in seed crops, grizzly bear mortality, and nearness of grizzly bears to humans have not been analyzed for the Yellowstone Ecosystem. Thus, we posed the following additional hypotheses:

H_{a4}: Distribution of grizzly bears with respect to human facilities differs between years of large and small seed crops, and among sex-age cohorts.

H_{a5}: Human-caused mortality differs between years of large and small seed crops, and by sex-age cohorts.

Herein, we test the hypotheses posed, and speculate on causal linkages between what we suspect are 2 major factors influencing grizzly bear mortality in the Yellowstone area: whitebark pine seed crop size and frequency of human-habituation among the bears; we also offer interpretations for management.

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STUDY AREA AND METHODS

Our 20,000-km^2 study area was centered on Yellowstone National Park and included portions of Wyoming, Montana, and Idaho. Study area characteristics have been described by Knight and Eberhardt (1985), Mattson et al. (1991) and Blanchard and Knight (1991).

Transects for monitoring whitebark pine cone production have been maintained since 1980 (Blanchard 1990). Cones were counted on each of 10 permanently marked trees after cone maturation, but before heavy cone use by seed consumers. Although the number of transects increased over the years from 9 to 21 (Blanchard 1990), we used only the 9 transects first established in 1980 to allow systematic comparison of results.

Food habits were estimated by fecal analysis, 1976–90 (Mattson et al. 1991), and included the frequency of whitebark pine seed remains in grizzly bear feces for August–October and for the entire year. An acute sigmoidal relationship was evident between frequency of pine seeds in feces and transect cone counts (Blanchard 1990). Consequently, we classified years as either characterized by widespread use (use) or virtually no use (nonuse), with the cut-off point between the two being 20% frequency of seeds in feces (corresponds to about 220 cones/transect).

We hypothesized that the current year's crop, reflected in August–October use, most influenced autumn behavior, and that the entire year's diet also influenced mortality. Consequently, we used August–October pine seed use to stratify analysis of mortality, movements and behavior, while we also used data for the entire year to stratify the mortality analysis. Stratification of data by August–October use and the entire year's use differed because during June–July bears extensively consumed pine seeds from a large previous year's crop that had survived

the winter either on trees or in red squirrel caches (Mattson and Jonkel 1990).

We categorized all radio-marked bears as human-habituated, human food-conditioned, or wary (i.e., non-habituated) using definitions synopsized by Herrero (1985:51). Bears that were known or suspected of making more than incidental use of human foods other than livestock were considered to be food-conditioned. Bears that were known to exhibit considerable tolerance of humans were considered to be human-habituated. These bears remained in an area despite close approach of humans or operated in areas near humans without apparent caution. The tendency of a bear to range near roads or developments by itself was not a basis for concluding that the animal was habituated or food-conditioned. Several bears maintained ranges near humans but did not exhibit the close-range tolerance of humans that we considered to be characteristic of human habituation.

We treated human habituation and food conditioning separately by 2 classifications, assuming, for example, that a bear could be food-conditioned by using human garbage at a dump and yet remain relatively wary of humans. Conversely, some bears were human-habituated but were never known to use human foods. Realizing that human habituation and food conditioning are continua, we used 3 categories for each: yes, no, and uncertain. Because major changes in management were instituted in 1982 to reduce food conditioning among bears by increased sanitation of human facilities (Knight and Eberhardt 1985), we pooled habituated and food-conditioned animals and tested (G-test) for independence of categories of cohorts, and by time period (1975–82 vs. 1983–90). We used the G_c-statistic corrected for continuity with tests that had 1 degree of freedom and the standard G-statistic elsewhere (Zar 1984:72).

Number of bear mortalities for the study area were derived from Craighead et al. (1988) and Knight et al. (1989, 1990). We used only known and probable human-caused mortalities (Craighead et al. 1988) because of their direct tie to human–bear conflicts. These mortalities accounted for 81% of all mortalities and 88% of mortalities of radio-instrumented bears between 1975 and 1988 (Craighead et al. 1988, Knight et al. 1988*b*, Knight et al. 1989). Mortalities were stratified by cohort, excluding cubs-of-the-year, and tested (Mann-Whitney test) for differences in levels between use and nonuse years. We also tested (G-test) for differences in frequency of mortalities between habituated or food-conditioned and wary bears, and for differences between bears that were food-conditioned and those that were habituated but not food-conditioned. Analysis of mortalities was further stratified by whether mortalities were recorded as occurring at major roads and developments (front-country) or in more remote settings (back-country), and by the amount of August–October use of pine seeds. Because we hypothesized that early-season use of the previous year's pine seeds could have influenced mortality, we also stratified mortalities by double-weighting August–October and single-weighting total-year pine seed use, employing the same cut-off point for use and nonuse. Management captures were stratified by the same year classifications as mortalities and were taken from unpublished Interagency Grizzly Bear Study Team data; management captures were considered to be any successful trapping done to either rectify or prevent human–bear conflict.

We also analyzed causes of mortality (from Craighead et al. [1988] and Knight el al. [1989, 1990]) for bears either human-habituated or food-conditioned, and for bears that were neither. Causes were stratified by whether management agency personnel were involved, in response to conflict endangering people or property other than livestock, or whether private citizens had acted illegally or in self defense. Illegal and self-defense mortalities were further stratified as those not involving livestock, either near roads or major developments or in the back-country, and those where livestock were the cause of conflict. A final category covered other causes, including natural, research accidents, and unknown. This stratification reflected whether the mortality was related to bear use of foods more closely associated with humans than livestock, to conflicts around concentrations of people (e.g., at garbage dumps or town-sites), and whether the mortality resulted from a judicious review of the bear's behavior. These issues in turn reflected the degree to which human habituation and food conditioning influenced cause of death.

Blanchard and Knight (1991) described methods for collection of bear radio-telemetry locations and Mattson et al. (1987) described methods for analysis of locations with respect to zones successively parallel to roads or concentric to human developments. Data were available

for this analysis from Yellowstone Park and for the period, 1977–86. We stratified locations (n = 3,080) by 1-km-wide zones from roads or developments. Only locations after 31 July (n = 1,681) were used for analysis of distributional changes between pine seed use and nonuse years, because this period corresponded with bear consumption of the current-year seed crop and the occurrence of most grizzly bear mortalities. Telemetry locations also were stratified by associated sex-age cohort, and included adult female reproductive status, and whether the bear was habituated, food-conditioned, or wary. We converted locations into densities by 1-km zone and further scaled these densities to the highest density among cohorts, to allow visual comparison of among-cohort patterns. We used actual zone frequencies when testing (G- and G_c-tests) for independence of distributions between use and nonuse years, and among cohorts. For analysis of sex-age cohort distributions, we doubled zone widths because of smaller cohort sample sizes. We tested for differences among cohort proportions within zones by a multiple-comparisons procedure using angular transformations (Zar 1984:401).

We did not pose a priori hypotheses about the exact pattern of distributional differences between use and nonuse years and among sex-age cohorts. Instead, we took an iterative approach that entailed first examining zonal distributions for major proportional breaks in the compared distributions, and then posing the hypothesis that distributions did not differ with respect to these major breaks. Consequently, break-points varied with the distribution being analyzed. This approach allowed us to identify the spatial extent of major changes in bear distributions associated with use and nonuse years, habituation status, and sex-age cohorts, and to make inferences about the differential spatial impacts of developments and primary roads.

The Yellowstone Ecosystem is described in terms of ecological landscape units called habitat types, that are further aggregated as series and split into phases (Steele et al. 1983). Virtually all bear use of whitebark pine seeds occurred in habitat types characterized by a high frequency of mature whitebark pine, including all of the whitebark pine series as well as the subalpine fir/grouse-whortleberry–whitebark pine (*Abies lasiocarpa/Vaccinium scoparium–Pinus albacaulis*) phase (Mattson and Jonkel 1990). Thus, percent area in these whitebark pine habitat types, by 1-km zone, corresponded to the distribution of pine seed feeding opportunities. We calculated percent area from the same digital map data used by Mattson et al. (1987). We analyzed the correlation of location density and arcsin transformed percent areas of whitebark pine types, by 1-km zone, using the Pearson correlation coefficient.

RESULTS

Grizzly bears made widespread use of whitebark pine seeds in our study area in 8 of 15 years during August–October and 8 of 14 years during the entire active season (Table 1). Years of use and nonuse were not evenly interspersed; strings of up to 3 successive use and 4 successive nonuse years were observed.

Distributions by Years of Pine Seed Use

Distribution of bear telemetry locations across zones parallel to roads and concentric to developments differed between use and nonuse years, with major shifts at 5 km from roads and 8 km from developments (Fig. 1). Locations occurred disproportionally more often within 5 km of roads and 8 km of developments during nonuse years (roads: G_c = 216.0, 1 df, $P < 0.001$; developments: G_c = 107.1, 1 df, $P < 0.001$), with proportionally 1.9 times as many locations within 8 km of developments, and 2.1 times as many within 5 km of roads. During use years, location densities were positively correlated with arcsin transformed percent coverages of whitebark pine types, across zones (n = 11; roads: r = 0.70, P = 0.017; developments: r = 0.66, P = 0.028). Conversely, during nonuse years, location densities were negatively correlated with cover of whitebark pine types along roads and to a lesser extent around developments (roads: $r = -0.73$, $P = 0.012$; developments: $r = -0.58$, $P = 0.060$).

Distributions of sex-age cohorts during nonuse years differed by 3 major proportional breaks relative to distance from roads and developments (roads: 0–2, >2 and ≤6, and >6 km; developments: 0–2, >2 and ≤8, and >8 km). Distributions of cohorts differed during nonuse years (roads: G = 32.1, 6 df, $P < 0.001$; developments: G = 25.2, 6 df, $P < 0.001$), primarily because proportionally fewer ($P < 0.05$) locations of adult males occurred within 8 km of developments, and fewer locations of subadult females and adult males occurred within 2 km of roads. Also, more locations of subadult males

Table 1. Whitebark pine cone production, grizzly bear use (U = widespread use; N = virtual nonuse of pine seeds), and grizzly bear captures by management personnel, Yellowstone Ecosystem, 1976–90.

Year	Transects *n*	Mean cones[a]/transect or crop rating *n*	Freq. whitebark[b] pine seeds in feces *n*	%	Cone use classification Aug–Oct	Year-long	Management[c] captures
1976	0	Good	23	69.0	U		3
1977	0	Poor	124	3.2	N	N	5
1978	0	Excellent	262	41.6	U	U	1
1979	0	Good	473	81.2	U	U	1
1980	9	257	191	33.0	U	U	3
1981	9	132	37	5.4	N	N	33
1982	9	160	76	1.3	N	N	24
1983	9	170	50	4.0	N	N	18
1984	6	60	146	7.5	N	N	22
1985	9	257	119	69.7	U	U	5
1986	8	13	212	9.4	N	U	32
1987	9	39[d]	208	58.2	U	U	10
1988	9	4	119	0.8	N	N	[e]
1989	9	493	285	42.8	U	U	3
1990	9	5	236	21.2	U	U	13

[a] Verbal ratings (1976–79) derived from relationships between cone counts and scat contents from 1980–90 data (see text).
[b] August–October data, pooled.
[c] For period after 31 July.
[d] Anomalous low count due to early cone maturation and late transect readings (Blanchard 1990).
[e] Excluded because of anomalous conditions associated with 1988 wildfires.

occurred within 2 km of both roads and developments, and because fewer locations of adult females occurred beyond 8 km of developments and 6 km of roads. Within intermediate zones, males were underrepresented around developments and subadults were underrepresented along roads. Overrepresentation of subadult males within 2 km of roads and developments was the most prominent feature when we analyzed only locations within 6 km of roads and 8 km of developments. Adult males also were underrepresented within 2 km of roads.

We investigated distributions of adult female reproductive cohorts separately, by the same 3 zones used for all cohorts. Distributions differed with respect to developments (G = 12.6, 4 df, P = 0.015), but not roads (G = 0.62, 4 df, P = 0.96). Differences were attributable to the relative underrepresentation ($P < 0.05$) of lone females within 2 km of developments, of females with young >1 year old that were >8 km away, and the relative overrepresentation of this same class (with older young) between 2 and 8 km away from developments.

Management Actions and Mortalities by Years of Pine Seed Use

The majority of management trappings (82%, n = 173) and human-caused mortalities (73%, n = 99) in the Yellowstone Ecosystem occurred after 31 July, coincident with availability of the current year's pine seeds and hyperphagia (Mattson et al. 1991). More (6.2 times as many) management trappings occurred during nonuse years compared to use years (Table 2). Similarly, 2.3 times as many adult females and 3.3 times as many subadult males died by human causes during nonuse years; total human-caused bear deaths increased 1.9 times. Subadult female deaths were uniformly low, and both subadult female and adult male deaths varied independently of use and nonuse years. Front-country bear deaths were associated more with intensity of pine seed use than back-country deaths, although both increased substantially (2.3 times and 1.9 times, respectively) during nonuse years.

Distributions by Habituation Class

Distributions of locations from habituated and non-habituated bears differed with respect to developments (G = 390.8, 2 df, $P < 0.001$) and roads (G = 393.5, 2 df, $P < 0.001$), primarily due to major shifts at 4 and 12 km from developments and 2 and 10 km from roads. Proportionally, locations of habituated bears were 2.9 times more frequent within 4 km of developments and 2.1 times more frequent within 2 km of roads compared to locations of non-habituated bears. Conversely, locations of non-habituated bears were 2.9 times as frequent beyond 12 km of developments and 4.2 times as frequent beyond 10 km from roads.

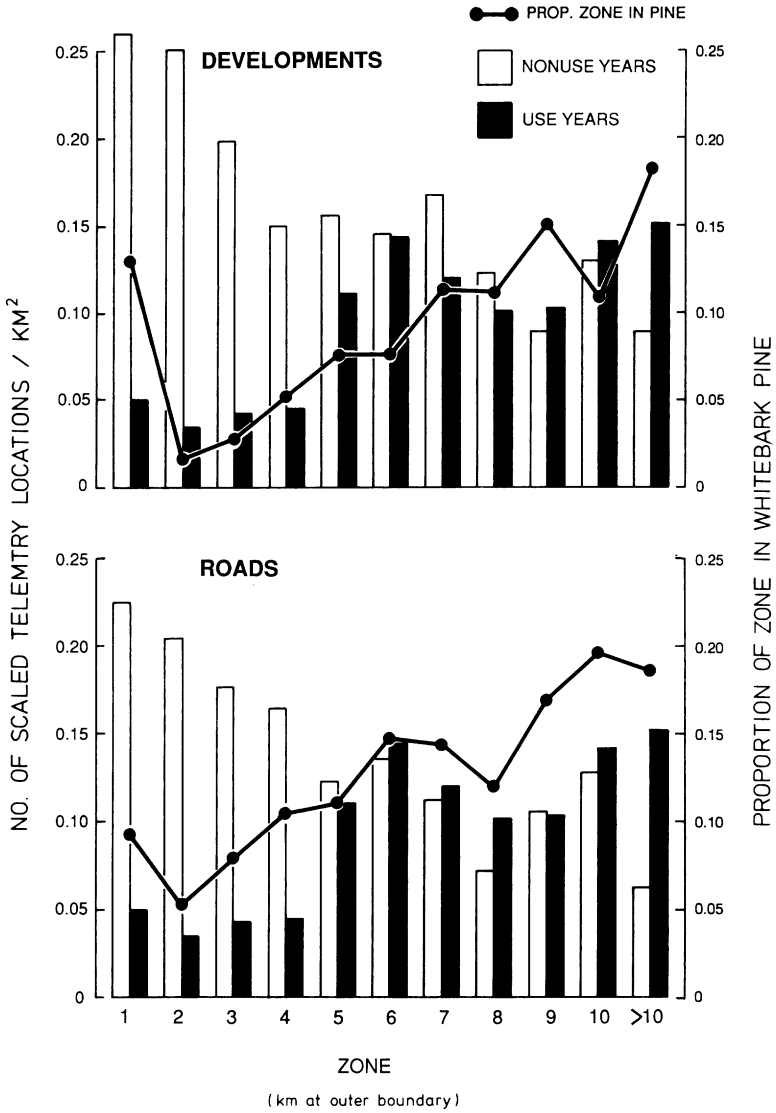

Fig. 1. Density of telemetry locations from radio-collared grizzly bears and proportion of each zone in whitebark pine habitats, relative to distance (km) from roads and developments in Yellowstone National Park and for years when pine seeds were widely used and were not used. Densities of nonuse-year telemetry locations were scaled to use-year densities to facilitate comparison of patterns. Locations occurred disproportionately more often within 5 km of roads ($P < 0.001$) during nonuse years.

Habituation and Food Conditioning by Cohort

Habituation and food conditioning did not vary independently of sex-age cohort ($G = 19.3$, 6 df, $P = 0.004$), primarily due to less habituation and food conditioning among adult males ($G = 13.6$, 2 df, $P = 0.001$). Only 13.3% of 45 adult males were known to be habituated or food-conditioned compared to 41.7% of all 139 other bears. Relative frequency of habituation and food conditioning did not vary independently of early (1977–82) and late (1983–90) time periods ($G = 6.58$, 2 df, $P = 0.039$), dropping from 42.7 to 25.9% between the 2 successive periods. The relative frequency of non-food-conditioned habituated bears among all habituated or food-conditioned bears increased between the 2 periods, from 2.8% of 35 to 30.0% of 30 bears ($G_c = 7.66$, 1 df, $P = 0.006$). Thus, as overall relative frequency of habituation and food conditioning decreased, habituation without food conditioning increased proportionally among affected bears.

Table 2. Mean number of grizzly bear captures by management personnel and human-caused mortalities during years with widespread whitebark pine seed use (U) and years of nonuse (N) in the Yellowstone Ecosystem, 1976–90.

	Aug–Oct use[a]				Year-long use[b]			
	$\bar{x}$ mortality/manage. captures				$\bar{x}$ mortality/manage. captures			
Category	U	N	χ^{2c}	P^d	U	N	χ^{2c}	P^d
Manage. captures[e]	3.1	19.3	8.14	0.00	8.5	20.4	3.94	0.05
Mortalities								
Adult female	1.0	2.3	5.29	0.02	1.6	3.4	4.07	0.04
Subadult female	0.2	1.0	1.86	0.17	0.9	1.0	0.05	0.82
Adult male	1.2	1.5	0.00	0.99	1.6	2.2	0.51	0.48
Subadult male	0.9	2.3	4.00	0.04	1.1	3.6	5.38	0.02
Front-country	1.2	2.8	3.46	0.06	2.6	4.4	3.23	0.07
Back-country	2.9	4.5	1.73	0.19	3.2	6.2	2.17	0.14
Total	4.1	7.3	3.58	0.06	5.9	10.6	4.90	0.03

[a] Sample size: U years = 8, N years = 5.
[b] Sample size: U years = 8, N years = 6.
[c] Chi-square approximation of the Mann-Whitney test for differences between management captures and human-caused mortality relative to use and nonuse of whitebark pine seeds.
[d] *P*-value for the Mann-Whitney test.
[e] All cohorts combined.

Mortality and Survivorship by Habituation Class

Humans did not kill human-habituated bears at different relative frequencies during use and nonuse years ($G_c = 0.028$, 1 df, $P = 0.88$). However, humans killed habituated bears proportionally 3.1 times more often (60.0% of 65) than non-habituated bears (19.1% of 89) ($G_c = 25.8$, 1 df, $P < 0.001$); there was no difference in proportions of food-conditioned and habituated (but not food-conditioned) bears killed by humans ($G_c = 0.12$, 1 df, $P = 0.74$). Similarly, humans killed habituated or food-conditioned adult females 3.8 times more often (47.4% of 19) than non-habituated adult females (12.5% of 32)($G_c = 5.78$, 1 df, $P = 0.02$). Overall, survivorship of non-habituated females from age 5 to age 13 was 1.4–1.6 times greater than habituated or food-conditioned females (0.771 [n = 161 bear-yr] vs. 0.470–0.549 [n = 101]; the difference in probabilities resulting from the difference in treatment of a bear whose fate is in question). We chose this range of ages because reproduction in most Yellowstone females started at ages 5–7, and peaked during ages 8–13 (Knight et al. 1988*b*).

Cause of Death by Habituation Class

We did not statistically analyze differences in cause of death between human-habituated or food-conditioned bears and bears that were neither, because 4 of the 10 cells had expected values <5 and could not logically be consolidated with others. However, major differences apparently existed: the majority (58%) of habituated or food-conditioned bears and none of the wary bears were removed during agency management actions. Management actions were taken in response to behavior that was considered to be unacceptable, such as destruction of property, aggression towards people, or persistent use of habitat near people (Craighead et al. 1988). Conversely, most (70%) of the wary bears that died did so in back-country incidents involving livestock or attractants, typically ungulate carcass remains, associated with outfitters and hunters.

DISCUSSION

Although our criteria for identifying human-habituated or food-conditioned bears were not rigorous quantitatively, we used the same criteria generally applied by managers in the Yellowstone Ecosystem. Our analysis is intended to address the implications of management distinctions and to extrapolate them to management situations. We also are confident that non-food-conditioned but human-habituated bears occurred in our study area (see Albert and Bowyer 1991). This type of bear represents a substantially different management problem than the food-conditioned bear, and while part of a continuum, distinction between these types in our analysis is important in addressing the implications of current management.

The proportionally greater frequency of male locations >6–8 km from roads and develop-

ments could simply be an artifact of their larger home ranges (Blanchard and Knight 1991) and/or trapping effort biased towards roads and developments. In other words, males with core ranges far from human facilities are more likely to be caught and marked than females with core ranges equally far from humans (see Bunnell and Tait 1985). We consequently expect proportionally more telemetry locations from adult males in more remote areas compared with their actual density. Given a mean female life-time home range of 884 km^2 (Blanchard and Knight 1991), we expect this bias to be most pronounced roughly beyond the radius of an equal-sized circular area, that is, beyond approximately 16.8 km of roads and developments. Only 17.0% of the area in Yellowstone Park is beyond this distance from roads and only 24.8% beyond this distance from developments. Thus, while this home-range size related bias likely existed, we concluded that it did not negate our results, because of the relatively small portion of our study area affected, and because our analysis emphasized areas within 12 km of roads and developments.

Given that human-habituated and food-conditioned bears are more likely to be trapped during management actions (Meagher and Fowler 1989), the frequency of these behavioral types would likely be affected by the frequency of bears in our sample that were first captured for management reasons. This potential bias would have affected the comparison of habituation and food conditioning between the earlier and later study periods especially if management-trapped bears occurred relatively more frequently in the earlier period sample. However, there were proportionally more bears (37.8% compared to 23.1%) first trapped during management actions during the later study period ($G_c = 3.78$, 1 df, $P = 0.052$). We concluded that this bias did not negate our results, and that habituated and food-conditioned animals occurred relatively more frequently during the earlier study period.

During years of widespread pine seed use, grizzly bears made very little use of areas near human facilities. This may have been a consequence of whitebark pine's high elevation distribution, typically in areas more remote from human facilities. However, during years of little or no pine seed use, areas near human facilities (<5 km from roads and <8 km from developments) were used intensively by bears. During these relatively frequent nonuse years, cohorts were distributed differently relative to human facilities.

Presumably, as a consequence of bears being nearer and in more frequent contact with humans, nearly 6 times as many bears were trapped by management personnel, and nearly 2 times as many bears were killed during nonuse years. Our results suggest that high nonuse year mortality among adult females and subadult males was a direct function of their tendency to range closest to humans of all cohorts (Dau 1989). Adult male mortalities did not vary with availability of pine seeds, probably because of their apparent ability to range farther, on average, from human facilities during nonuse years, and because of the motivation to do so implicit to low frequency of habituation in this cohort. For reasons that are not obvious, subadult females escaped high mortality during nonuse years, despite ranging nearer to human facilities and exhibiting a higher frequency of habituation than adult males.

The low incidence of mortality among subadult females compared with adult females and subadult males does not contradict the hypothesis posed by Mattson (1990) that subadult males and especially adult females with cubs-of-the-year experience the greatest energetic stress of all sex-age cohorts, especially compared with adult males and subadult females. If this hypothesis is true, subadult males and adult females in pursuit of feeding opportunities would be more likely to tolerate humans, and would be at greater risk of conflict with humans (Mattson et al. 1987, McLellan and Shackleton 1988, Mattson 1990, Albert and Bowyer 1991). Subadult males also are more likely to disperse long distances from maternal ranges compared to subadult females (Blanchard and Knight 1991). Therefore, subadult males may have been less familiar with local bears and foraging options and consequently more willing than subadult females to tolerate humans as a means of minimizing competition with other bears (Mattson et al. 1987, McLellan and Shackleton 1988, Mattson 1990). Certainly, the contrast between subadult female and subadult male mortality and the considerable concentration of subadult male telemetry locations near human facilities during nonuse years do not contradict this hypothesized scenario.

Habituated and food-conditioned bears were 3–4 times more likely to be killed compared

with wary bears, and possibly because of differential energetic stressors and habituation evident among sex-age cohorts, this risk was disproportionally borne by adult females and subadult males. The low incidence of habituation among adult males conceivably resulted from the death of most habituated males as subadults. Among females however, habituated subadults were likely to survive to adulthood. Thus, the consequences of habituation appear to have been played out more frequently among adult females, presumably exacerbated by energetic demands associated with providing food and security for dependent young (Pearson 1975, Sizemore 1980, Pond 1984, Stelmock and Dean 1986, Dau 1989). Our results also suggest that behavior associated with habituation played a major part in managers' perceptions of risk, and decisions to remove bears.

MANAGEMENT IMPLICATIONS

Management changes instituted in 1982 apparently resulted in a decreased relative frequency of food-conditioned habituated grizzly bears. Our results suggest that this change was achieved by killing most food-conditioned bears, in concert with increased sanitation of human facilities (Knight et al. 1988*a*). However, substantial numbers of habituated bears still exist, and our results suggest that a greater portion of these animals are not tolerating humans as a means of acquiring human-related foods, but rather in the course of using native foods near human facilities. Consequently, behavior of this type of bear is less likely to be modified by manipulation of human foods. This type of bear also is likely to be near humans because it has fewer options in more remote areas (Mattson et al. 1987, McLellan and Shackleton 1988, Mattson 1990).

Preserving habituated bears that live near humans primarily to acquire native foods may be a sound rationale. Without these animals, the number of bears supported by the Yellowstone Ecosystem would likely decline, because habitat near humans would be underused (McArthur Jope 1985, Keating 1986, Mattson 1990). Indeed, we attribute the consistent underuse of areas near human facilities in Yellowstone National Park (Mattson et al. 1987, Reinhart and Mattson 1990, Gunther 1990) to the higher mortality of habituated than of wary bears, primarily as a result of management removals. This consideration of habitat effectiveness (Weaver et al. 1986) is not trivial (Keating 1986). Our results suggest that habituated bears account for most habitat use in 24%, and a substantial portion of use in 69%, of Yellowstone National Park. If human-habituated bears are not preserved, then a successful non-lethal means of increasing wariness of bears near humans, or a means to minimize the number and extent of human facilities must be found (Knight et al. 1988*a*, Mattson 1990, Mattson and Reid 1991).

Because human–bear conflicts are so closely tied to whitebark pine seed crops, annually varied management designed to minimize mortality risk to bears and based on an assessment of seed crop size could be instituted. Given the 3-year maturation of whitebark pine cones (Lanner 1990), crop size determinations could be made 1 or 2 years in advance. If small crops are anticipated, then temporary closure of areas to people and more restrictive management of human activity around facilities could be instituted.

Ideally, management strategies for grizzly bears should be based on prior experience and knowledge of food conditions. Because good and poor pine seed crops can occur in a series of several years, observations during a 1–2 year period can be misleading. For example, Meagher and Phillips (1983) asserted that "trends" towards decreased sightings of bears around developments, decreased control actions, and decreased human injuries, punctuated by the years 1978 and 1979, were evidence of future trends associated with the Yellowstone grizzly bear population's successful transition from foraging around dumps and developments to foraging on native foods. However, we interpret the low levels of conflict and sightings, especially during 1978 and 1979, as a consequence of large pine seed crops. During the series of small crops starting in 1981, the level of human-bear conflicts escalated again.

LITERATURE CITED

ALBERT, D. M., AND R. T. BOWYER. 1991. Factors related to grizzly bear-human interactions in Denali National Park. Wildl. Soc. Bull. 19:339–349.

BLANCHARD, B. M. 1990. Relationships between whitebark pine cone production and fall grizzly bear movements. Pages 362–363 *in* W. C. Schmidt and K. J. McDonald, compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. U.S. For. Serv. Gen. Tech. Rep. INT-270.

———, AND R. R. KNIGHT. 1991. Movements of Yellowstone grizzly bears. Biol. Conserv. 58:41–67.

BUNNELL, F. L., AND D. E. N. TAIT. 1985. Mortality rates of North American bears. Arctic 38:316–323.

CLAAR, J. J., R. W. KLAVER, AND C. W. SERVHEEN. 1986. Grizzly bear management on the Flathead Indian Reservation, Montana. Int. Conf. Bear Res. and Manage. 6:203–208.

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, Wildl. and Parks, Craighead-Wildl.-Wildlands Inst., Interagency Grizzly Bear Stud. Team, Natl Fish and Wildl. Found. 104pp.

DALLE-MOLLE, J. L., AND J. C. VANHORN. 1989. Bear–people conflict management in Denali National Park, Alaska. Pages 121–128 *in* M. Bromley, ed. Bear–people conflicts: proceedings of a symposium on management strategies. Northwest Territ. Dep. Renewable Resour., Yellowknife.

DAU, C. P. 1989. Management and biology of brown bears at Cold Bay, Alaska. Pages 19–26 *in* M. Bromley, ed. Bear–people conflicts: proceedings of a symposium on management strategies. Northwest Territ. Dep. Renewable Resour., Yellowknife.

DENNIS, B., P. L. MUNHOLLAND, AND J. M. SCOTT. 1991. Estimation of growth and extinction parameters for endangered species. Ecol. Monogr. 61:115–143.

GARSHELIS, D. 1989. Nuisance bear activity and management in Minnesota. Pages 169–180 *in* M. Bromley, ed. Bear–people conflicts: proceedings of a symposium on management strategies. Northwest Territ. Dep. Renewable Resour., Yellowknife.

———, AND M. R. PELTON. 1981. Movements of black bears in the Great Smoky Mountains National Park. J. Wildl. Manage. 45:912–925.

GRENFELL, W. E., JR., AND A. J. BRODY. 1983. Seasonal foods of black bears in Tahoe National Forest, California. Calif. Fish and Game 69:132–150.

GUNTHER, K. A. 1990. Visitor impact on grizzly bear activity in Pelican Valley, Yellowstone National Park. Int. Conf. Bear Res. and Manage. 8: 73–78.

HERRERO, S. 1985. Bear attacks—their causes and avoidance. Nick Lyons Books, New York, N.Y. 287pp.

JOPE, K. L. 1985. Implications of grizzly bear habituation to hikers. Wildl. Soc. Bull. 13:32–37.

KEATING, K. A. 1986. Historical grizzly bear trends in Glacier National Park, Montana. Wildl. Soc. Bull. 14:83–87.

KENDALL, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. Int. Conf. Bear Res. and Manage. 5:166–173.

KNIGHT, R. R., B. M. BLANCHARD, AND L. L. EBERHARDT. 1988*a*. Mortality patterns and population sinks for Yellowstone grizzly bears, 1973–1985. Wildl. Soc. Bull. 16:121–125.

———, ———, AND D. J. MATTSON. 1988*b*. Yellowstone grizzly bear investigations: annual report of the Interagency Study Team, 1987. U.S. Natl. Park Serv., Bozeman, Mont. 80pp.

———, ———, AND ———. 1989. Yellowstone grizzly bear investigations: annual report of the Interagency Study Team, 1988. U.S. Natl. Park Serv., Bozeman, Mont. 34pp.

———, ———, AND ———. 1990. Yellowstone grizzly bear investigations: annual report of the Interagency Study Team, 1989. U.S. Natl. Park Serv., Bozeman, Mont. 15pp.

———, AND L. L. EBERHARDT. 1984. Projected future abundance of the Yellowstone grizzly bear. J. Wild. Manage. 48:1434–1438.

———, AND ———. 1985. Population dynamics of Yellowstone grizzly bears. Ecology 66:323–334.

———, AND ———. 1987. Prospects for Yellowstone grizzly bears. Int. Conf. Bear Res. and Manage. 7:45–50.

LANNER, R. 1990. Biology, taxonomy, evolution, and geography of stone pines of the world. Pages 14–24 *in* W. C. Schmidt and K. J. McDonald, compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. U.S. For. Serv. Gen. Tech. Rep. INT-270.

MATTSON, D. J. 1990. Human impacts on bear habitat use. Int. Conf. Bear Res. and Manage. 8:33–56.

———, B. M. BLANCHARD, AND R. R. KNIGHT. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. Can. J. Zool. 69:1619–1629.

———, AND C. JONKEL. 1990. Stone pines and bears. Pages 223–236 *in* W. C. Schmidt and K. J. McDonald, compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. U.S. For. Serv. Gen. Tech. Rep. INT-270.

———, AND R. 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. For. Serv. Gen. Tech. Rep. INT-257.

———, ———, AND B. M. BLANCHARD. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. Int. Conf. Bear Res. and Manage. 7:259–273.

———, AND M. M. REID. 1991. Conservation of the Yellowstone grizzly bear. Conserv. Biol. 5: 364–372.

MCARTHUR JOPE, K. L. 1983. Habituation of grizzly bears to people: a hypothesis. Int. Conf. Bear Res. and Manage. 5:322–327.

MCCRORY, W. P., S. HERRERO, AND G. JONES. 1989. A program to minimize conflicts between grizzly bears and people in British Columbia Provincial Parks. Pages 93–98 *in* M. Bromley, ed. Bear–people conflicts: proceedings of a symposium on management strategies. Northwest Territ. Dep. Renewable Resour., Yellowknife.

MCLEAN, P. K., AND M. R. PELTON. 1990. Some

demographic comparisons of wild and panhandler bears in the Smokey Mountains. Int. Conf. Bear Res. and Manage. 9:105–112.

MCLELLAN, B. N., AND D. M. SHACKLETON. 1988. Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat use and demography. J. Appl. Ecol. 25:451–460.

MEAGHER, M., AND S. FOWLER. 1989. The consequences of protecting problem grizzly bears. Pages 141–144 *in* M. Bromley, ed. Bear–people conflicts: proceedings of a symposium on management strategies. Northwest Territ. Dep. Renewable Resour., Yellowknife.

———, AND J. R. PHILLIPS. 1983. Restoration of natural populations of grizzly and black bears in Yellowstone National Park. Int. Conf. Bear Res. and Manage. 5:152–158.

PEARSON, A. M. 1975. The northern interior grizzly bear (*Ursus arctos* L.). Can. Wildl. Serv. Rep. Ser. No. 34. 86pp.

POND, C. M. 1984. Physiological and ecological importance of energy storage in the evolution of lactation: evidence for a common pattern of anatomical organization of adipose tissue in mammals. Symp. Zool. Soc. London. 51:1–32.

REINHART, D. P., AND D. J. MATTSON. 1990. Bear use of spawning cutthroat trout streams in Yellowstone National Park. Int. Conf. Bear Res. and Manage. 8:343–350.

SIZEMORE, D. L. 1980. Foraging strategies of the grizzly bear as related to its ecological energetics. M. S. Thesis, Univ. Montana, Missoula. 67pp.

SLOBODYAN, A. A. 1976. The European brown bear in the Carpathians. Int. Conf. Bear Res. and Manage. 3:313–319.

STEELE, R., S. V. COOPER, D. M. ONDOV, D. W. ROBERTS, AND R. D. PFISTER. 1983. Forest habitat types of eastern Idaho–western Wyoming. U.S. For. Serv. Gen. Tech. Rep. INT-144. 122pp.

STELMOCK, J. J., AND F. C. DEAN. 1986. Brown bear activity and habitat use, Denali National Park—1980. Int. Conf. Bear Res. and Manage. 6:155–168.

USTINOV, S. K. 1976. The brown bear on Baikal: a few features of vital activity. Int. Conf. Bear Res. and Manage. 3:325–326.

WEAVER, J., R. ESCANO, D. MATTSON, T. PUCHLERZ, AND D. DESPAIN. 1986. A cumulative effects model for grizzly bear management in the Yellowstone ecosystem. Pages 234–246 *in* G. P. Contreras and K. E. Evans, compilers. Proceedings—grizzly bear habitat symposium. U.S. For. Serv. Gen. Tech. Rep. INT-207.

ZAR, J. H. 1984. Biostatistical analysis. Second ed. Prentice-Hall, Inc., Englewood Cliffs, N.J. 718pp.

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