CHANGES IN MORTALITY OF YELLOWSTONE'S GRIZZLY BEARS

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Abstract: Records of grizzly bear (*Ursus arctos*) deaths are currently used by managers to indicate trends in actual grizzly bear mortality and to judge the effectiveness of management. Two assumptions underlie these current uses: first, that recorded mortality is an unbiased indicator of actual mortality, and second, that changes in mortality after implementation of management strategies are sufficient grounds to infer the effects of management. I examined the defensibility of these 2 assumptions relative to alternate explanations, circumstantial evidence, and the potential costs of error. The potentially complex relation between actual and recorded mortality, as currently tallied and used, was reason to expect that the association between these 2 values would be weak. This expectation was supported by the prevalence (60–76%) of radio-marked bears among recorded deaths, the variation in apparent likelihood of documentation among causes of death, and variation in the prevalence of different causes over time. For these reasons, recorded mortality is likely to be an unreliable indicator of actual mortality. Use of whitebark pine (*Pinus albicaulis*) seeds by grizzly bears had a major effect on annual variation in recorded mortality. Low numbers of recorded deaths, 1984–92, were attributable to relatively frequent large whitebark pine seed crops. There was little or no residual trend potentially ascribed to management intervention during 1976–92. Management intervention was probably responsible for observed changes in recorded causes of death and stabilized recorded mortality over the period covered by this analysis.

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Key words: grizzly bear, mortality, trend, *Ursus arctos*, whitebark pine, Yellowstone.

Numbers of recorded grizzly bear deaths are used to guide grizzly bear management in the Yellowstone Recovery Area. Recorded deaths are used in calculations of allowable mortality (U.S. Fish and Wildlife Service 1993) and to infer trends in actual mortality, where actual mortality is the total number of bears that die in a given year and recorded mortality is the fraction of that total registered in official documents such as Craighead et al. (1988) or Knight and Blanchard (1994). Recorded mortality is also used by managers and scientists to judge the effectiveness of management. If the number of dead bears declines following implementation of a management strategy, then some managers conclude that management intervention was directly responsible.

Managers in the Yellowstone area are, in fact, concluding that recent declines in recorded grizzly bear mortality closely reflect trends in actual mortality and are ascribing these changes to management interventions (e.g., Salwasser 1994, Fitzwilliams 1995). However, Yellowstone's grizzly bear population is vulnerable if these conclusions are in error (Mattson et al. 1996). Undue optimism could lead to liberalized management and increased bear mortality under circumstances where detection of declines is uncertain (Craighead et al. 1995) and recovery from over-harvest is inherently slow (Miller 1990). Furthermore, because the Yellowstone population is isolated, it can not be naturally augmented through immigration (Mattson et al. 1995).

The assumptions behind current uses of recorded grizzly bear mortality have not been critically examined (Mattson and Craighead 1994, Craighead et al. 1995). Given the importance of these counts to management decisions, including the possible delisting of Yellowstone's population from its present "Threatened" status under the Endangered Species Act (16 U.S.C. 1531–1544; U.S. Fish and Wildlife Service 1993), an evaluation of assumptions is warranted. Specifically, current applications implicitly assume that recorded mortality is an unbiased indicator (*sensu* Eberhardt 1978) of actual mortality, especially with respect to time and cause. In other words, annual variation in recorded mortality is assumed to be highly correlated with annual variation in actual population mortality (Mattson 1997). A second assumption is that the likelihood of documenting a bear death is equal between legal and illegal causes and between human and natural causes.

Unfortunately the hypotheses implicit to these assumptions cannot be directly tested with available data. Independent and reliable annual estimates of actual population mortality do not exist. Given that human-caused grizzly bear mortality results from both the frequency and lethality of bear contact with humans (Mattson et al. 1996), it is also logistically infeasible to directly evaluate the merits of the second assumption. This assumption primarily relates to the lethality of human–bear encounters and can only be evaluated by controlling for the effects of encounter frequency. Control of this factor is contingent upon obtaining currently unavailable estimates for the annual frequency of contact between bears and people, and information on the extent to which variation in contact depends upon variation in bear foods or bear population size, as opposed to direct management intervention. Even so, it is not necessary nor safe to uncritically adopt the assumptions underlying current uses of recorded griz-

zly bear mortality just because the definitive information required to directly test them is unavailable (Shrader-Frechette and McCoy 1993).

Data used in this paper were collected by many people, most under auspices of the Interagency Grizzly Bear Study Team, under the direction of R. Knight. H. Pac and A. Dood of Montana Department of Fish, Wildlife, and Parks provided me with information and have been responsible for tabulating, verifying, and archiving grizzly bear mortalities from the Yellowstone ecosystem. The US Geological Survey Forest and Rangeland Ecosystem Science Center and the former U.S. Biological Service, through R.G. Wright, funded this research. H. Reynolds and 3 anonymous reviewers provided helpful comments.

A Conceptual Model

The construction of a conceptual model that relates the metric (recorded mortality) to the parameter of interest (actual population mortality) is important to an evaluation confronted by the degree of uncertainty identified here (Ratti and Garton 1994). Logically, if the relationship between recorded and actual grizzly bear mortality were diffuse and affected by numerous factors that were not controlled, there would be *prima facie* justification for questioning the reliability of the metric. More importantly, a conceptual model can serve to identify relevant ancillary hypotheses that are able to be tested using available biological information.

The number of recorded grizzly bear deaths is related to the number of actual deaths through several probabilistic events, in turn likely affected by a number of extraneous factors (Fig. 1). A certain number of bears will die, but only a fraction of these will be detected, and of these only a fraction will be officially documented. The detection of dead bears and their documentation by humans are logically affected by the number of humans, the level and dispersal of human access in grizzly bear habitat, and by human behavior (Mattson et al. 1996). The number of radio-marked bears and their proportion of the total population, in turn a reflection of research effort, is likely to affect recorded mortality because deaths of these animals are virtually certain to be documented. Human

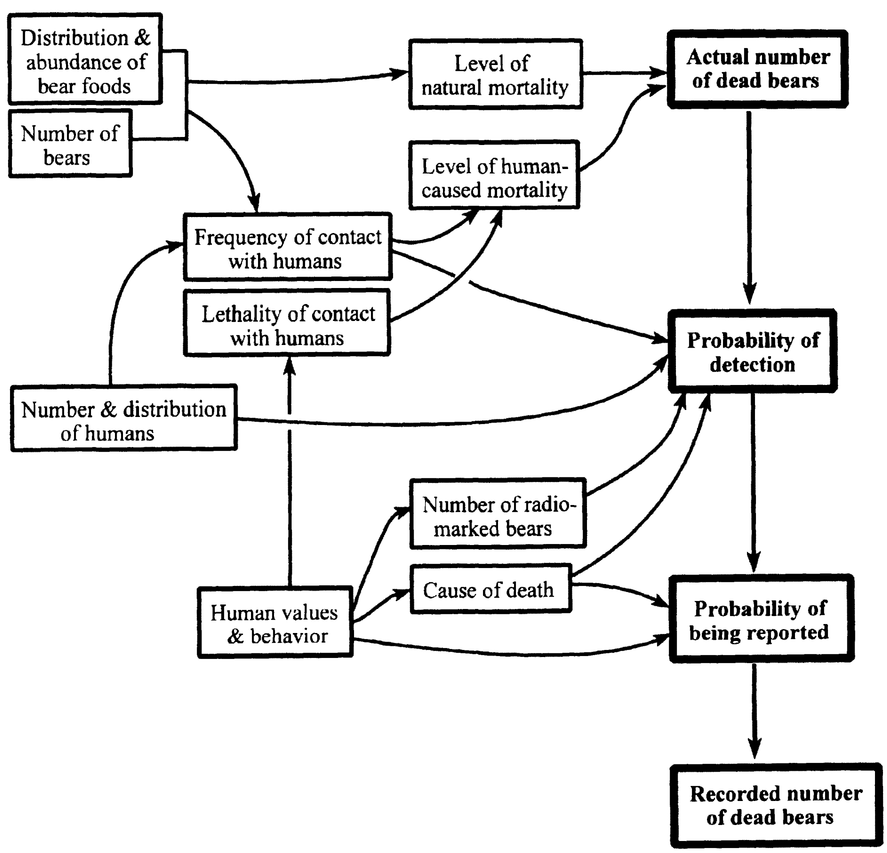

Fig. 1. A simplified conceptual model of the relationship between recorded and actual grizzly bear mortality, identifying factors likely to affect the number, detection, and documentation of dead bears.

behavior (e.g., how we respond to encounters with bears, live or dead) is furthermore likely to be affected by the level of interest in grizzly bears by managers, communication of this interest to others, and other incentives or disincentives to report dead bears. In particular, legal deaths will be more often documented than illegal deaths (Knight and Eberhardt 1985).

Numbers and distributions of grizzly bears also likely affect the frequency of contact with humans (Mattson 1990, Mattson et al. 1992) and the likelihood that they will die under circumstances favoring documentation. When using foods such as whitebark pine seeds and army cutworm moths (*Euxoa auxiliaris*), which occur at high elevations remote from human facilities, live or dead grizzly bears are less likely to be encountered by humans (Mattson et al. 1991, Mattson et al. 1992, French et al. 1994). The opposite is true for grizzly bears using cutthroat trout (*Oncorhynchus clarki*) spawning in streams tributary to Yellowstone Lake, many of which are near roads and recreational developments (Reinhart and Mattson 1990, Mattson and Reinhart 1995). In short, there are a number of factors that likely influence the relationship of recorded to actual mortality that can vary without any obvious relationship to the number of bears dying either by natural or human-related causes.

Under these circumstances, declines in recorded bear mortality could be observed for a number of reasons: (1) actual mortality could be declining; (2) the mortality rate could be stable or increasing, but offset by a declining bear population; (3) bears could also be distributed farther away from front-country human facilities and dying in equal or greater numbers, but under conditions where documentation is less likely; (4) humans could be killing as many or more bears under otherwise similar circumstances, but by poaching, and thus managers would be receiving proportionally less information for their records; or (5) all else equal, recorded mortality would decline if the number of radio-marked bears declined. These less than exhaustive and potentially over-lapping alternate explanations are all plausible and further help to identify relevant and testable hypotheses.

Testable Hypotheses

If annual variation in recorded grizzly bear mortality could be explained by causes that did not include management intervention, then it would be conservative relative to the cost of potential errors to assume that changes in recorded mortality were not attributable to human management (Shrader-Frechette and McCoy 1993). If recorded mortality also included proportionally few bears that had died under circumstances where detection by humans was unlikely (e.g., unmarked poached bears), then it would be similarly conservative to assume that present methods employed to record mortality of unmarked (or untrapped) bears are ineffective. Heavy reliance on marked bears to document deaths in turn allows for the existence of bias attributable to differences in the probability of documentation among individual causes, especially if those causes have varied in relative prominence over time. Without knowing the true ratio of recorded to actual mortality by cause, this condition would also be consistent with low annual correlation between these 2 values over all causes of death.

To address these issues I estimate the relationship between recorded mortality and alternate explanatory variables and estimate the proportion of recorded mortality attributable to radio-marked bears or other circumstances highly favorable to documentation. I test the following ancillary hypotheses (H_N): (1) annual variation in recorded grizzly bear deaths was not related to bear use of whitebark pine seed crops or number of radio-marked bears; (2) causes of mortality did not proportionally change among 3 periods of approximately 6-years each, 1976–93; and (3) mortalities with inherently high likelihood of documentation did not proportionally vary among causes. Referring to Figure 1, hypothesis 1 pertains to the effects of number of radio-marked bears and the distribution and abundance of an important food, emphasizing whitebark pine because previous work has shown a negative relationship between numbers of recorded grizzly bears deaths and use of whitebark pine seeds by bears in the Yellowstone ecosystem (Mattson et al. 1992). Hypotheses 2 and 3 pertain to the effects of cause-of-death. For lack of data, human behavior, values, numbers and distribution were not addressed.

Together, these tests can be used as a basis for judging the merits of assuming that numbers of recorded and actual deaths are highly correlated and that changes in numbers of recorded deaths over time are attributable to management intervention. More specifically, this analysis provides grounds for judging whether it is both safe and defensible to assume that current management has actually reduced Yellowstone grizzly bear mortality.

METHODS

Data and Stratifications

I used annual records of known and probable grizzly bear deaths (*sensu* Craighead et al. 1988) for this analysis, including totals by all causes and by human causes alone, and for all bears and for adult females only. Adult

females were considered to be greater than or equal to 5 years old, unless accompanied by cubs at a younger age (Knight and Eberhardt 1985, Eberhardt et al. 1994). Craighead et al. (1988) and H. Pac and A. Dood of Montana Department of Fish, Wildlife, and Parks (Helena, unpubl. data) provided records of known and probable bear deaths that included causes of death and information on whether the bears had been trapped or were radio-marked at time of death. Annual numbers of radio-marked bears were tallied from individual grizzly bear histories (dated 19 March 1993) maintained by the Interagency Grizzly Bear Study Team. These histories were also used to confirm deaths of radio-marked bears recorded in the mortalities data base. Intensity of use of whitebark pine seeds, 1976–92, was determined from fecal analysis (Mattson et al. 1992, Knight et al. 1993, and Knight and Blanchard 1994) and was considered to be intensive when pine seeds were present in ≥20% of all collected grizzly bear feces (Mattson et al. 1992). I treated whitebark pine seed use as a 0–1 variable because of the well-established dichotomy in seed consumption that partly reflected an abrupt inflection in the relationship of bear use to cone availability (Mattson and Reinhart 1994).

I categorized mortality by 6 general causes. These were "natural," "management," "hunter-related," "livestock-related," "other illegal," and "other." Natural mortality included all bears that died by causes not directly related to humans or human facilities and consisted primarily of dependent young dying from unknown causes, intra-specific predation, and deaths from "old age." Management-caused mortality included those instances of bears removed by managers for humane reasons or because the bear posed a threat to human safety, but did not include bears removed by managers because of conflict over livestock or back-country camps with attractants. Hunter-related mortality, some of which was illegal, resulted from chance encounters with big-game and bird hunters, encounters over bear baits, or encounters involving camps of outfitters catering to hunters. Livestock-related mortality, some of which was also illegal, derived from conflict over livestock, primarily sheep. Other illegal mortality could loosely be considered poaching that was not clearly associated with livestock or hunting. Finally, all other causes (e.g., road-kills, accidental death during a research capture) were lumped under "other."

I stratified deaths according to 3 categories that reflected *a priori* differences in likelihood of documentation. These categories were: radio-marked bears ("marked"); bears that were otherwise likely to be documented ("UM likely"), associated with road kills, electrocutions, management actions, and research trappings; and remaining bear deaths that were comparatively less likely to be either detected or recorded ("UM unlikely"). Marked and UM likely deaths were mutually exclusive.

I stratified the data by 3 periods to analyze proportional changes in causes of death and the categories that reflected likelihood of documentation. These intervals were of 6 years each: 1976–81, 1982–87, and 1988–93. The last period consisted of 4 years in most analyses (1989–92) because some data for 1993 were not available and because I excluded the anomalous conditions associated with extensive wildfires during 1988 (~560,000 ha burned [Schullery 1989]). These fires led to unusual foraging, including consumption of fire-killed ungulates and unusual interactions between bears and humans (Blanchard and Knight 1990). I did not exclude 1988 when analyzing differences in numbers or fractions of radio-marked bears because I assumed that fire-related biases were not as germane to this question.

The 3 periods corresponded to substantive changes in either bear management or the structure of bear habitat. My analysis began with 1976 because I assumed mortality directly related to closure of open-pit dumps in Yellowstone National Park during 1969–70 was negligible by that time (Craighead et al. 1995). Efforts to protect bears and sanitize human facilities were increased after 1982 (Gunther 1994), while wildfires during 1988 caused major changes in vegetation structure and composition in a large part of grizzly bear habitat.

Analysis

I used general linear models to test hypothesis 1 and throughout set $\alpha = 0.1$. Recorded number of deaths (either total or human-caused, or for all bear classes or just adult females) was the dependent variable. Whitebark pine seed crop use, number of radio-marked bears (either total or just adult females, depending upon the dependent variable), and sequential year were independent variables. Tallies of deaths and radio-marked bears were converted to normalized ranks (Iman and Conover 1979) to condition these otherwise non-normal discrete data (Potvin and Roff 1993). Whitebark pine seed use was treated as a class variable, and other effects were estimated by analysis of covariance. Sequential year ($t = 1, 2, ..., 17$) served partly as a means for alleviating serial correlation (Seber 1977) as well as a surrogate for the hypothesized time-specific effects of management in the Yellowstone ecosystem (e.g., Gunther 1994). A significant negative coefficient for "sequential year" would be consistent with the assumption that management had become increasingly effective, conditional upon ultimate expla-

nations for residual variation. I also used the Durbin–Watson test for first-order auto-correlation (Durbin and Watson 1950), where $D \gg 2$ indicates that none was present.

I used the log-likelihood statistic (G^2) to test whether the relative frequency of categories related to cause or likelihood of documentation varied independently of time period (hypotheses 2 and 3, respectively). Where columns were binomial and rows ordered by time (e.g., marked versus unmarked dead bears) I used the Mantel-Haenszel X^2 test (Mantel 1963). I did not use continuity corrections because marginal totals were not fixed. Where I was interested in equality of locations among the 3 periods, I used non-parametric analysis-of-variance (rank transforms [Conover and Iman 1980]). Protected multiple comparisons used analogs of the Tukey-Kramer procedure (Zar 1983), either on angular transformed proportions or rank transformed counts. I used Bonferroni confidence intervals that varied with number of recorded deaths in both periods when comparing relative frequencies (Miller 1981).

RESULTS

Annual Patterns in Recorded Mortality

Annual number of recorded grizzly bear deaths was strongly related to whitebark pine seed use in all models (Table 1). Pine seed use explained between 31 and 50% of the variance in recorded mortality, for total mortality, all causes, and for total human-caused mortality, respectively. In all instances recorded mortality was much greater (1.8–3.3 X) during years when pine seeds were not intensively used (Table 2).

Sequential year and number of radio-marked bears combined explained only 3–16% of annual variation in recorded mortality. Parameter estimates for both were also not different from zero except in 1 case (Table 1). Human-caused mortality of all classes exhibited a weak negative relationship to sequential year (i.e., it declined with time), and explained 10% of total variance. This contrasted with the 50% explained by whitebark pine seed use in the same model.

Most residuals exhibited consistent patterns among years in all 4 models and were only auto-correlated in the analysis of total human-caused mortality (D = 2.89 and auto-correlation = -0.48 for this model; D = 1.98–2.22 for other models). For total human causes, annual recorded mortality that was greater than expected tended to be followed by mortality that was less than expected. Recorded mortality was also substantially greater than expected by all models (i.e., residuals were comparatively large) during 1990 and substantially greater than expected during 1989 and 1991. During 1991 no known or probable mortalities were recorded. Recorded mortality of all classes, total and human-caused, was greater than expected during 1985, when 7, an unusually large number of natural cub mortalities, were documented.

Some positive effect other than use of whitebark pine seeds was strongly implicated only if numbers of deaths were less than 1 adult female and 6 total mortalities during years of little pine seed consumption and no adult female mortalities and 4 total during years of heavy pine seed consumption (Table 2). In other words, the absence of recorded adult female deaths during a year of heavy

Table 1. Results of statistical analysis for linear models relating annual recorded grizzly bear mortality (human caused and total, all classes and just adult females) to level of whitebark pine seed use (class variable), sequential year (1–17), and number of radio-marked bears, for the Yellowstone Recovery Area, 1976–92, excluding 1988.

	Whitebark pine seed use		Sequential year		No. of marked bears[a]		Total model		
Recorded mortality[a]	Coefficient[b]	P^c	Coefficient[b]	P^c	Coefficient[b]	P^c	R^2	F	P^d
All classes									
Total[e]	-0.314	0.025	-0.046	0.349			0.360	3.66	0.055
Human-caused	-0.495	0.001	-0.098	0.092	0.058	0.184	0.650	7.45	0.004
Adult females									
Total	-0.436	0.009	-0.027	0.453	0.003	0.802	0.465	3.48	0.050
Human-caused	-0.413	0.012	-0.023	0.497	0.002	0.826	0.438	3.13	0.066

[a] Rank transformations used.
[b] Coefficients were standardized based on % variance "explained".
[c] P-values are for test that coefficients = 0.
[d] In all cases df = 3, 12, except for "total, all classes", where df = 2, 13.
[e] No. of radio-marked animals was dropped to achieve an acceptable model (with this variable P = 0.121).

Table 2. Mean annual recorded grizzly bear mortalities for years when grizzly bears showed high and low levels of use of whitebark pine seeds in the Yellowstone Recovery Area, 1976–92, excluding 1988.

	High use years (n = 11)			Low use years (n = 5)		
Recorded mortality[a]	$\bar{x}$	90% CI	90% Bounds	$\bar{x}$	90% CI	90% Bounds
All classes						
Total	7.1	4.9–9.2	0.6–13.6	13.0	9.0–17.0	6.0–20.0
Human-caused	5.4	3.8–7.0	0.6–10.2	11.6	8.2–14.9	5.8–17.4
Adult females[b]						
Total	1.1	0.5–1.8	0.0–3.5	3.6	2.1–5.5	1.2–7.1
Human-caused	1.1	0.5–1.8	0.0–3.5	3.5	2.0–5.2	1.2–6.6

[a] 90% confidence intervals (CIs), and 90% bounds (within 1.65 standard deviations of $\bar{x}$).
[b] Estimates for adult females used data transformed by $(\bar{x} + 0.5)^{1/2}$. Displayed values were back-transformed.

pine seed use was consistent with the effects of whitebark pine seed use alone. These results assume a dominant effect of pine seed consumption on levels of recorded mortality and, given $\alpha = 0.1$, that "unusually" few bear deaths would be any number <1.65 SDs below the mean for a given type of seed use year. Furthermore, the observed drop in recorded mortality during 1984–92 (excluding 1988) compared to 1976–83 (U.S. Fish and Wildlife Service 1993) was consistent with a greater tendency towards more frequent heavy use of pine seeds by bears during the more recent period ($G^2 = 2.76$, 1df, $P = 0.097$).

Changes in Causes and Likelihood of Documentation

Causes-of-death and categories corresponding to likelihood of documentation differed proportionately among the three 6-year periods (P = 0.056 and 0.004, respectively) (Table 3). Simple contingency tables corroborated this apparent dependence of cause ($G^2 = 27.86$, 10df, P = 0.002) and documentation ($G^2 = 9.65$, df = 4, $P = 0.047$) upon period. Neither causes nor categories related to likelihood of documentation varied with annual level of whitebark pine seed use (Wald X^2 P = 0.201 and 0.710, respectively, for cause and likelihood of documentation using log-linear models).

Dead bears that were radio-marked or likely to be documented for other reasons accounted for the majority of recorded mortality during all 3 periods, with this pattern becoming more pronounced over time. Specifically, radio-marked bears increased as a percentage of recorded mortality (Mantel-Haenszel $X^2 = 5.10$, $P = 0.024$), reaching a maximum of 76% during 1988–92 (Table 3). There was a similar but weak trend toward increasing percentages of recorded deaths that were likely to be documented for all reasons (marked and UM likely combined) (Mantel-Haenszel $X^2 = 2.41$, $P = 0.121$), reaching a maximum

Table 3. Percent grizzly bear mortalities in the Yellowstone Recovery Area, 1976–92, by cause and likelihood of documentation (marked, marked + UM likely) for 3 periods. Percentages followed by the same letter in rows are not different, except the last column, where those followed by the same letter in the column are not different.

	Time period			%
	1976–81 (n = 62)	1982–87 (n = 62)	1988–93 (n = 37)	Marked + UM likely[a]
Cause				
Management	8.1b	32.3a	8.1b	100.0
Hunter-related	25.8a	21.0a	24.3a	42.1b
Livestock-related	17.7a	8.1ab	2.7b	70.6a
Other illegal	17.7a	9.7a	16.2a	60.9a
Natural	12.9b	21.0ab	35.1a	73.5a
Other	17.7a	8.1a	13.5a	95.2
Likelihood of documentation				
% marked	53.2c	64.5b	75.7a	
% marked + UM likely	67.7b	67.7b	83.8a	
$\bar{x}$ no. radio-marked bears[b]	33.3b	42.5ab	50.5a	

[a] Management and other causes were not included in the statistical analysis and so are not identified with a statistical population by a letter.
[b] Includes unmarked dependent young.

of 84% also during 1988–92 (Table 3). These increases could partly be ascribed to an increase in the number of monitored radio-marked bears and their dependent young ($F = 3.94$, 2df, $P = 0.046$) (Table 3).

The portion of recorded deaths that consisted of radio-marked bears or was attributable to circumstances otherwise ensuring documentation varied among causes. By definition, all management-caused mortality was documented. The causes comprising "other," such as road-kills and accidental deaths during research captures, were similarly highly predisposed to documentation (Table 3). Considering the remaining 4 causes of mortality, there was significant variation in the percentage of recorded deaths that occurred under circumstances tending to ensure documentation ($G^2 = 8.50$, 3df, $P = 0.037$) (Table 3). Of these causes, hunter-related mortality was significantly different from the rest and depended least upon radio-marked animals for its documentation.

The relative frequency of causes-of-death differed among all combinations of the 3 periods. Livestock-related mortality proportionally decreased and natural mortality proportionally increased from 1976–81 to 1988–93 (Table 3). However changes in the proportion of management-related deaths dominated differences among time periods, reaching a maximum during 1982–87. Proportional increases primarily in poaching (i.e., "other illegal"), "natural," and "other" complemented the proportional decline in management-related deaths between 1982–87 and 1988–93. In other words, recorded mortality shifted from a cause that was inherently detectable (management) to causes that were inherently much less so, combined with greater apparent dependence upon radio-marking for documentation. Interestingly, radio-marked bears also comprised the largest part of total recorded mortality (80%) in recent years (1988–93) outside of Yellowstone Park, compared to between 57 and 65% of recorded mortality either during other years or inside Yellowstone Park for the same period.

DISCUSSION

I did not reject H_N 1, that variation in recorded deaths was not related to whitebark pine seed crops or the number of radiomarked bears. The availability of whitebark pine seeds and their use by grizzly bears did affect the annual variation of recorded mortality. Declines in recorded deaths can be ascribed to the effects of large pine seed crops, including low levels of mortalities recorded during 1989–92, that coincided with unusually frequent large pine seed crops. This interpretation is strengthened by a plausible causal mechanism. During years when grizzlies heavily used pine seeds, the bears were distributed in areas remote from human facilities, and recorded conflicts with humans were less frequent. Conversely, during other years bears made much greater use of areas near humans and caused more problems typically addressed by management trapping (Blanchard and Knight 1991, Mattson et al. 1992, Blanchard and Knight 1995). This is not to say that actual mortality varied for these reasons, but rather that observed variation in recorded mortality can thus be plausibly explained.

There is little support for the assumption that management intervention caused declines in recorded mortalities. Only human-caused mortality for all classes exhibited a relationship to time, controlling for the effect of whitebark pine seed crops. However, this negative trend was weak. This is not to say that management actions such as sanitation of human facilities, removal of sheep, and law enforcement had no effect. The beneficence of these actions is indisputable (e.g., Mattson 1990, Gunther 1994). Rather, such management probably served to prevent background levels of recorded mortality from rising in the face of adverse trends such as increasing road access and numbers of people in Yellowstone's grizzly bear habitat (Glick et al. 1991; Pease and Mattson, In Press). Even so, these conclusions hold only for recorded mortality and do not address whether patterns and putative causes observed for recorded mortality are synonymous with those of actual mortality.

The dependence of documentation of mortalities on radio-marking is one result that casts doubt on the relationship of recorded to actual mortality. It is very unlikely that radio-marked bears would comprise as large a fraction of recorded mortality as was observed if the deaths of unmarked bears were being recorded at even close to the same rate as marked bears. This point is illustrated by the following simple exercise: If one assumed that actual mortality was 2 times recorded mortality (Knight and Eberhardt 1984, Dood et al. 1989) and further assumed that the proportion of radio-marked bears in recorded mortality (0.70) was the same as the proportion of marked bears in the total live population and that marked bears had 2 times the death rate of unmarked bears (Pease and Mattson, In press), then a marked sample of 40 bears would give a population size (~230) substantially less than the 300–400 bears that most likely resided in the Yellowstone Recovery Area during the period of this analysis (Mattson et al. 1995, Eberhardt and Knight 1996). This substantial deviation below the best current population estimate strongly implies that the odds of recording deaths of

unmarked bears were very low and that recorded mortality was therefore insensitive to variation in deaths of these animals.

More than simply being possible, a low correlation between recorded and actual mortality was likely. The proportion of recorded deaths that occurred under circumstances favoring documentation varied with cause of death, and the relative prominence of causes varied over time. As might be expected, there was a marked disparity in the apparent likelihood of documentation between management removals and livestock-related mortality, natural deaths, and poaching (i.e., "other illegal"). While proportionally fewer bears died in recent times because of conflicts with livestock, fewer were also being removed by managers. At the same time, poaching and natural causes were accounting for proportionally more bear deaths. In short, because the part of recorded mortality attributable to radio-marked bears increased to 75% at the same time that causes shifted to those with low apparent likelihood of documentation, there is no reliable basis for inferring from recorded mortality that actual mortality had declined during 1988–92 compared to earlier years, whatever the cause for declines in recorded mortality.

Similarly I did not reject hypotheses that causes of mortality did not change among time periods (H_N2) or that mortalities with a high likelihood of being documented did not proportionally vary among causes (H_N3). Thus, there is no basis in this analysis for concluding that recorded mortality was highly correlated over time with actual mortality. *Prima facie*, this relationship is likely to be weak. A number of factors potentially influence documentation of dead bears, including numbers, distributions, and behaviors of both bears and humans (Fig. 1). None of these extraneous factors were controlled in either making or interpreting tallies (Craighead et al. 1988, U.S. Fish and Wildlife Service 1993).

MANAGEMENT IMPLICATIONS

These results do not support assumptions that actual grizzly bear mortality in the Yellowstone ecosystem has declined, or that declines in recorded mortality have occurred because of successful management intervention. Of the 5 potential explanations for declines in recorded mortality identified in the introduction, this analysis is consistent with the potential effects of a decline in actual mortality, constant or increasing mortality rates offset by a declining bear population, bears dying in more remote areas where they are less likely to be documented, or, all else equal, bears dying by causes that are less likely to be documented. To adopt only the first of these explanations is not defensible nor precautionary (Shrader-Frechette 1991).

Management apparently has been successful at changing the nature of human-caused mortality, in recent years primarily by proportional reductions in livestock-related deaths and management removals. This is consistent with the beneficial effects of sanitizing human facilities and removing sheep from occupied grizzly bear habitat.

Some recent analyses of population growth based on survival and reproduction of radio-marked bears (Eberhardt et al. 1994, Eberhardt 1995) and trends in tallies of unduplicated females with cubs-of-the-year (Knight et al. 1995) have suggested that the Yellowstone grizzly bear population is increasing. However, these recent estimates of population growth have been affected by optimistically biased methods (time at risk was not censored for intervals when bears were not radio-marked; Hovey and McLellan 1996), selective use of inherently optimistic data (only a fraction of the marked bears, those that were substantially wary of humans, were used for analysis; Pease and Mattson, In Press), or use of methods otherwise potentially affected by substantial uncontrolled biases (determination of counts of unduplicated females with cubs-of-the-year was substantially subjective [Craighead et al. 1995], and trends in these counts were affected by sightability and search effort [Mattson 1997]). Another recent analysis of population trend suggests that the Yellowstone population increased very little from 1975 to 1995 (Pease and Mattson, In Press). Therefore, managers should consider these factors and be cautious in their interpretations of recorded grizzly bear mortality as well as cautious in their judgments about the overall effectiveness of current management practices.

Given these cautionary conclusions, recorded mortality may yet provide useful information. First, it is important to acknowledge the effect of whitebark pine seed use on recorded mortality in the Yellowstone ecosystem. Based on this relationship, attribution of reductions in recorded mortality to management programs should only be made when such reductions are greater than what might be expected by bear use of whitebark pine seeds. However, for years when grizzlies are heavily using whitebark pine seeds, this level includes no adult female mortality. A better test would be to determine whether recorded mortality consistently dropped to <1 adult female and ≤6 bears total, during years when grizzlies were making less intensive use of pine seeds.

Recorded mortality may also provide more information about actual mortality if the effects of cause are controlled. However, this is contingent on the availability of unbiased estimates or indicators of the likelihood that different causes can be detected and documented. Such estimates could be obtained by leaving the remains of dead radiomarked bears *in situ* and recording the number of these deaths that were detected by means other than radio telemetry. Secondarily, these counts would be more useful if the effects of human effort were controlled, including the effects of radio-marking, observer numbers, and variation in efforts to otherwise document observed mortalities. However, the models presented here suggest that annual variation in radio-marking has a minor effect, and control of the remaining factors is likely to be difficult.

Given the biases potentially affecting inferences from grizzly bear mortality as currently recorded in the Yellowstone ecosystem, other means of monitoring based on estimates of death rate may be preferable. However, calculation of death rate is predicated on obtaining comparable estimates of dead and live bears. Such a task potentially relies on intrusive and expensive methods, employs its own set of assumptions and is potentially affected by several biases. No one approach is likely to be uniformly superior by all criteria.

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