

SUSTAINABLE GRIZZLY BEAR MORTALITY CALCULATED FROM COUNTS OF FEMALES WITH CUBS-OF-THE-YEAR: AN EVALUATION

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Abstract

Unduplicated counts of female grizzly bears Ursus arctos horribilis with cubs-of-the-year are currently used to estimate minimum population sizes used, in turn, to calculate allowable (assumed to equal sustainable) mortality for grizzly bear populations in the contiguous United States of America. This calculation assumes that unduplicated counts are an unbiased and accurate indicator of population size and that the ratios of minimum population size and known mortality to their respective totals are equal. Neither of these assumptions can be directly tested. However in this paper I use data from the Yellowstone ecosystem, 1977–1990, to evaluate two directly related but alternate hypotheses: (1) annual variation in unduplicated counts is explained by factors extraneous to the number of adult females in the population (i.e. search effort and sightability of females with cubs); and (2) there is > 10% risk of allowing unsustainable mortality (actual mortality rate > 6%) given a plausible, uniform range of population and mortality ratios. My results are consistent with accepting both of these hypotheses. I therefore concluded that unduplicated counts varied without a known relationship to population size and that, by normal standards, the method currently adopted for management of grizzly bear populations in the contiguous United States was not a conservative basis for calculating maximum allowable mortality. I suggest that using lower mortality rates and conservative bounds of confidence limits for the estimated parameters used in calculations of allowable mortality could substantially reduce the risk of unintentionally allowing excessive mortality. © 1997 Published by Elsevier Science Ltd

Keywords: population index, search effort, sightability, unduplicated, Yellowstone National Park.

INTRODUCTION

In theory, many grizzly bear populations can sustain 6% per annum mortality (Harris, 1986a; Miller, 1990;

US Fish and Wildlife Service, 1993). Managers of threatened grizzly bear populations in the contiguous United States of America have accordingly set maximum allowable death rates at 4%, somewhat less than this theoretical maximum and at a level that is thought to be conservative (US Fish and Wildlife Service, 1993). It is, however, very difficult to determine whether death rates are at acceptable levels because extensive forest cover, low bear densities, and limited management resources often preclude reliable estimates of total mortality and population size. Standard methods have been plagued by variability and high bias (Erickson and Siniff, 1963; Harris, 1986b) or, in the case of remote cameras (Mace *et al.*, 1994), may not be suited to estimating wide-spread, low-density populations (Kasworm & Thier, 1994). Managers and researchers have consequently settled on using minimum population estimates derived from an index to calculate maximum allowable mortality and on using records of known and probable bear deaths from all sources to monitor mortality (US Fish and Wildlife Service, 1993).

The index used to calculate allowable mortality is called 'unduplicated counts of females with cubs-of-the-year (COY)'. These counts are simply an estimate of the individual females represented by all sightings of this class by all sources within a given year. This determination is based upon the physical characteristics of females and their cubs, and spatial disjunction and temporal synchrony of sightings. Because this class is endowed with several diagnostic features, it is assumed that there is sufficient information from sightings to determine the number of individual adult females represented by uncontrolled observations (Knight *et al.*, 1995). Because most female grizzly bears in the contiguous US have a three-year reproductive interval, it is further assumed that a three-year summation of unduplicated counts, minus known adult female mortality for that period, will provide a minimum number of adult females present in a population. Minimum population sizes (including males) are then calculated, based upon an estimate of the proportion of adult females in the population, and a 4% mortality rate is applied to derive

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an estimate of sustainable mortality (US Fish and Wildlife Service, 1993). Thirty per cent of this mortality is allowed to be females (US Fish and Wildlife Service, 1993).

Although methods for determining unduplicated counts have been described (Knight *et al.*, 1995), and the performance of these counts as an indicator of population trend has been investigated (Eberhardt *et al.*, 1986; Harris, 1986c; Knight *et al.*, 1995), application of three-year sums to calculation of sustainable mortality has not yet been critically assessed. Although several authors have pointed out that this metric is an uncertain population index and, on its own, an inappropriate basis for inferring short-term variation in population size (Eberhardt *et al.*, 1986; US Fish and Wildlife Service, 1993; Knight *et al.*, 1995), unduplicated counts are used as a reliable indicator of population size in calculations of allowable mortality (AM_t). Calculations directly use three-year sums of unduplicated females with COY (where NF_t = the count for the current year t) (US Fish and Wildlife Service, 1993):

$$AM_t = (((NF_t + NF_{t-1} + NF_{t-2}) - (D_t + D_{t-1} + D_{t-2}))/0.284) * 0.04 \quad (1)$$

As three-year sums increase, so does allowable mortality, conditional upon known adult female deaths (D_t) during this interval. This phenomenon is illustrated in Fig. 1 using historical data for the Yellowstone ecosystem for a period when this method was not yet applied. Thus, if unduplicated counts increase, it is implicitly assumed that the population can sustain more mortality and/or that the efficiency of detecting dead adult females varies 1:1 with the efficiency of detecting live females with COY.

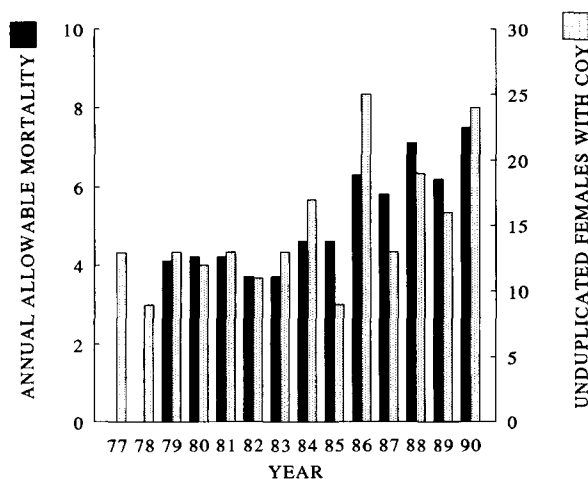


Fig. 1. Annual counts of unduplicated grizzly bear females with COY and calculated total allowable mortality (US Fish and Wildlife Service, 1993) for the Yellowstone ecosystem, 1977–1990. Calculations are used to illustrate the performance of this method and were not the actual standards for allowable mortality applied during this period.

There are several factors that potentially complicate use of this calculation to set mortality ceilings. Most important, the degree to which recorded mortality reflects actual mortality will depend upon the relative level of two ratios: minimum (or 'known') to total population size, and known to total mortality. Disparity in these ratios can result in actual mortality rates substantially different from assumed rates. Actual rates will predictably be greater than applied rates when the population ratio is less than the mortality ratio. Unfortunately, because neither total mortality nor population size can be reliably estimated on an annual or three-year basis (Eberhardt & Knight, 1996), managers cannot reliably estimate these respective ratios, and consequently run a risk of allowing unsustainable mortality even applying a 'conservative' 4% allowable mortality rate.

In summary, there are two key assumptions implicit to the adopted method of calculating allowable mortality: first, that minimum population estimates based upon unduplicated females with COY are precise and accurate indicators of total population size (N), and, second, that the ratio (or proportion) of known to total population (p_p) is less than or equal to the ratio of known to total mortality (p_m). These assumptions can be construed as null hypotheses: minimum population estimates are unrelated to total population size, and $p_p > p_m$. Neither hypothesis can be directly tested simply because there are no independent and reliable annual estimates of population size and mortality from areas where this method is being applied. However, as relevant to testing these assumptions, it could alternately be hypothesized (1) that variation in unduplicated counts is explained by causal factors (e.g. search effort and sightability of bears) that have no known or direct relationship to population size, and (2) that the probability of allowing unsustainable mortality (mortality rate $> 6\%$) is high (e.g. $> 10\%$) given a plausible range of population and mortality ratios. These two hypotheses are consistent with assuming that unduplicated counts will vary annually without a known relationship to population size and that the current method of calculating allowable mortality will result in a high risk of allowing unintended population declines.

I evaluate the defensibility of these alternate hypotheses in this paper and otherwise assess bias, variability, and risk associated with the currently adopted method for calculating maximum allowable mortality for grizzly bear populations in the contiguous US. I identify factors that potentially affect the relationship of unduplicated counts to actual numbers of adult females in the grizzly bear population in and near Yellowstone National Park, analyze the relationship of unduplicated counts to sightability and search effort within the Yellowstone ecosystem, and specify the risks associated with calculating allowable mortality from these counts. I furthermore suggest how this metric could be used in mortality calculations, but in ways that reduce risk and acknowledge potential error.

METHODS

A conceptual model

A conceptual model that relates three-year sums of unduplicated females with COY to the number of adult females in a population is clearly relevant to judging hypothesis (1) (Fig. 2). Observations of females with COY are affected by a number of probabilistic events ('filters' in Fig. 2) as well as at least six extraneous factors related to food availability and human behaviour. The chance that a field observation will be recorded and the probabilities of both encountering and sighting bears are intuitively important links between unduplicated counts and numbers of females in a population. The probabilities of encountering and sighting a female with COY are, in turn, likely to be conditional upon the probability that these animals will be in the open or near human facilities. Human effort (trapping, radio-relocations, observation flights, solicitation of observations, and number of humans at large), distribution and abundance of foods and other bears, and public atti-

tudes and awareness, are furthermore potentially important to making and recording sightings of females with COY. The conceptual model in Fig. 2 also identifies several likely sources of error, including the probability that a black bear *Ursus americanus* with COY or a grizzly bear with older young will be counted, the probability that a single female will be counted more than once in the 'unduplicated' tally, and the possibility of an inaccurate estimate of reproductive interval. Of these four errors, three are more likely to inflate rather than deflate the tally of females with COY relative to the actual number of females represented by sightings.

A statistically testable model

Several factors have probably influenced sightability (i.e. the probability that a given adult female will be seen with her COY) in the Yellowstone ecosystem over the last two decades. Increasing numbers of grizzlies have been observed eating adult army cutworm moths *Euxoa auxiliaris* in alpine talus, especially since 1985 (Mattson *et al.*, 1991). This annually varied use is best

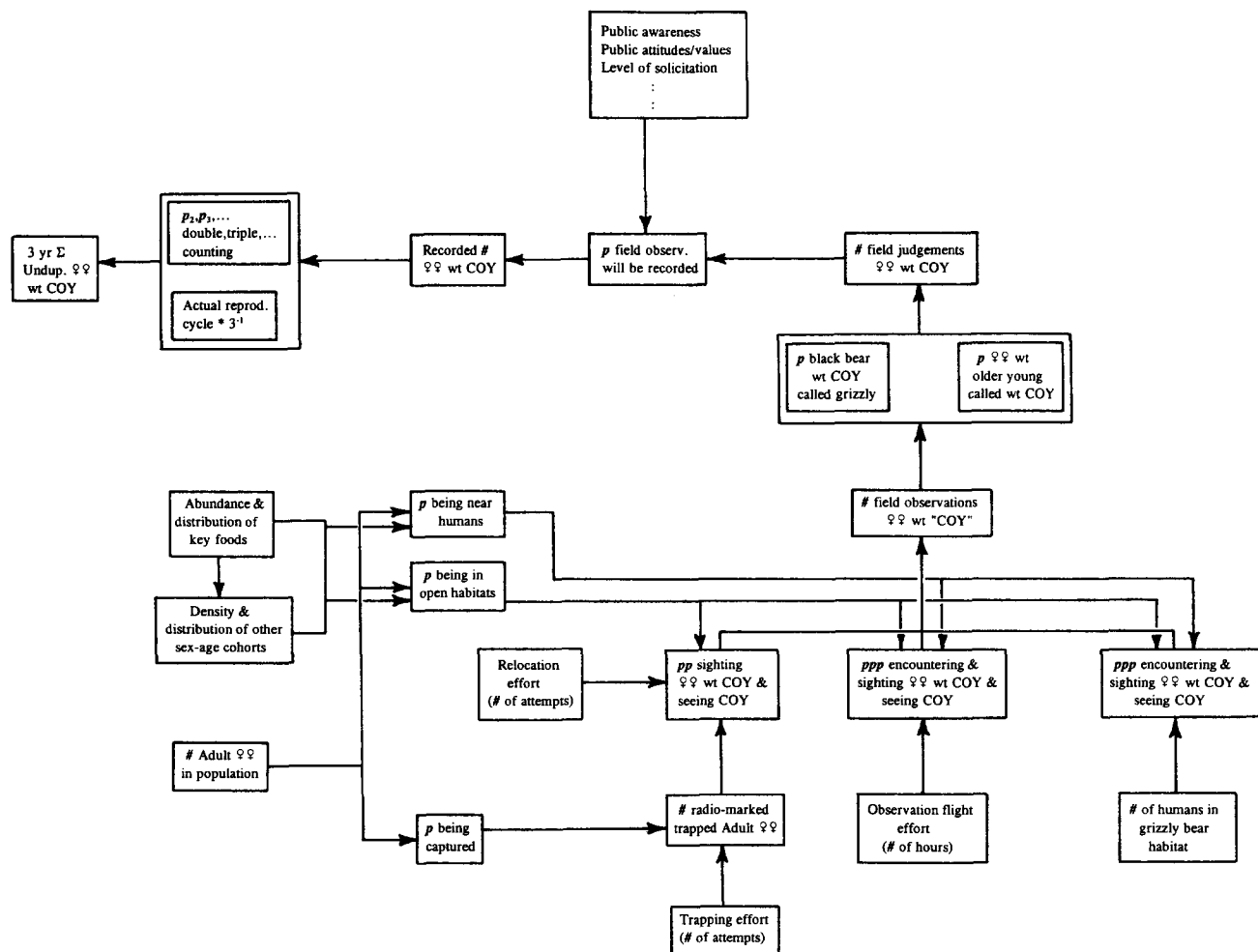


Fig. 2. A conceptual model of the relationship between three-year sums of unduplicated female grizzly bears with COY (three-year Σ Undup ♀♀ wt COY) and number of adult females in the population (no. Adult ♀♀ in population). Model elements include filters and levels, typically denoted by 'p' and '#', respectively. Levels correspond to system states that can be expressed as enumerations while filters correspond to probabilistic events. Filters included in a single box together affect a transition from one level to another.

indicated by the average total number of grizzlies seen per successful flight (i.e. when at least one bear was seen on a moth site) per year (Mattson *et al.*, 1991). Given the predictable and open nature of moth feeding sites, this increased use of moths has plausibly caused a larger portion of Yellowstone's grizzlies to be visible to aerial observers.

Supporting this argument, an increasing proportion, and most recently a majority, of unduplicated females with COY have been first observed at moth feeding sites (Knight *et al.*, 1993). Similarly, as more adult female grizzlies are radio-marked, the probability that a female will be seen with COY also predictably increases, given that the chances of locating and observing these marked animals are inherently greater than for unmarked animals. It is thus relevant that the number of radio-marked females has varied among years (cf. Knight *et al.*, 1991).

Two variables calculated from observations of radio-marked females potentially reflect the sightability of this class. Assuming that marked females with COY are representative of this class at large, the proportion of times these bears were seen during a radio-relocation effort would indicate the sightability of this class at large. Similarly, the proportion of all sightings of all marked bears during radio-relocation efforts that were attributable to females with COY would indicate both the relative number of this class in the radio-marked sample as well as this class's relative sightability.

Of all the factors related to effort, there is reliable information available concerning only two variables. The number of radio-marked females is again relevant through reflecting efforts to trap bears. All else being equal, the greater the effort the greater the number of radio-collared bears. Otherwise, hours of observation flights by Yellowstone researchers (the Interagency Grizzly Bear Study Team [IGBST]), where bear sightings were sought without the aid of radio-telemetry, have been recorded for each year (Knight *et al.*, 1991). This is not a trivial indicator of effort given that typically one-third of all unduplicated females with COY were first seen during these flights. Of equal importance, females with COY seen during observation flights have accounted for an increasing proportion of sightings in the Yellowstone ecosystem and, furthermore, account for virtually all of the increase in unduplicated counts during recent years (Fig. 3). Sightings from other sources have shown no obvious trend (Knight *et al.*, 1991).

Thus, parts of the more complex conceptual model can be reduced to a simpler and statistically testable model, relating annual counts of unduplicated females with COY to hours of observation flights and estimates of sightability. These estimates include total number of bears observed on moth sites, number of radio-marked adult females, the proportion of times these females with COY were seen during a radio-assisted relocation, and the proportion of all radio-marked bear sightings attributable to this class.

Analysis methods

Given that all four variables related to sightability were positively correlated (Table 1) and that some were complex functions of others, I chose not to use these measures individually for regression analysis because of likely problems with multicollinearity. Instead, I integrated information from these inter-related variables through principal components analysis (Johnson & Wichern, 1992). I analyzed the correlation matrix of untransformed values and used annual scores from the

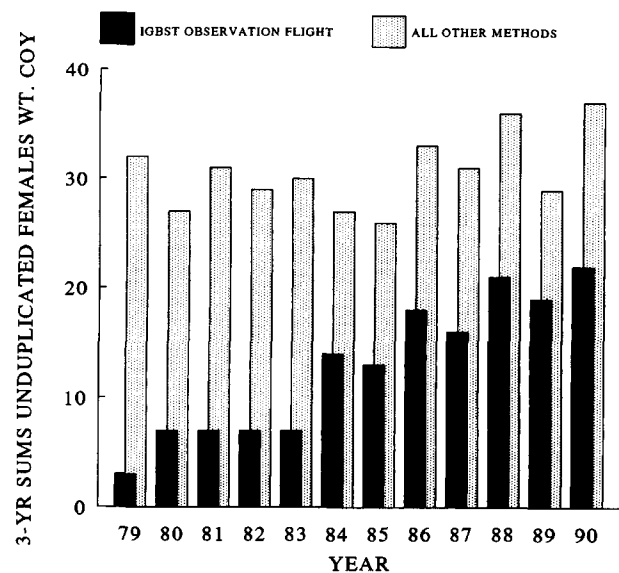


Fig. 3. Three-year sums of unduplicated female grizzly bears with COY attributable to research (IGBST) observation flights and all other sources, for the Yellowstone ecosystem, 1977–1990. Sums start with 1979 because of the implicit three-year lag. Other sources include research observation flights for other species, flights for telemetry location of radio-marked bears, and ground observers.

Table 1. Estimated correlation (Pearson r), and probability that $r=0$ (in parentheses), between four variables thought to be related to annual sightability of female grizzly bears with cubs-of-the-year (COY) in the Yellowstone ecosystem, 1977–1990 ($n=14$)

Variables	Variables		
	No. of bears at moth sites	No. of adult female bears radio-marked	% of marked females wt COY sighted
No. of adult female bears radio-marked	0.856(0.000)		
% of marked females wt COY sighted	0.684(0.007)	0.373(0.188)	
Females wt COY as % of total	0.573(0.032)	0.664(0.010)	0.449(0.107)

first principal component (accounting for 70.5% of total variance, with an eigenvalue = 2.82) as an aggregate measure of 'sightability'. The first principal component had loadings for number of bears on moth sites, number of radio-marked adult females, percent of marked females with COY seen during a relocation effort, and these sightings as a percent of the total for all marked bears, of 0.558, 0.524, 0.434 and 0.474, respectively. This satisfactorily integrated information pertaining to sightability from four variables into one, better suited to a regression analysis with $n = 14$. The resulting principal component was also subject to straight-forward interpretation as an aggregate positive indicator of sightability.

I used regression analysis to address hypothesis (1), with α for rejection = 0.1 for the entire model and for individual parameters. I estimated probabilities of type I error by use of parametric models and by randomization ($n = 5000$) (Manly, 1991). Following the logic of Gilbert (1989) and Sokal and Rolf (1981), I used ordinary least-squares regression even though the independent variables were measured with error. I also converted unduplicated counts of females with COY into normalized ranks. This allowed me to employ parametric models as non-parametric procedures (Iman & Conover, 1979; Potvin & Roff, 1993).

The serial nature of these data also posed potential problems. I dealt with this issue by introducing an independent time variable ($t = 1, 2, \dots, 14$) (Seber, 1977) and by testing for remaining first-order autocorrelation with the Durbin-Watson test (Durbin & Watson, 1950). The time term was also of interest as a surrogate for population trend (Harris, 1986c).

My analysis covered the period 1977–1990 and did not include more recent years because I lacked information to calculate some independent variables after 1990. I also used individual-year counts of females with COY, rather than three-year sums, because independent variables were calculated by year, and to avoid additional problems with serial autocorrelation. This approach also more closely reflected hypothesis (1).

I calculated the probability of over-harvest (P_{oh} ; $d_c > 6\%$) for a plausible spectrum of proportions (i.e. ratios) of known mortality (p_d) and population size (p_p) relative to their respective totals.

$$P_{oh} = [(p_{pmax} - (p_{pmin}d_e/d_c))(p_{dmax}d_c/d_e) - p_{dmin}]2^{-1} / [(p_{pmax} - p_{pmin})(p_{dmax} - p_{dmin})] \quad (2)$$

where d_c is the calculated mortality rate (in this case 4%), d_e is the threshold to over-harvest (6%), and $p_{p,dmax}$ and $p_{p,dmin}$ are the maximum and minimum proportions, respectively, considered for analysis. P_{oh} can be recalculated if these bounds change. The equation can also be solved for d_c and d_a so that P_{oh} can vary as a function of these factors.

I chose 0.1–0.9 as the range of proportions for both mortality and population size and, for lack of information to the contrary, assumed that the true combination of

proportions had a uniform probability of occurring within these bounds. It is very unlikely that real values lie outside these extremes, and this range also contains existing point estimates (Knight & Eberhardt, 1985; Montana Department of Fish, Wildlife & Parks, 1986; Aune & Kasworm, 1989; Pease & Mattson, unpublished data). Perhaps more important, an assumed uniform distribution is conservative with respect to errors potentially leading to the unsustainable killing of bears (Shrader-Frechette & McCoy, 1993).

RESULTS

The conceptual model summarized in Fig. 2 reveals a number of factors unrelated to grizzly bear population size that potentially affect unduplicated counts of females with COY. The model presents an argument that is consistent with accepting hypothesis (1), and is potential grounds for concluding that three-year sums of unduplicated females with COY are not closely related to the number of adult females in a population. It is therefore potential grounds for reaching the same conclusion regarding the relationship of minimum population estimates to total population size. All of the parameters possibly influencing key relationships (human effort, attitudes, and awareness, and the distribution and abundance of bear foods and other bear cohorts) could vary among years with little or no relationship to numbers of reproducing females (Mattson *et al.*, 1992, 1996; Johnson & Snepenger, 1993; Reading *et al.*, 1994). Moreover, none of these extraneous sources of variation is controlled in deriving and applying unduplicated counts to calculations of allowable mortality (US Fish and Wildlife Service, 1993; Knight *et al.*, 1995). However, this assessment by first principles is strengthened by the statistical examination of data from the Yellowstone ecosystem that reflect on the influences of sightability and research effort.

Results of the regression analysis were also consistent with accepting hypothesis (1). Unduplicated counts were related to aggregate sightability and to hours of observation flights (d.f. = 3/9, $F = 7.62$, $p = 0.008$, and $R^2 = 0.717$; by randomization $p = 0.006$). This model was fitted to data that did not include an outlying observation for 1989. The model was still significant including 1989 ($p = 0.029$; $p = 0.023$ by randomization), but the observed value for 1989 was much less than predicted, and had a Cook's D value far larger (> 1.6 times) than any other. There was also a biological rationale for removing 1989 from the analysis, given that this year followed singular and extreme fire conditions during 1988 (approximately 560 000 ha burned (Schullery, 1989)), coupled with a failure of the white-bark pine *Pinus albicaulis* seed crop. As implied by the negative residual, less than expected cub production could be anticipated the following year under these scenarios (e.g. Mattson & Reinhart, 1994).

Table 2. Estimated regression parameters by randomization and by use of ranks in parametric models and tests for parameters = 0 for the relationship between annual counts of unduplicated grizzly bear females with COY (normalized ranks) and aggregate sightability, hours of IGBST observation flights, and sequential years. Results are for the Yellowstone ecosystem, 1977–1990, excluding 1989 ($n = 13$)

Parameter	Standardized coefficients	Parametric model wt ranks		
		<i>t</i>	<i>p</i>	<i>p</i> ^a
Sightability ^b	1.39	3.53	0.006	0.004
Observation flights (h)	0.67	2.52	0.032	0.029
Sequential year	-0.99	-2.10	0.065	0.065
Intercept	—	1.68	0.126	

^aBy randomization ($n = 5000$).

^bScores from the first principal components, derived from annual numbers of bears on moth sites, numbers of radio-marked adult females, % of relocations at which these females with COY were seen, and these sightings as a % of the total from the entire radio-marked sample.

Standardized regression coefficients and *t*-tests for whether parameter estimates = 0 (Table 2) suggested that unduplicated counts were positively and most strongly related to aggregate sightability and secondarily related to hours of observation flights and sequential year. As expected, the partial relationship to hours of effort was positive. The relationship to year was negative. If an explanation of residual variation did not substantially change the partial relationship of unduplicated counts to year, the result would be consistent with a declining rather than increasing population (Harris, 1986c). This contrasts with the results of Eberhardt *et al.* (1994) and Knight *et al.* (1995). The intercept was not different from 0, suggesting that the model could explain even very small annual counts of unduplicated females with COY. The Durbin-Watson *D* statistic = 2.26 ($D \approx 2$ indicates that there is no first-order autocorrelation (Durbin & Watson, 1950)). I therefore assumed that the analysis was not confounded by first-order autocorrelation.

My results were also consistent with accepting hypothesis (2). Even with the mortality ceiling (d_c) at an ostensibly conservative level of 4%, there was still a 29% probability that an actual death rate > 6% could occur for the range of conditions that was considered. This assumed that recorded mortality was at maximum allowable levels and that there was a uniform joint distribution (Fig. 4). Under the least optimistic conditions, where $p_p = 0.9$ and $p_m = 0.1$, actual mortality rate (d_c) = 36%. Conversely, under the most optimistic conditions, $d_c < 1\%$. By this assessment, mortality rates used in calculations of allowable mortality would need to be < 2.1 and 1.6% if the risk of allowing excessive mortality (P_{oh}) were to be reduced to < 10 and 5%, respectively. It is important to note that these figures include no buffer against error in tallying unduplicated females with COY from total observations. Earlier this error was shown to more likely increase rather than decrease the level of allowable mortality. Error and uncertainty in estimating reproductive interval and the proportion of reproducing females are also not considered.

DISCUSSION

Wildlife managers and researchers have long recognized that indices of population size will accurately reflect *N* only if bias related to such things as effort and setting is somehow controlled (e.g. Grinnell, 1914; Dice, 1931). This can be achieved through prior design and corrective models, including such approaches as double sampling (Caughley, 1974; Eberhardt & Simmons, 1987). Similarly, any index that exhibits a complex and highly contingent relationship to the parameter of concern is not a good candidate for reliable information (Eberhardt, 1978). Although unduplicated counts of females with COY might uncritically appear to have a simple relationship to population *N*, the conceptual model shows that this is potentially not the case. Furthermore, the model shows that several factors, currently not controlled either through design or correction after the fact, could affect this relationship.

The results presented here are consistent with accepting hypothesis (1), that unduplicated counts of females with COY vary primarily because of variation in search effort and variation in sightability of this class. Even so, several alternate models could be constructed, and just because the specified model was not rejected does not make it true (Quinn & Dunham, 1983). Likewise, unduplicated counts and population *N* could be highly correlated not only to each other but to effort and sightability. Notwithstanding these reservations, the results presented here are cause for cautious use of the existing approach to calculating allowable grizzly bear mortality for the following reasons.

1. It is more fruitful to judge competing hypotheses in terms of their relative defensibility rather than simply the possibility that one or the other might describe a system. Posed as two competing hypotheses (Chamberlin, 1965)—(a) unduplicated counts are correlated with population *N*, and (b) unduplicated counts are a function of factors with no direct relationship to *N*—(b) is better supported by these results than is (a). Furthermore, the

position implicit to (a) has little scientific utility because there will probably never be the information (i.e. reliable annual estimates of population N) to directly test it (cf. Platt, 1964). Even though (b) is not the singular alternative to (a), it is the one with the best conceptual and statistical support to date.

2. Bear populations are especially vulnerable to overharvest. Inherently low population growth rates caused by late sexual maturity, small litters, and relatively long inter-birth intervals make population recoveries slow and tenuous (Miller, 1990). The described approach to calculating sustainable mortality is being applied to grizzly bear populations in the contiguous US that are not only legally threatened (US Fish and Wildlife Service, 1993) but also vulnerable because of varying degrees of isolation (Mattson *et al.*, 1995). This situation thus leaves little margin for error; any approach must accordingly minimize discrepancies between calculated and actual mortality rates if managers and society do not want to incur high risks of unintended population declines.
3. It is also important to realize that all errors and uncertainties are not of equal consequence to society (Shrader-Frechette, 1991; Reckow, 1994). Erroneously concluding that a bear population has increased is far more serious than erroneously concluding that it has declined (Miller, 1990). The former error can result in unintentional extirpations while the latter merely faces managers with the problem of managing more bears than had been anticipated.

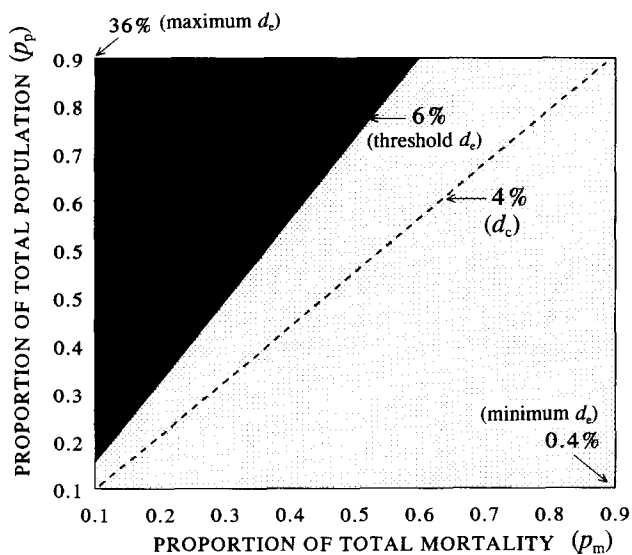


Fig. 4. The relationship of expected mortality rate (d_e) to the proportions of known mortality and population size to their respective totals (p_d and p_p , respectively), given a 4% calculated mortality rate (d_c) and ranges of 0.1 to 0.9 for both p_d and p_p . Extreme d_e s for $d_c = 4\%$ are < 1 and 36%.

Calculating maximum allowable mortality as 4% of three-year sums of unduplicated females with COY is, by common scientific and social standards, not conservative. Three-year sums are likely to vary with sightability and search effort, and with no known relationship to population N . Furthermore, because reliable annual information on p_p and p_d is lacking, there is additional risk of precipitating unintentional population declines, even assuming that unduplicated counts were unbiased and accurate indicators of N .

Recommendations

Logically, management decisions and plans are made in ways that minimize the risk of costly mistakes (Ludwig *et al.*, 1993; Reckow, 1994). The calculation of sustainable mortality for low-density grizzly bear populations living in largely forested environments will probably always be fraught with uncertainty and plagued by a corresponding lack of reliable estimation techniques. Managers may therefore have to continue relying upon indices such as unduplicated females with COY as a basis for calculations (Harris, 1986c). The trick will be to use this metric in ways that reduce risk to tolerable levels and without needing the costly data collection that is often associated with use of a corrective model.

There are two measures, taken together, that could contribute to this end; (1) reduce the mortality rate used in calculations and (2) incorporate uncertainty into the minimum estimate of adult females. As shown earlier, rates of 2.1 and 1.6% could reduce the risk of allowing unsustainable mortality to 10 and 5%, respectively. Even so, this only considers potential variation in the ratios of known mortality and population size to their respective totals and is contingent upon the simplifying assumptions made in this analysis. Given a different range of conditions and a different level of acceptable risk, other rates could be calculated using an appropriate solution to eqn (2).

However this does not remedy the potential for errors in determining 'unduplicated' counts or in estimating the reproductive cycle of adult females and their proportion in the population. In the case of unduplicated counts, some of this uncertainty could be accommodated by calculating confidence intervals (CIs) that are based on some agreed-upon preceding time interval and, given a conservative approach to the bias towards overestimation, by using the lower bound of the CI as a multiple of the estimated reproductive interval. If variation residual to the model tested above (28%) is ascribable to error and n corresponds to the number of years sampled for each estimate (i.e. = 3), then σ_x could be estimated as:

$$\hat{\sigma}_x = \sqrt{0.28\hat{\sigma}^2/3} \quad (3)$$

For example, 90 or 95% CIs could be calculated for the mean, based upon annual counts minus the number of observed adult female deaths each year, over three years

preceding and including the current year. The lower bound could be multiplied by the reproductive interval (in this case = 3) to estimate the minimum number of adult females represented by these observations. In 1990, this approach would have given an estimate of 47.4 and 44.8 females, at 90 and 95% confidence, respectively, for the Yellowstone ecosystem; 89 and 84%, respectively, of the 53 females calculated by rote summation. Similarly, applying 2.1 and 1.6% death rates in eqn (1) to 47.4 and 44.8 adult females gives maximum allowable annual mortalities of 3.5 and 2.5 bears; 47 and 33%, respectively, of the 7.5 bears calculated using 53 females and a 4% rate. Using the current standard that provides for no more than 30% of allowable mortality to be females (US Fish and Wildlife Service, 1993), these alternate calculations would allow for no more than 1.0 and 0.8 dead females per year, respectively.

However, even with these remedial measures some critical issues remain unresolved. For one, the use of 6% mortality as a standard for sustainability is open to question. Uncertainties in the long-term future (Mangel & Tier, 1994), the potential for deviation from assumptions behind the 6% standard (Harris, 1986a), and variation in the environmental conditions that often drive grizzly bear mortality (e.g. whitebark pine seed crops in the Yellowstone ecosystem (Mattson *et al.*, 1992)) argue for a more conservative standard. Uncertainty and potential bias in estimates of reproductive interval and the proportion of reproducing females have also not been addressed. Again, the resolution logically entails deriving unbiased estimates for each parameter and using the conservative bound from their respective confidence intervals (the lower for reproductive interval and the upper for proportion of adult females) in the calculation of allowable mortality. I have also not directly addressed risks of population decline or extirpation, but only the risk that mortality could exceed 6%. These parameters are of fundamental importance to management, and consequently worth directly investigating prior to adopting any approach to calculating allowable mortality for grizzly bear populations in the contiguous US.

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