

APPENDIX K

MODELING SUSTAINABLE HARVEST RATES FOR GRIZZLY BEARS

Richard B. Harris
Montana Cooperative Wildlife Research Unit
University of Montana

Part 1. Data Requirements

The ideal model for determining allowable harvest rates for a grizzly bear population would incorporate the following information:

1. Natality rates (preferably age-specific). In bears, natality rates are actually made up of 3 components:
 - a. Litter size
 - b. Breeding interval
 - c. Age at first reproduction
2. Age-specific survival in the absence of hunting
3. Relative vulnerability to hunting by age and sex class
4. Initial age-structure, and
5. Response of rates #1, #2, and #3 to lowered density caused by hunting ("density response" or "compensatory response").

Of these, only #1 is available for more than a very few grizzly bear populations. Age-specific survival rates are available only for the unhunted Yellowstone area population. We can make reasonable guesses at #3, based on general knowledge of bear behavior and hunters, but we have no hard data. The initial age-structure is generally unknown, although an appropriate stable age distribution can be simulated if #1, #2, and #3 are known. We have very little information on #5. McCullough (1981) modeled compensatory responses in the Yellowstone population of 1959-1972. The work of Fowler et al. (1980) and Eberhardt and Siniff (1977) has provided guidance to modelers regarding the expected response of vital rates of populations of large mammals to changes in density.

Further, the concept of sustainable yield is itself valid only in a probabilistic way. Given enough time or enough variability in vital rates, any harvest will eventually drive a model population to extinction. However, some harvest rates do so with a vanishingly small probability, or require longer times to do so than are reasonable to consider. Additionally, Harris (1984) has shown that the concept of sustainable yield is not independent of the size

of the population in question. Smaller populations were shown to decline at slightly smaller proportional harvests than were larger populations.

Part 2. Modeling sustainable yield of grizzly bear populations using a stochastic simulator.

Sustainable yields of grizzly bear populations were simulated using a stochastic, age-structured simulation model which I term URSIM. Details of the model are available in Harris (1984). The following gives a summary of the procedures and results.

A grizzly bear simulation model was built in 1984 for purposes of examining age-structures of harvested samples. The analysis of age-structures appeared in Harris (1984). Here, I used the identical model to examine sustainable yields, focusing on the stable portion of the sustained yield curve (Fig. 1). The vital rates used in this modeling effort were identical to those in Harris (1984), and are summarized in Table 1. These rates were intended as average birth and death rates of typical southern interior grizzly bear populations, and were written using data from Montana (Jonkel 1982, Aune and Stivers 1983, Martinka 1974, Craighead et al. 1974, Knight et al. 1983, Knight and Eberhardt 1985) and British Columbia (McClellan 1983, Mundy and Flook 1973). Relative vulnerabilities to hunting were guessed, based on discussion with grizzly bear biologists, and knowledge of home range size (e.g. Bunnell and Tait 1980) and legal status (e.g. protection of females with cubs). A review of model assumptions is appended.

In Harris (1984), 4 slightly different mechanisms of population regulation were modeled. For this exercise, I used only 1; the "specific model" termed DMADM in Harris (1984). In this "specific model", all 3 natality functions (age at first reproduction, litter size, and breeding interval) are considered density-independent, i.e., they are influenced by yearly changes in carrying capacity (assumed to represent favorable and unfavorable years), but are not influenced by the density of the population relative to its carrying capacity. Survival rates of all sex/age classes are density-dependent. Survivorship of males younger than 4 years and independent of their mother is a function of the number of males older than 4 years in the population. Survivorship of all other sex/age classes is a function of the total number of animals in the population. This model closely resembles the view of population regulation of bears suggested by Bunnell and Tait (1981). In building a separate survivorship function for sub-adult males, I intended to mimic the compensatory processes thought to occur when adult males are removed from a population (e.g. Kemp 1976, Young and Ruff 1982). Populations simulated using this model were intermediate in their resilience to harvest compared to the other 3 used by Harris (1984).

Methods

Ten independent unharvested age-structures were generated for starting the simulations. Each was generated using the same parameters: carrying capacity was set at 475, the carrying capacity of adult males was set at 76 (.16 of K, a value found earlier to be the mean proportion adult males of simulated populations, Harris 1984), and environmental variability was modeled such that 95% of yearly carrying capacities varied from 380 to 594. In specifying K, it should not be concluded that I claim to know what the equilibrium number of animals in any given area is. The simulation model requires specification of K because density-dependence operates with respect to K. The value 475 was chosen to produce sustainable harvests at population sizes near those estimated by Dood et al. (1985). It was expected that the variability of yearly carrying capacities would reduce the actual number in the population from the 475 figure; preliminary simulations suggested that unharvested equilibrium would occur at about 450. Thus, only populations from 445 to 455 were considered candidates for the initial age-structures. The 10 actually averaged 448 (s.d. = 3).

Each of these 10 age structures was then harvested for 60 years at 20, 22, 24, 26, 28, 30, 32, and 34 animals per year. Mean harvest rates were computed starting at year 20, when it was assumed age-distributions would have stabilized in response to harvest.

Results

None of the 50 simulations at harvests of 26 per year or higher produced sustainable yields because all populations declined chronically. Instantaneous rates of change (r) of the 10 simulations at each harvest were as follows:

Instantaneous rate of change (r)

Harvest per year	Mean	Standard Deviation
26	-0.0349	0.0125
28	-0.0402	0.0199
30	-0.0481	0.0161
32	-0.0666	0.0132
34	-0.0744	0.0158

None of the simulations at harvests of 20 or 22 per year declined chronically. Three of the simulations at a harvest of 24 per year produced population extinction; 3 others had significantly ($p < .001$) negative trajectories during years 20-60, and were judged to be on their way to extinction. The remainder of this paper deals with those simulations

using harvests of 20-24 per year only, because those harvested at 26 or greater never stabilized to allow computation of average harvest rates.

Table 2 summarizes the results of simulations performed with 20-24 animals per year harvested. There are 2 ways to interpret these results: i) in terms of the harvest rate, irrespective of sex of the animal, and ii) as separate harvest rates for males and females.

i). Overall harvest rates. Simulated harvests of 6.35% of the total population or less did not lead to population decline. At mean harvest rates of 6.6%, 6 of 10 populations declined chronically. Thus, the maximum sustainable yield (defined as the hunt that had 10% or less chance of producing chronic decline within 60 years) of these simulated populations was apparently between 6.35 and 6.6%. A lower probability of decline would have required harvests of less than 6.35%. Note that these harvests consisted of approximately 69% males; harvests with higher proportions of males would have had higher sustainable yields; those with lower proportions would have had lower sustainable yields. Note also that the standing population was approximately 60% females, due primarily to the predominately male harvest.

ii). Separate sex harvest rates. Proportional harvest of males were much higher than of females. Mean female harvest rates at 20 animals per year were 2.94%; at 22 animals per year they were 3.54%. The 4 non-declining populations harvested at 24 per year had female harvest rates of 3.6%; the 6 that declined had female harvest rates of from 3.8 to 7.7%. Non-declining populations had male harvest rates averaging 8.8 to 11.2% (20 to 24 per year harvested). It appears that simulated populations were much less sensitive to male harvest rates than to female harvest rates.

Implications

It appears that up to approximately 6.5% of a grizzly bear population having similar properties as the modeled populations may be harvested without causing declines. Note however, that among this population's attributes are relative vulnerabilities to harvest highly skewed toward males. The average proportion of males in harvested samples was usually close to 70%. Viewed another way, the number of females harvested appeared to be critical. Harvests of 3.5% of the female segment did not lead to extinction; harvests of 3.6% did. It appears that a safe practice would be to keep harvests of females in populations similar to those modeled at 3% or below.

The maximum overall sustainable man-caused mortality rate derived here is greater than the 3% suggested by Sidorowicz and Gilbert (1981) for the Yukon Territory, and

the maximum female sustainable man-caused mortality is greater than the 2% recommended by Tompa (1984) for British Columbia. Both Sidorowicz and Gilbert (1981) and Tompa (1984) used more conservative estimates of population-wide natality rates than the present effort. The maximum sustainable mortality rates presented here are slightly greater than the 4.5-5.9% suggested by Cowan (1972, p. 353) as appropriate for grizzlies in North America.

Review of Assumptions

The model considers only a single, isolated population. Because no ingress or egress is possible, dispersal is equivalent to death. The environment in which the population exists is abstracted into the single variable K. All biotic and abiotic factors that affect the potential size of the population (e.g. prey species, competing species, availability of denning sites, berries, carrion, etc.) are subsumed by K. Further, variation in K is considered independent of population size, that is, populations are incapable of reducing their carrying capacity (e.g. by overgrazing). The carrying capacity varies each year independently of previous years, i.e. serial correlation and cycles are not modeled. As well, the variability in K is assumed proportional to K (i.e. distributed log-normally), with relatively good and poor years equally likely. Finally, the 13% coefficient of variation for year K is assumed representative of ecosystems for southern interior grizzly populations.

All hunting occurs in the fall, no spring hunt is modeled. The number killed, rather than the effort expended, is considered constant each year. The implicit assumption is that, at least over a broad range of bear densities, grizzly bear hunters exhibit no functional response. The hunt modeled is opportunistic rather than trophy-oriented. Relative vulnerabilities by age/sex class are determined by inherent behavioral properties of bears, as opposed to conscious selection by hunters (except for legal protection of family groups). Age/sex specific behaviors that result in different relative vulnerabilities are also assumed independent of both bear population density and hunting pressure.

Life-history events that actually occur over a period of time are condensed into essentially instantaneous events, each occurring only once per year, and always in the same order. In nature, deaths probably occur at all times of the year; the model condenses natural mortality into the period between fall hunting and spring family breakup. This order creates a small amount of compensatory natural survival following a hunt, because mortality is lower when acting on a slightly smaller post-hunt population than an unhunted population.

Responses of density-dependent rates are assumed to follow the general pattern for large-mammals described by Fowler et al. (1980). Thus, populations below the level at which density effects are felt have intrinsic growth rates close to the maximum biologically possible. Specific birth, death, and vulnerability to hunting rates are based as closely as possible on empirical data. In some cases, the best available data are weak or non-existent. Rates with the weakest supporting data include survival rates (particularly for orphaned cubs and sub-adults), relative hunting vulnerabilities, and values for all rates when the population is greater than K.

Finally, genetics is not treated. Inbreeding depression, as well as founder and bottleneck effects leading to loss of genetic diversity, while important considerations for conservation of the species, are assumed not to materially affect the age-structures of hunted samples.

Implications for Management of Grizzlies in Montana

The state of Montana has managed the harvest of grizzly bears under a quota system for the past few years. This modeling effort can aid in developing quotas of sustainable yield when population size can be estimated. Two types of quotas may be used:

Population quotas (defined as the proportion of the entire population that can be removed annually by man without causing chronic decline) cannot be greater than about 6.5% of the total population if mean harvests are at least 70% male. If mean harvests are less than 70% male, quotas of 6.5% of the total population may lead to chronic decline. With small sample sizes typical of Montana grizzly bear removals (15-25 yearly) it may take some years before sample sizes are large enough for harvest sex ratio statistics to be reliable. One approach to insure that sex ratio is sufficiently weighted toward males is to require that the lower bound of a specified (binomial) confidence interval around the sampled sex ratio be greater than 70%.

Female quotas (defined as the proportion of the female segment of the population that can be removed annually by man without causing chronic decline) should not exceed 3% of the female segment. An additional unknown in generating female quotas is the proportion of the population estimate made up by females. Sex ratios obtained in the field from trapping are known to be biased, but the exact amount of bias is usually unknown. However, the simulations suggest that grizzly bear populations exposed to moderate harvest levels with males much more vulnerable than females stabilize at approximately 60% females (Table 2). Thus, it seems reasonable to calculate allowable female mortality assuming 60% females in the standing population. Maximum

allowable man-caused losses of females under these assumptions would then be

Population estimate X 0.60 X 0.03

If a sport hunting season is desired, this argues strongly for management efforts at producing harvests heavily weighted toward males. Hunting seasons in early spring or late fall may aid in keeping harvests predominately male.

Managers should keep in mind that the model considers only a single, homogenous population while real populations may vary geographically in recruitment, mortality and harvest pressure. Thus for example, while a 3% or less population-wide removal rate of females should not cause a population-wide decline, some sub-populations may decline while others may expand. Further, it must be emphasized that the values presented here are approximations derived from a modeling effort. Total mortality quotas based on these values may be above or below the maximum sustainable if harvest parameters misrepresent the response of a particular grizzly bear to total mortality, or if population estimates to which the total mortality rate are applied are inaccurate. The guidelines are intended for maximum sustainable harvest management, and may or may not be appropriate for other management goals.

Table 1. Vital rates used in URSIM, the stochastic model to simulate grizzly bear populations. Sources from which rates were approximated appear in text. Accuracy of the estimations of sustainable yields depend on accuracy of these rates.

Recruitment Functions

Age at 1st reproduction:	5	6	7	8
Percent:	65%	26%	9%	1%
Mean age at 1st reproduction:	5.50			
Litter size:	1	2	3	
Percent:	19%	55%	26%	
Mean litter size:	2.07 cubs			
Breeding interval:	2	3	4	5 (years)
Percent:	14%	63%	20%	2%
Mean breeding interval:	3.09 years			
Mean cub/reproductive female/year:	.670			

Average Natural Survival Rates *

Age	Mean Survival	
	Females	Males
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0	91.4%	91.4%
1	91.4%	91.4%
2	88.0%	88.0%
3	77.4%	77.4%
4	90.0%	90.0%
5	95 %	95 %
to		
12	95 %	95 %
13	90 %	90 %
to		
20	90 %	90 %
21	75 %	75 %
to		
24	75 %	75 %

Hunting Vulnerability

	Relative Vulnerability to Hunting
Cub with mother	0.05
Older juvenile with mother	0.20
Lone female, age 0-4	2.00
Lone female, age 5-24	0.80
Female with young	0.20
Lone male, age 0-4	7.00
Lone male, age 5-24	1.00

* These rates are based on maximum survivorships, which occur at population levels below carrying capacity. The rates for ages 0-4 are composite averages of rates applied to young with mothers and young on their own for whatever reason.

Table 2. Sustainable yields and sex ratios from populations harvested at 20, 22 and 24 animals/year. Populations harvested at 20 and 22/year were stable over the 60 years of simulations. Tabulated values for simulations at harvests of 26 animals/year are for the 4 stable populations only because 6 simulated populations declined chronically, preventing calculations of sustainable yield. All entries in the table are means.

Statistic	Harvest/year (all animals)		
	20	22	24 (stable)
Sample size	10	10	4
Overall harvest rate	5.37%	6.35%	6.60%
Female harvest rate	2.94%	3.54%	3.60%
Male harvest rate	8.85%	10.40%	11.24%
Percent males in harvest	69.55%	68.88%	68.65%
Percent females in population	60.33%	60.44%	62.17%

SUSTAINED YIELD CURVE

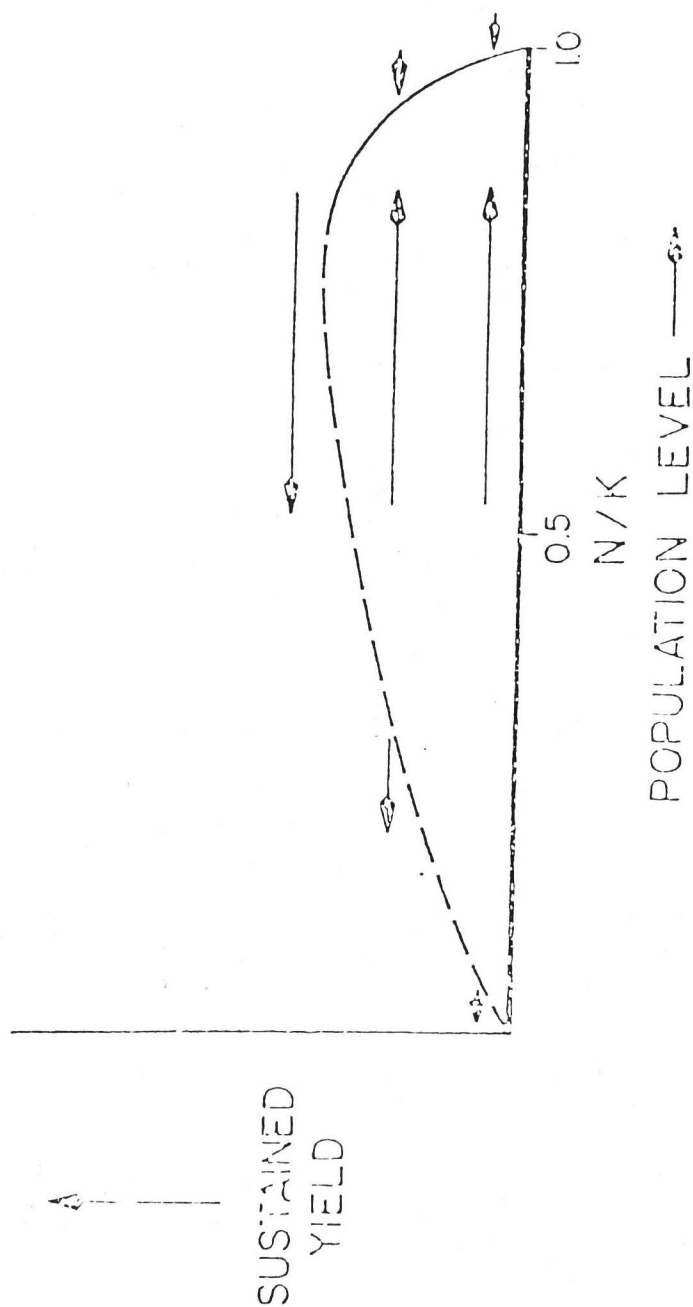


Figure 1. A generalized sustained yield curve, showing trajectories of populations. Populations along the descending right-hand portion (solid line) are stable; those along the left-hand portion (dashed line) are unstable and either decline to extinction or increase to the right-hand portion. This study identified the top of the curve for simulated grizzly bear populations.

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