

BEARS IN MODELS AND IN REALITY — IMPLICATIONS TO MANAGEMENT

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Abstract: The use of computer simulation models as an aid to understanding of biological data was demonstrated using a number of simulated bear populations. Data from black (*Ursus americanus*), brown (*U. arctos*), and polar bear (*U. maritimus*) populations were employed. Population models without feedback were used to compute mortality isoclines as a function of reproductive measures and to document the unreliability of age structure as an indicator of population growth form. A simple Leslie matrix projection was modified to include the effects of population density and hunting. The resulting models provided a consistent explanation for some of the sex and age ratios reported in the literature. The importance of spatial and temporal distributions of hunting pressure were documented, and management implications of hunting patterns, population biology, and dispersion of bears were summarized.

Of the enormous amount of detail known about bears, not all is amenable to simulation modeling; similarly, not all modeling techniques are appropriate to simulation of bear biology. Here we deal with the intersection of bears in models and reality. Our scope is broad taxonomically but narrow ecologically. We present analyses of black, brown, and polar bear populations but limit ourselves largely to the examination of population dynamics. Analyses are extended to encompass some relations with habitat through the influences of habitat on man as hunter. We limit our discussion largely to the simplest forms of models, those adapting the Leslie matrix formulation without feedback. Models incorporating more biological relationships of bears and thus more complexity are treated in Bunnell and Tait (1978). The approach involves (1) a brief review of the nature of models, including their advantages and disadvantages; (2) documentation of the usefulness and limitations of the basic form of population projection, the Leslie matrix; and (3) a summary of the implications of these analyses to research and management. The major emphasis is towards delimiting the intersection between bears in reality and in models, and thus towards finding ways in which models can facilitate our actions in the real world.

All models are simplified representations of reality and, in their broadest sense, include any set of simplifying assumptions or abstractions. The key to successful modeling lies in developing the appropriate abstraction and aggregation of the real system. This process of simplification has inherent advantages and disadvantages. The major advantages are straightforward — it is quicker, socially more expedient, and far less costly to explore the consequences of research or management activities in a model than in the real world. On the other hand, it may prove extremely dif-

ficult to determine whether the simplification adequately represents reality (Bunnell 1973, 1974). Because the process of abstraction or simplification attempts to grasp the essence of biological relationships, the ideas in ecological models, whatever their mathematical nature, are almost always nontrivial. One consequence is that the results of such simplification are not always intuitively obvious (see Fig. 2 for an example). A second consequence is that the concepts may not be amenable to rigorous analytical techniques. The implications are best explored by mimicking (simulating) the biological responses.

All models of population dynamics invoke the simple tautology that changes in population size are due to the net change in rates of immigration, emigration, deaths, and births. The models make assumptions about the rules that modify these rates. Rules for change are applied to a population at time t that produces the population size at time $t + 1$, to which the rules are again applied for as long as the projection continues.

Population $t \rightarrow$ rules for change \rightarrow Population $t+1$

Clearly, the important factors are the assumptions made concerning the rates and the rules for changing these rates. Furthermore, the rules must be sufficiently general to apply to any interval of time. Rules we have invoked are discussed in association with specific models.

Many of the concepts explored in this paper evolved from discussion with C. Jonkel, A. Pearson, K. Scoullar, and I. Stirling. S. Buckingham prepared the figures. The development of models for bear populations was supported by a grant to F. L. Bunnell from the British Columbia Fish and Wildlife Branch as part of the Computer Assisted Resource Planning Program.

POPULATION MODELS WITHOUT FEEDBACK

Our theme is that even the most simple models can be used constructively to both bound and extend our understanding of bear population dynamics. First, we use a very simple, biologically incomplete model of population projection, the Leslie matrix (Appendix) to demonstrate the utility and limitations of a modeling approach. This simplest model applies constant sex- and age-specific survival rates to the number of bears in each age-class to generate the number of bears in the next oldest age-class in the next year of the projection. The number of cubs is calculated by applying constant age-specific natality rates to the number of female bears in each age-class. We treat the assumptions of such models explicitly. Explicit treatment can place boundaries on the population responses that are biologically possible and can *explain* seemingly counterintuitive observations, thus increasing our insight into the dynamics of bear populations.

Bounding the Biologically Possible

Following the rationale presented by Stirling et al. (1976), a near-absolute upper limit on the harvest rate can be generated by assuming that all mortality is due to hunting and that the mortality rate is constant for all age-classes. Cubs are assumed to die only if the mother is part of the kill. The mortality rate due to hunting is balanced against the natality rate essential to generate a stationary (nondeclining) population. The computed

average mortality rate is thus the upper limit to the sustainable rate of harvest. Fig. 1 illustrates isoclines of the upper limit of maximum sustainable rates of harvest for populations with different average natality rates and different average ages of first reproduction. The natality rate is for reproductive females and is computed by dividing the average litter size by the interval between reproduction. Using this formulation, it is easy to compare populations of black, brown, and polar bears.

For example, a brown bear population in which females first breed at age 6.5, first reproduce at age 7, have an average litter size of 1.5, and breed every 3 years (natality rate = $1.5/3 = 0.5$) can sustain no greater harvest than 10.7 percent per year. Similarly, a black bear population in which females conceive at age 2.5, reproduce at age 3, and produce a litter of 2.0 cubs every 2 years (natality rate = 1.0) can sustain an absolute maximum rate of harvest of 23 percent per year. Note that these values are for maximum sustainable *mortality*. If the brown bear population was experiencing a 6 percent mortality in addition to hunting mortality, the harvest rate could be no greater than 5 percent per year. Isoclines such as those in Fig. 1 can be developed for other population measures; their use lies in providing some limits to what is biologically possible.

Exploring Counterintuitive Observations

The life table dilemma. — Even the simplest models, by enforcing explicit treatment of the inherent assumptions, often produce counterintuitive results. Gross (1972) has demonstrated this point elegantly for simple models of maximum sustainable harvest that incorporate density-dependent feedback. The phenomenon, however, is general and applies to the simplest models of population dynamics — life tables and survivorship curves — employed in wildlife management. Consider as an example the 3 age structures presented in Fig. 2. Each curve has been plotted, in classical fashion, relative to a juvenile base of 1,000, and represents 3 consecutive years of the same projected population. Although the numbers depict a representative, unbiased sample, a manager confronted with such data could easily be deceived. One obvious interpretation is that the population suffered somewhat less mortality between years 1 and 2 and then experienced heavy juvenile mortality between years 2 and 3. In short, the data might suggest a potentially dangerous situation if conditions in year 3 persist.

In actuality the population is thriving. The changes experienced by the population are nearly the opposite of those inferred from the sample. Actual changes are

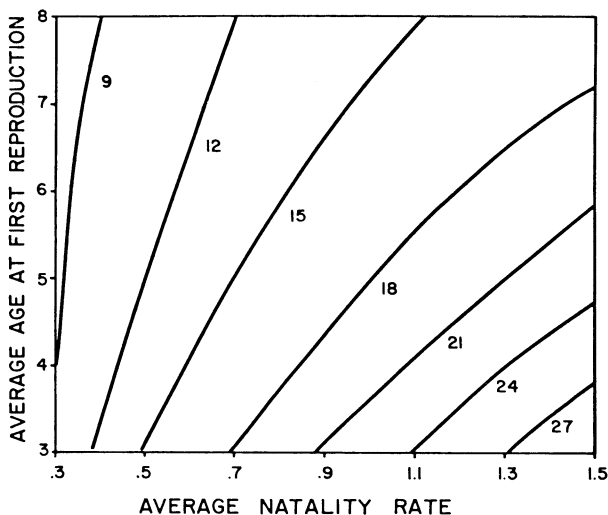


Fig. 1. Isoclines of maximum sustainable mortality (percent/year) as a function of average age at first reproduction and average natality rate (litter size/years between litters).

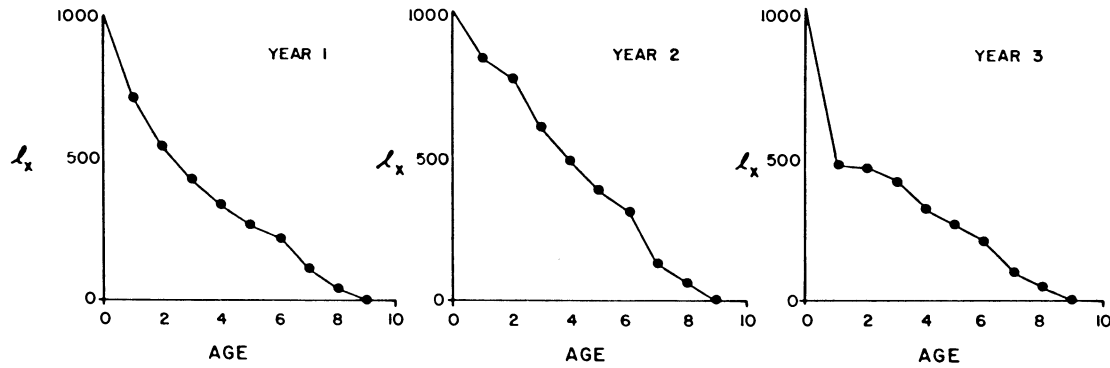


Fig. 2. Unbiased and representative samples of age structure from subsequent years in a hypothetical population. (The survivorship curves are from the population in Table 1).

summarized in Table 1 and result from the following modifications of rates of survival and natality:

- Year 1 to 2: decline in first-year survivorship from 0.7 to 0.6, with concomitant reduction from 0.5 to 0.33 in young/females of 2+ years of age.
- Year 2 to 3: first-year survivorship back to 0.7 from 0.6, and young/females back to 0.5 from 0.33.

The apparent high juvenile mortality is the result of the relatively large recruitment into the first-year age-class (Table 1).

Caughley (1974) addressed a simpler but analogous problem treating sex and age ratios in ungulates. He concluded that (1) what is occurring within a population is not intuitively evident from sex and age ratios, and (2) the growth form of a population cannot be determined from these ratios. The results of Fig. 2 imply a broader conclusion: In general it is not possible to infer from a single age structure or series of age structures what has happened in the past to generate the

current structure of a population. Nor is it possible to predict what will happen over the next few years. It is not our intent to generate an aura of hopelessness, but to distinguish potentially futile exercises from useful ones.

Incongruent sex and age ratios. — There are several phenomena common to black, brown, and polar bear populations where simple models can reconcile seemingly incongruent observations. One broad area concerns differences in the sampled sex and age ratios of hunter kill and actual populations. We consider 2 phenomena: (1) In heavily hunted bear populations where selection by the hunter is predominantly for males, the sex ratio of the kill is close to parity. (2) A preponderance of males in the harvest generally implies a preponderance of females in the population. Both of these phenomena superficially appear to be counterintuitive.

Consider the first situation in which a heavily hunted population experiencing high selectivity for males shows an even sex ratio in the kill. Males may be 3-4 times as vulnerable as females to hunting, females with cubs may be legally protected, and still the sex ratio of

Table 1. Parameters and unbiased samples of these parameters for a changing population. (Unbiased sample is illustrated in Fig. 3.)

Age-class	Underlying parameters		Population numbers			Unbiased sample		
	Survivorship	Young/female	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
0- 1	0.70	0	100	70	98	100	100	100
1- 2	0.77	0.1	70	60	49	70	86	49
2- 3	0.80	0.5	54	54	46	54	77	47
3- 4	0.80	0.5	43	43	43	43	61	44
4- 5	0.80	0.5	34	34	34	34	49	34
5- 6	0.80	0.5	27	27	27	27	39	27
6- 7	0.50	0.5	22	22	22	22	31	22
7- 8	0.50	0.5	10	10	10	10	14	10
8- 9	0		5	5	5	5	7	5
9-10			0	0	0	0	0	0
Total			365	325	334	365	464	338

the total kill can (and most likely will) be close to even. Expressing the intuitive observation, Pearson (1975:75) noted that "Inasmuch as two out of every three mature female grizzlies should be protected from hunting because they are accompanied by cub(s) of the year or yearling young, there should be significantly fewer females than males harvested." In fact, the apparent incongruity is a natural and unavoidable consequence of heavy hunting.

Fig. 3a illustrates the age distribution of male and female bears in a heavily hunted population in which the males are about twice as vulnerable to hunting as females (i.e., the probability of an individual male bear being harvested is twice as great as the probability of an individual female being harvested). Prior to the hunting season, the first legally hunted age-class contains equal numbers of males and females. We assume that the sex ratio at birth is even and that natural mortality factors do not discriminate between young males and females. Because males are twice as vulnerable to hunting as females, twice as many males from the first hunted age-class appear in the harvest (Fig. 3b). Next year there will be fewer males than females in the next older age-class. Eventually the age-class of the males will be only half the size of the female age-class. The sex ratio of the harvest of that age-class will be even. The sex ratio of the harvest of all older age-classes will favor females because there will be few older males left to hunt. The total female harvest could thus equal the total male harvest and the first counterintuitive phenomenon is clarified.

A simpler rationale is to extend the concept of a heavily hunted population to assume that *all* mortality is due to hunting — every bear born eventually appears in the harvest. Since equal numbers of both sexes are assumed to be born, equal numbers must be harvested. This latter explanation, valid also for populations in which 1 sex is more vulnerable to hunting, obscures the underlying dynamics of the age distribution and the effects of changing sex ratios in the population.

Now, the second counterintuitive phenomenon mentioned is no longer counterintuitive. The population illustrated in Fig. 3a is predominantly female, with an even sex ratio in the kill. Males constitute a large portion of the harvest in the younger age-classes (Fig. 3b). In a population in which the harvest contains a greater proportion of males than in that illustrated in Fig. 3, conditions are similar except that some females are not harvested and die a natural death. Under such conditions, we would observe an even greater proportion of females to males in the population.

Fig. 3a,b was constructed from a simple Leslie matrix form of model, using parameters estimated from harvest data of a black bear population in North Carolina (Collins 1974). The population was assumed to be stationary and to be experiencing a constant rate of mortality due to hunting. Thus, the mortality estimate could be generated by regressing the log of the number of bears in the harvest on age. The age structure observed by Collins (1974) and the structure predicted by our estimation of mortality rates are summarized in Table 2. Mortality rates estimated by re-

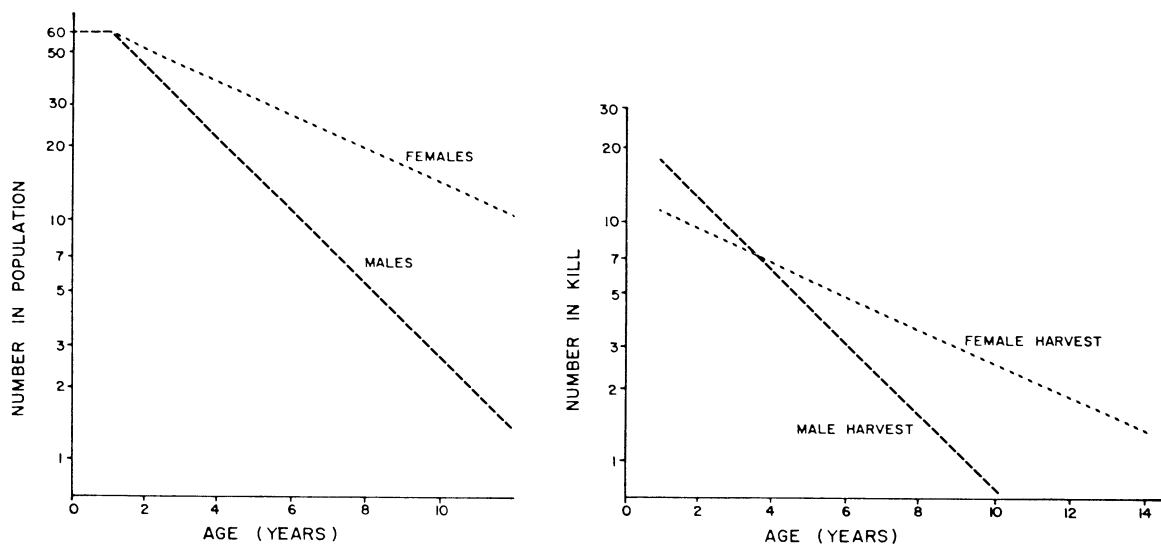


Fig. 3. Simulated age structures in the population (a) and kill (b) of a stationary bear population experiencing constant mortality due to a hunting.

gression are 30 percent per year for males and 15 percent per year for females. The regression model accounts for 80 percent of the variation in mortality rates of males and 76 percent of the variation in mortality rates of females.

Table 2. Observed and predicted age structures of black bears.

Age-class (years)	Numbers of males		Numbers of females	
	Observed ^a	Predicted ^b	observed ^a	predicted ^c
0.75	3	25	4	13
1.75	32	18	12	11
2.75	12	13	5	9
3.75	6	9	9	8
4.75	8	6	5	7
5.75	2	4	10	6
6.75	5	3	8	5
7.75	1	2	3	4
8.75	3	2	7	3
9.75	1	1	3	3
10.75	1	1	1	3
11.75		1	3	2
13.75	1	0		
14.75	1	0	1	1
15.75			1	1
17.75			1	1
21.75	1	0		
22.75	1	0		

^aObserved values are from Collins (1974: Table 2).

^b $Y = 32.7e^{-0.35 \text{ age}}$; $r = 0.89$.

^c $Y = 14.59e^{-0.16 \text{ age}}$; $r = 0.87$.

There are 2 independent estimates of the relative vulnerability of males and females to hunting. The first estimate is simply the ratio of the number of males of the first harvested age-class to the number of females of the first harvested age-class, 32:12 or 2.7. The second estimate is given by the ratio of the average instantaneous mortality rates, assumed to be the sex-specific harvest rates. The instantaneous mortality rates (regression coefficients) are 0.35 for males and 0.16 for females, a ratio of 2.2. It thus appears that male black bears in North Carolina are about 2.0-2.5 times as vulnerable to hunting as are females.

The general pattern depicted in Fig. 3 is a recurrent theme in the literature of hunted bear populations. Harvests of brown bears on the Kodiak Islands, for example, had a sex ratio of 188 males to 100 females (Troyer 1961) whereas the sex ratio in the population was even for the younger age-classes and was 36 males to 100 females for bears 4 years old and older (Troyer and Hensel 1964). Erickson (1964) reported that although the verified sex ratio in black bear harvest data from Michigan was not significantly different from even,

there were more male than female cubs shot and more female than male animals shot in older age-classes.

In Washington, Poelker and Hartwell (1973) noted that the average age of 135 known-age black bears was 3.7 years for males (maximum age, 14) and 6.6 years for females (maximum age, 27). They also reported a sex ratio of 100 males to 69 females in the 23,000 bear kills by sport hunters between 1967 and 1971. In their only sample of the population, as opposed to the kill, the sex ratio was 100 males to 138 females, not statistically different from even. On the basis of these observations, Poelker and Hartwell (1973) suggested a sex ratio of 100:100 for black bears in Washington, with a slight imbalance in favor of males. We conclude from our analyses and simple models that the sex ratio in the population is probably significantly biased in favor of females. The major assumption necessary to account for these observations is that hunter kill is a large portion of total mortality. The isoclines of Fig. 1 illustrate the maximum total mortality that populations can sustain and suggest that in many hunted populations, harvest does dominate the total mortality rate. The assumption has been addressed more explicitly for polar bears and grizzly bears by Stirling et al. (1976).

We conclude that the apparent incongruities between sex and age ratios of heavily harvested populations are natural and unavoidable consequences of the population dynamics of bears.

Exploring Alternative Hypotheses

We present 1 example to illustrate the manner in which the simplest models can be utilized to examine alternative hypotheses relevant to the same data. We have chosen the study of Pearson (1975) as our example because it contains sufficient data to provide a workable framework. The relevant data are life tables generated from kill data for male and female grizzlies in the Yukon Territory and the Mackenzie Mountains of the Northwest Territories during 1965-69. The sex ratio in the kill data is 146 males to 100 females. "After reaching sexual maturity the data show an initially elevated mortality rate, more pronounced in males than in females, and a fairly constant rate of 10-11 per cent in males and 15-16 per cent in females with the males having subsequently a greater longevity than the females" (Pearson 1975:62). Pearson noted further that to have a nondecreasing population, given the female age structure of the kill data and the low observed rates of natality (0.25 female yearling/mature female), the average mortality rate for females from their second to their seventh year of life could be no

more than 7 percent per year. This value is less than half the estimated mortality rate of the mature females, 15-16 percent annually.

We play devil's advocate by first rejecting the conclusion that the rate of subadult mortality is only 7 percent, thus forcing a critical exploration of the underlying assumptions. The first assumption questioned was that the hunted population was stationary. A simple population model was "harvested" heavily, causing a decline in the computed population size. The only constraint was that the age distribution of the kill be the same as that observed by Pearson (1975). We found that with a constant harvest rate applied to all adult females, we could not change the subadult mortality rate of 7 percent more than about 2 percent without significantly changing the shape of the age distribution of the kill. Our inability to reject that assumption of a 7 percent subadult mortality rate even in a nonstationary population forced us to examine critically the other assumptions.

The problem, from the point of view of a modeler examining consistency of data, was that too few cubs were being recruited to the population because there were not enough adult females producing cubs. As a result, what few cubs could be recruited required a low mortality rate in order to generate sufficient adults. As Pearson (1975:60) pointed out, the use of kill data in analyses of life tables required "that every bear had an equal chance of being selected." If we assume that female grizzly bears have a declining vulnerability to hunting with age, or equivalently, that a female that escaped the hunt last year has a better than average chance of escaping the hunt the next year, then a number of incongruent observations can be reinterpreted.

Our new assumption is completely plausible biologically. We are assuming that some bears in a population, by virtue of their *behavior* or *location*, are more likely to be shot than others and that they retain this higher vulnerability until they are shot and die. If we then look at the average vulnerability in an age-class from year to year, we find that the average vulnerability decreases as the cohort ages.

One result of declining vulnerability to hunting with age is that the number of bears per age-class in the hunter sample will represent a progressively smaller proportion of the number of bears per age-class in the population, when increasingly older age-classes are considered. A life table generated from such kill data would diminish too rapidly in the older age-classes, and any mortality estimate would thus be too high. It is

noteworthy that the estimated female mortality rate (15-16 percent) reported by Pearson (1975) is 50-60 percent higher than the estimated rate of male mortality (10-11 percent) despite the fact that there are 46 percent more males harvested than females. If hunting is a major source of mortality, males rather than females would be expected to have the higher mortality rate. A consequence of underestimating the number of older females in the population is an underestimate of potential cub recruitment and therefore a low apparent rate of subadult mortality.

Our change in assumption, that the average female has a declining rather than a constant vulnerability to hunting, provides an alternative and consistent interpretation of Pearson's data. We do not have to assume and rationalize a low rate of subadult mortality. Nor do we have the problem of a relatively high female mortality rate with a low female harvest. It should be noted that we have presented only an alternative hypothesis or interpretation. The explanation offered by Pearson is also consistent with the data. The 2 interpretations could most easily be distinguished by an estimate of the sex ratio of the live population. Our interpretation suggests that females would significantly outnumber males, whereas Pearson's interpretation suggests that males would outnumber females.

POPULATION MODELS WITH FEEDBACK

The Leslie matrix form of model treated in the preceding section contains a major weakness that makes it unsuitable for population projection and management planning at all but the most general level. Because the mortality rates and natality rates are constant, the simulated population will either grow exponentially to infinity, decline exponentially to zero, or remain exactly level. The natality and/or mortality rates must change either directly or indirectly with density before a viable or biologically reasonable population can be maintained. A more comprehensive discussion of models treating density dependence in bears is presented in Bunnell and Tait (1978). Here we treat spatial distribution and vulnerability.

We have seen that individual vulnerabilities of animals can produce the kinds of changes in the sex and age ratios of harvest that have been observed. We also suggested age-induced changes in vulnerability as an alternative explanation for patterns observed in some data. Here we explore in greater detail the concept of changing vulnerability of bears as it interacts with hunting.

The vulnerability of bears is the result of the interaction between man the hunter and bear the prey. An understanding of vulnerability thus requires an understanding of both human and bear behavior. Our first model of man as a hunter depicts man as an ambush predator. We do not mean that the hunter remains hidden and motionless but that during a hunt he remains within a limited area while the bear moves over a much larger area. This description approximates the nonresident's method of fall hunting used in the Yukon and elsewhere. Nonresidents generally hunt over short distances from outfitters' camps while the adult male bear is roaming over a home range of 287 km² (Pearson 1975). If we extend the model and consider a hunter randomly entering an area and waiting to encounter a bear, then the probability of the hunter-bear encounter is proportional to the area of the bear's home range.

We can modify the model to a second formulation by allowing the hunter sufficient mobility to move relatively quickly or frequently along a specific route — a road, river, or trail. The probability of encountering randomly distributed bears is then roughly proportional to the square root of the bears' home range. This second model would encompass incidental encounters with bears shot while moving along a road, hunting for black bears from charter boats in Prince William Sound (McIlroy 1972), and spring hunting for grizzly bears along navigable rivers in the Yukon (Pearson 1975). For black bears with their smaller home ranges, the model may approximate the encounter rate for hunters who move consistently along a trail. Both models suggest that the relative vulnerability of male and female bears to hunting should be related to the relative sizes of their home ranges.

When the second model (hunter following a fixed path) is used, the average relative vulnerability of male black bears to hunting is 2.4 times that of females (Table 3). The observed relative vulnerability of male to female black bears in North Carolina was 2.2-2.7

(Table 2). Because brown and black bears seem to maintain permanent home ranges (Jonkel and Cowan 1971, Pearson 1975), the model of man as hunter following a fixed route generates a declining average vulnerability with increasing age.

Fig. 4 illustrates a road (or river) that intersects the home ranges of 2 male grizzlies and 2 female grizzlies. The relative sizes and orientations of the home ranges are taken from Pearson (1975); the road is hypothetical. Grizzly female C is less vulnerable to hunting as a result of her relative isolation from the road. As the vulnerable bears (A, B, and D) are removed, they will

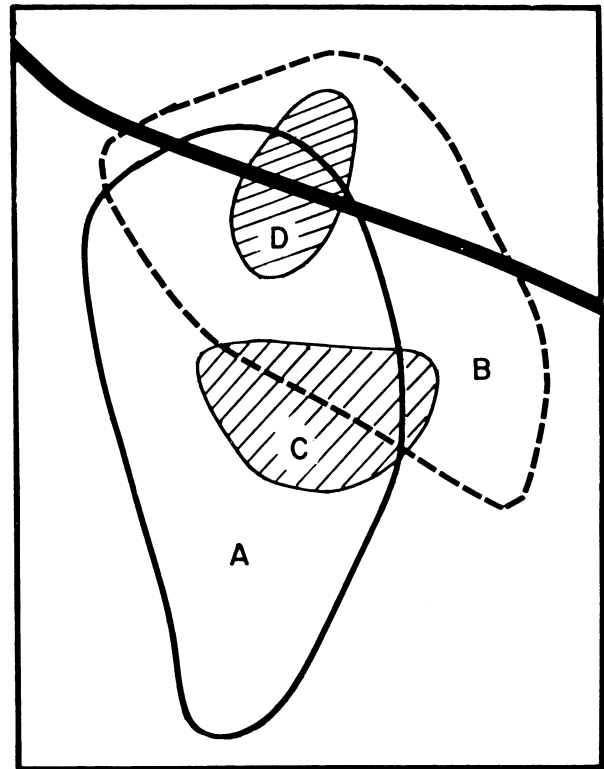


Fig. 4. Idealized home ranges of grizzly bears; A and B are males, C and D are females. Relative size and orientation of home ranges are from Pearson (1975); the solid band or road is hypothetical.

Table 3. Relative sizes of home ranges of male and female bears.

Bear species	Location	Average male home range (km ²)	Average female home range (km ²)	Male/female home range	Square root of male/female home range	Source
Black	Michigan	51.8	25.9	2.0	1.4	Erickson and Petrides (1964) ^a
Black	Montana	30.8	5.2	5.9	2.4	Jonkel and Cowan (1971) ^a
Black	Washington	85.0	5.3	16.0	4.0	Poelker and Hartwell (1973) ^a
Black	Idaho	112.1	34.3-48.9	2.3-3.3	1.5-1.8	Amstrup and Beecham (1976)
Average		-	-	6.7	2.4	
Brown	Yukon	287.0	86.0	3.3	1.8	Pearson (1975)

^aStandardization to km² by Amstrup and Beecham (1976).

be replaced by young animals that will also be vulnerable. Female C, however, may live to an old age. The male bears, on the other hand, as a result of their larger home ranges, are less likely to have home ranges that do not come in contact with the activities of man. A decrease in average vulnerability with a decrease in density due to hunting may provide a density-dependent feedback that will encourage populations at low densities.

The above models of man as hunter are idealized approximations. As hunting pressures increase, or as hunters become more mobile relative to the bears, hunting will cover increasingly extensive areas and the effect of home range will diminish. At the extreme, one can envision the bears as being relatively stationary while man moves about. There would be no apparent differences associated with male and female bears, and the relative vulnerability would be 1. The only method of hunting reported by Poelker and Hartwell (1973) for black bears in Washington that had significantly more females than males in the kill was hunting with dogs. Use of dogs generates a pattern of hunting that had man moving over larger areas rather than along traditional paths. We suggest that the use of dogs reduces the relative vulnerability of male to female bears to hunting to approximately 1 and that the reported sex ratio (100 males to 127 females) in the kill reflects the sex ratio in the population.

Trapping, the only other form of hunting reported by Poelker and Hartwell (1973) that yielded a sex ratio significantly different from even, represents the other extreme model, man as a stationary hunter. The sex ratio of animals trapped was 100 males to 59 females and is consistent with the general difference in sizes of home ranges.

IMPLICATIONS TO MANAGEMENT

We have shown that even an elementary understanding of the population dynamics of bears, particularly as these are affected by man, incorporates some set of simplifying assumptions or model. All implications of even the simplest models are not intuitively obvious (Fig. 2). If management consists of acting knowledgeably on information, the manager must first organize and simplify relevant information into some model(s), then develop understanding of the model(s). By *gaming* or exhausting the implications of his assumptions, we feel that the manager can only improve on the quality of his decisions.

Some of the implications to management were presented in the preceding discussion. Others were not

stated explicitly. For example, the nature of the density-dependent regulation suggests that control of black bear populations that concentrates on the more vulnerable male portion of the population may encourage population growth (Kemp 1976, Bunnell and Tait 1978). Acknowledging only this phenomenon suggests that control must be selective for females. A further implication that can be drawn from the discussion also concerns density-dependent response — the control must be operative at both high and low densities. In populations with a low reproductive rate, unrestricted hunting may permit no effective response at low densities. Quota systems will probably prove an insufficient regulatory device and limited-entry permits may be the only effective means of sustaining populations.

We can summarize many of the implications to management by treating a real-world example and by examining the intersection of the models presented and the data (reality). Consider the problem of managing the polar bear population in the area of James Bay and the Belcher Islands, described by Jonkel et al. (1976:6): “. . . the proposed annual quotas for the area . . . could be as high as 18% of the total population.” From Fig. 1, the maximum sustainable rate of mortality for a polar bear population with an average litter size of 1.7 and age of first reproduction of 7 years is about 11 percent. Examination of the kill data by age and sex reveals that the average ages of female bears killed in James Bay and in the Belcher Islands are lower than the average ages of male bears. This trend is opposite to that illustrated in Fig. 3b, and suggests that females may be more vulnerable to hunting than are males. The kill taken by the Ontario Indians is predominantly female and reflects the sex-specific patterns of movement of female polar bears to their denning area in Ontario. The phenomenon is analogous to that illustrated in Fig. 4. From analyses such as those of Bunnell and Tait (1978), we know that slight overharvesting with a selection for females would produce no appreciable difference in the total population of adults nor in the success of hunters over the short term. The first few years of overharvest would affect the recruitment of the population with a lag of about 6 years before the total population of adults would reveal the impact. Lowered recruitment would not be evident in kill data. After about 6 years, the population would appear to decline rapidly. It is important to note that once the effect of overharvest became evident, it would take many years for countermeasures to reverse the trend.

We chose the example of Jonkel et al. (1976) not because their data have unique implications to man-

agement but because the example represents in a simple fashion the manner in which simple models can facilitate interpretation of data and consideration of management actions. Our plea is for increased examination

of assumption by any means. We feel that simulation models can help to keep managers from joining that group of individuals so aptly described by St. Augustine as those who “saw the effect but not the cause.”

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APPENDIX

Our “models without feedback” have been referred to as a Leslie model because the results could be duplicated by a Leslie-Lewis matrix, the assumptions embedded in our model and the Leslie-Lewis matrix are equivalent, and our results have the same characteristics as a Leslie-Lewis matrix — a constant growth rate and eventual stable age distribution. However, our modeling approach is not strictly that of Leslie (1945) in that we do not use a Leslie-Lewis matrix nor do we use matrix algebra to arrive at our solution. Our model simulates the following set of difference equations:

$$N_{x+1}(t + 1) = S_x \times N_x(t) \quad x = 0, 1, 2, \dots, \text{upper age limit (maximum} = 30)$$

$$N_0(t + 1) = \sum_x N_x(t + 1) \times F_x$$

where

$$N_x(t) = \text{number of females aged } x \text{ in year } t,$$

S_x = proportion of females aged x that survive age x , and

F_x = average number of female offspring of a female of age x .

The upper limit on x is not allowed to exceed 30 and may be lower, depending on the particular survivorship schedule, S_x . As an example, the fecundity rate, F_x , used to represent a bear population with an average age of first reproduction of 5 years and an average natality rate of 0.9 cubs/year (0.45 females/sow) would be:

$$F_x = 0 \quad x = 0, 1, 2, 3, 4$$

$$F_x = 0.45 \quad x = 5, 6, 7, \dots, \text{upper age limit}$$

By systematically choosing alternative values of S_x and simulating, one finds that with $S_x = 0.827$ for all ages (Fig. 1), the population size remains constant.

Density-dependent effects and hunter harvests were incorporated by appropriate time- or density-dependent modifications of S_x .