HARVEST YIELDS FROM MOOSE POPULATIONS SUBJECT TO WOLF AND BEAR PREDATION

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Abstract: A simple conceptual model is presented that links several important variables based on the ratio of moose per predator at equilibrium. This ratio is determined by annual predator kill rates, the potential rate of increase of moose, and mortality of moose due to hunting. This conceptual model guided our thinking in the construction of a simulation model desiged to illustrate how predation by wolves (*Canis lupus*) and bears (*Ursus* spp.) affected harvest yields for humans. A model moose population that displayed sigmoid population growth resulting from density dependent mortality and fecundity formed the heart of the model. Demographic parameters were typical of certain Alaskan moose populations. Maximum sustained yield for bull plus cow harvests fell to 40% of predator free conditions when predation by wolves or bears was intense. Under these conditions, bull only hunts provided an equivalent numerical yield to either sex hunts but had a much higher margin of safety for management errors. Predation intensities that reduced sustained yields for humans to zero were determined; management implications are discussed.

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In recent years moose managers in several diverse areas of North America have had to deal not only with the impact of increasing human pressures on moose and their habitat, but also with problems caused by efficient wild predators that seemed capable of reducing harvest yields for humans. Management strategies have ranged from severe curtailment of human harvests to severe reductions of predators, both with the expectation that future yields to hunters would improve. Often, managers who applied these actions had too few data and too little understanding of the inter-relationships between hunting, predation, weather, forage supplies, and moose numbers, and it was seldom clear how all of these factors interacted to produce variable yields. The net result has generally been poor understanding of: (1) the extent to which a given intensity of predation can reduce harvest yields, (2) when to initiate predator reductions to maximize long term yields, (3) when to stop predator reductions, and (4) what to expect when more than one species of predator is operating.

The purpose of this paper is to address points 1 and 4 above. Our approach was to construct a model moose population that closely mimicked certain natural populations, and then to subject the model population to various intensities of predation and hunting. We felt that this artificial process could provide insight into natural systems if our assumptions were explicit and our models were realistic. We entered into this venture with the belief that simplified abstractions were necessary in order to illustrate certain problems. Accurate, precise field data on necessary parameters covering the full range of possible interactions are not and may never be available. Thus, the reduction of yields by predation is a problem ideally suited to a modeling approach.

MOOSE/PREDATOR/HUNTER INTERACTIONS

Before describing our moose population model, we must first provide a conceptual model of moose/predator interactions and define relationships between hunting and predation. This will be necessarily brief but these topics are central to questions of population regulation, harvest theory, and one's own view of how the world works.

Caughley (1976) discussed the roles of fecundity and mortality in ungulate population dynamics and suggested that many such populations display sigmoid (if not logistic) growth curves. Sigmoid growth implies that a population ultimately reaches an equilibrium that, in the absence of predators, is due to per capita reductions in food supply, reduced fecundity, and increased mortality. Caughley (1976) rejected the notion that ungulate populations are typically cyclic or chaotic; equilibria are features of ungulate population dynamics. This does not deny that equilibria may be dynamic nor does it suggest that fluctuations are rare. It does provide some fundamental concepts to those working with moose population models. Crete et al. (1981) adopted these concepts, as did we.

Caughley (1977) and McCullough (1979) suggested that predators divert deer (Odocoileus spp.) and moose populations to new and lower equilibria than those typical of predator-free environments. This assumes constant habitat conditions that might include the mature vegetation types that many North American moose populations seem to occupy. Again, this is a valuable concept, but it may not apply if human exploitation of predators or prey is excessive or if habitats are transitional. Also, there is little agreement as to the relationships between predation induced equilibria and those created by food shortage and competition.

For obligate predators, nutritional constraints limit predator population growth. Rates of increase for such predators are closely tied, in turn, to per capita biomass of ungulate food supply (Keith 1983; Packard and Mech 1980). Thus, nutritional constraints are imposed by the predators themselves through their impact on prey numbers. McCullough (1979) maintained that equilibrium densities of deer were established on the deer's qualitative characteristics; selection of young, old, and infirm prey by wolves is well known. These relationships are less clear for predators such as bears whose population fluctuations may be poorly correlated with ungulate abundance. The effects of bear predation on prey numbers has received little attention.

Fundamental variables that determine the impact of predation on prey numbers for a one-prey-one-predator system include the number of prey killed per predator per year, the potential rate of increase of prey on an annual basis, and the ratio of prey to predators. If hunting acts to reduce the rate of increase of prey, the proportion of the annual increment removed by hunting must also be known. These concepts treat predation as a force acting to reduce the rate of increase of prey below that in predator-free situations. Predator:prey ratios, annual kill rates, and rates of increase of prey are viewed as fundamental variables that each integrate numerous others including fecundity and survival rates of prey, functional and numerical responses of predators, abundance of alternate prey, and effects of human exploitation on both predators and prey. Viewed in this way, predation loses much of the complexity and mystique that have characterized the existing literature.

Keith (1983) suggested that crude estimates of the number of prey required per predator to prevent prey populations from declining could be determined by:

$$N = \frac{K}{(\lambda - 1)(1 - H)}$$

where N = moose numbers per predator in spring before births

λ = potential finite rate of increase of moose

H = proportion of annual increment of moose removed by hunting

K = number of moose killed per predator annually.

This assumes that predation and hunting mortality are largely additive and do not merely replace other mortality factors.

This provided the elements of a simple conceptual model that underpinned our thinking about moose/predator/hunter relationships.

MOOSE POPULATION MODEL

The model moose population occupied a hypothetical area of 1000 km^2 so that when it numbered about 1000 it approximated predator-free equilibrium densities typical of interior Alaska. Reductions in birth rates began at a threshold precalving density of 0.6 moose/km^2 and reached minimum values at 0.8 moose/km^2 or higher. Mortality rates increased above densities of 1.0/km^2. Decreasing birth rates and increasing mortality as density increased produced sigmoid population growth, a maximum λ of 1.14, and a predator-free equilibrium density of 1.04 moose/km^2. Birth rates, densities, mortality rates, and other population parameters were obtained from the literature and from Van Ballenberghe's unpublished data on moose populations in interior and southcentral Alaska. Age specific mortality was modified when necessary to force the model population to reach equilibrium. Fecundity and mortality parameter values are shown in Tables 1 and 2.

Table 1. Fecundity of model moose.

Precalving Population Density	Births per 1 + female
$<0.6/km^2$	1.15
$0.6\text{–}0.79/km^2$	-0.7 (density[1/]) + 2.2
$\geq 0.8/km^2$	0.8

[1/] Moose/mi^2

Table 2. Age specific mortality of model moose under predator-free conditions.

Age	Fall Density	
	$<1.0/km^2$	$\geq 1.0\ km^2$
0-6 mos	0.50	0.60
6-12 mos	0.10	0.15
1-2 yrs	0.05	0.10
2-3 yrs	0.02	0.05
3-4 yrs	0.02	0.05
4-5 yrs	0.02	0.05
5-6 yrs	0.03	0.05
6-7 yrs	0.03	0.05
7-8 yrs	0.03	0.05
8-9 yrs	0.05	0.05
9-10 yrs	0.07	0.07
10-11 yrs	0.10	0.25
11-12 yrs	0.10	0.25
12-13 yrs	0.15	0.25
13-14 yrs	0.20	0.40
14-15 yrs	0.30	0.40
15-16 yrs	0.40	0.40
16-17 yrs	0.50	0.50
17-18 yrs	0.50	0.50
18-19 yrs	0.50	0.50
19-20 yrs	0.50	0.50

The simulation model consists of data files that store information on moose population parameters and certain model outputs and programs that provide for modifications to the files, calculate moose numbers, and print out selected information generated by the model. The model population has an age distribution of 21 cohorts that have age specific mortality rates. Given certain initial conditions, the model calculates calf crops, calf mortality during summer, and adult and calf mortality during winter, all on the basis of rates that vary with density, and then prints out population statistics for December 1 of each year.

We recognize that age specific mortality and fecundity rates in nature are variables, not constants, and that stochastic, not deterministic, processes are common. But all models must be simplified abstractions of nature that focus on fundamental relationships. Deterministic approaches do not necessarily sacrifice insight; they do confine the spectrum of possible outcomes. We chose to use a model that closely follows processes that characterize moose populations and that employs reasonable data from one part of North America. Our goal throughout was to concentrate on relationships rather than strive for accuracy of predicted numbers.

Hunting and Predation

The model population could be subjected to hunting and/or predation for any series of years chosen by the user. We normally loaded selected cohorts and allowed 50 years to pass in order to approximate a stable age distribution. Hunting and/or predation were then applied for an additional 20 years before we examined moose population statistics.

Bulls, cows, or both could be hunted in the model population. Vulnerability factors were those of Crete et al. (1981) wherein young bulls had the highest vulnerabiltiy. Adult sex ratios were therefore slightly skewed toward females after several years of hunting. For bull only hunting we employed the hunter/effort curve of Crete et al. (1981) such that maximum bull yields occurred at bull densities of 0.18 bulls/km2 or higher. This was used to prevent bull:cow ratios from attaining excessive skewness.

Bear and wolf predation on model moose were considered to have fundamentally different demographic effects. Recent literature (Ballard et al. 1981, Franzmann et al. 1980) suggests that bear predation acts mainly to lower calf survival. Accordingly, we simulated bear predation by increasing mortality rates of calves during their first 6 months and assuming that predation on adults was compensatory. Wolf kill rates were modified from the data of Fuller and Keith (1980). One pack of wolves feeding exclusively on moose during winter was assumed to kill 63 moose annually, distributed among age groups as shown in Table 3. The age distribution of any total kill for wolves was determined from these proportions. Recent literature (Peterson 1977) suggests that annual kill rates are relatively constant for wolf packs of varying sizes. We assumed that all mortality of 12 year-old or older moose was due to predation whenever wolves killed 40 or more moose per year.

Table 3. Age distribution of wolf killed moose by seasonal periods.

	Total kill	
	Summer[1]	Winter
Adults	5	36
Calves	3	19

Age	Proportion of adult kill
1	0.15
2-6	0.15
7-11	0.25
12 +	0.45

[1] Summer = 15 May - 15 September

MODEL OUTPUTS

Of the many possible simulations combining various predation rates and hunting intensities we focused on only those few that best illustrated certain conditions in Alaska. For example, our estimated yields do not include calves because calves are not typically harvested here. Thus, our maximum sustained yields (MSY) are numerically lower than those theoretically possible and lower than those derived for European moose populations (Ericksson and Sylven 1979).

MSY Simulations Without Predators

In the absence of bears and wolves, the model moose population grew to a mean equilibrium of 1042 with a maximum λ of 1.14. As density increased, fall calf:cow ratios fell from a maximum of 42:100 to 25:100 at equilibrium. Sex ratios of adults were even throughout.

By extracting constant annual harvests from the population after it had reached equilibrium, we estimated MSY for bull only hunting and for either sex hunting by the technique of successive approximations, referred to as the sturdy workhorse of wildlife management by Caughley (1976). Density constraints on the harvest allowed bull:cow ratios to fall as low as 32:100 with bull only hunting; MSY of bulls with these constraints was 55. Up to 75 bulls could be harvested annually with bull cow ratios as low as 12:100, but this was not deemed a satisfactory management goal. Mean equilibrium at MSY of 55 was 1019 with fall calf:cow ratios of 25:100. Clearly, the model mimicked natural populations subject to bull harvesting strategies in that total numbers remained high with accompanying low productivity (McCullough 1979).

MSY when both bulls and cows were harvested totalled 100 at a mean equilibrium of 739. Adult sex ratios reflected the higher vulnerability of bulls to hunting and stabilized at 61:100. Fall calf:cow ratios, as expected, were much higher than those occurring with bull only hunting; they averaged 40:100. The well known tendency of populations to decline when harvests exceed MSY only slightly was illustrated when harvests of 105 moose per year were attempted. This produced rapid population declines.

Our assumption that hunting moratility and natural mortality were additive resulted in a conservative MSY compared to natural populations. For either sex hunting, MSY cropped 12% of the prehunt model population of 839 total moose. MSY could be increased numerically if calf harvests were a viable option.

Wolf Predation and MSY

With hunters and bears absent, MSY for wolves was 95 moose annually at a mean equilibrium of 834 moose. Wolf and human MSY differed slightly because wolves and humans selected different categories of moose (as they do in nature) and each category made different demographic contributions.

MSY for humans resulting from bull only and either sex harvests at varying wolf predation intensities are shown in Tables 4 and 5, respectively. When the annual kill for wolves is 60, thus approximating the kill for one pack, either sex MSY for humans is only 40 or 40% of MSY under wolf-free conditions. However, bull-only MSY for humans at the same wolf predation level is also 40 or 73% of that without wolves. Of major importance here is the difference in equilibrium for these two scenarios, 766 vs. 916. With either sex hunting near MSY density, a slight increase in harvest would send the population into a sharp decline accelerated by rapid changes in wolf:moose ratios. With bull only hunting the margin for error is much greater because an increased harvest would only further distort the adult moose sex ratio. In addition, the higher equilibrium with bull only hunting would provide more relative insurance against sharp declines due to altered wolf:moose ratios.

Table 4. Equilibrium moose numbers at various wolf and human kill rates for the model moose population. Human harvests are bulls and cows; bears were absent.

Human Harvest	Annual wolf kill 20	40	60	70	80
20	992	919	893	860	-
30	886	885	880	-	-
40	876	876	766	-	-
50	863	869	-	-	-
60	853	823	-	-	-
70	817	640	-	-	-
80	654	-	-	-	-
90	-	-	-	-	-

Table 5. Equilibrium moose numbers at various wolf and human kill rates. Human harvests are bulls only; bears were absent.

Human Harvest	Annual wolf kill 20	40	60	80	100
20	997	996	913	904	-
30	994	995	912	900	-
40	1006	995	916	-	-
50	999	-	-	-	-
60	-	-	-	-	-

Bear Predation and MSY

Simulated effects of increasing calf mortality on equilibrium number, λ , and fall calf:cow ratios are shown in Table 6. Predation by bears can lead to mortality rates as high as 0.75 during the first 6 months of life for certain Alaska moose populations; this can severely depress numbers, growth rates and calf:cow ratios to the point where additional kills by either humans or wolves could produce rapid declines of moose. For example, at this level of bear predation, MSY for wolves is only 15 at an equilibrium of 699 moose with no allowable harvest for humans.

Table 6. Effects of increasing calf mortality on certain population statistics of model moose. Hunters and predators were absent.

Calf Mortality				December calves: 100 cows	
Low Density[1]	High Density[2]	Equilibrium Number	Maximum Finite Rate of Increase	At Maximum Growth Rate	At Equilibrium
0.5	0.6	1042	1.14	42	25
0.5	0.7	992	1.14	42	20
0.6	0.7	981	1.11	35	20
0.7	0.7	957	1.05	28	20
0.75	0.7	808	1.05	24	20

[1] < 1 moose/km^2

[2] ≥ 1 moose/km^2

We arbitrarily adopted calf mortality rates of 0.7 and 0.7 for low and high density mortality during the first 6 months of life, for our bear scenarios. At these mortality rates with wolves absent MSY for humans is 40 moose per year irrespective of whether bulls and cows or bulls alone comprise the harvest. This was identical to the bear-free scenario when wolves killed 60 moose per year. Similar cautions apply regarding the dangers involved in increasing either sex harvest yields beyond MSY levels.

Finally, when bear predation at our specified intensity is acting, at what level of wolf predation did MSY for humans drop to zero? For MSY calculated for either sex harvests, this occurred at an annual wolf kill of 45 and an equilibrium of 623 moose. However, bull only harvests could still be extracted from such a moose population at a MSY of 20 per year.

MANAGEMENT CONSIDERATIONS

In Alaska during the 1970's several important moose populations declined greatly from peaks reached in the early to mid-1960's. This occurred during a time when demand for moose by hunters was increasing and more emphasis on meat production for subsistence uses was occurring. Wolf and bear densitites were generally high throughout the state. Despite efforts to reduce human harvests after moose declines had begun, moose populations generally continued to decline. In the early 1980's most have stabilized following predator population declines, and one, the Tanana Flats population, has increased dramatically as a result of intensive wolf control applied for several years.

It is not surprising that the rate of decline of these populations was extreme in light of the rapid declines model moose displayed when subjected to slight increases in harvests above MSY. Of the various factors contributing to the moose declines in Alaska, hunting emerges as one of the most significant when cows as well as bulls were shot, and when large numbers of hunters had long seasons and good access to populations that were subject to intense bear and wolf predation.

Modeling exercises point out the need for good data in order to derive accurate predictions and adjust management actions. Data on numbers of moose and predators are critical but are often too expensive or too difficult to obtain over large areas. The rate at which moose management in the north evolves from an art to a science may well depend on how well moose biologists can census moose and predators in the future. Those who gather field data and employ simulation models must strive for better measurements of age specific death rates of moose and better understanding of variations in λ from population to population.

McCullough (1979) suggested that several aspects of cervid management were not at all obvious; some, in fact, were counterintuitive. One less than obvious conclusion that emerged from our simulations is that as predation increases, MSY for bull only and MSY for either sex harvests tend to converge. This is in marked contrast to predator-free conditions wherein yields are much higher when both sexes are harvested.

Finally, one management lesson stands out as a result of these simulations — bull only hunting appears to be the only viable option for moose heavily killed by bears, wolves, or both. Even under intense predation by bears and wolves there is normally some room for bull harvests, albeit at only a small fraction of the yield possible when predators are absent. The manager who recommends a limited bull harvest when predators are dense will not be courting disaster, unlike his colleague who tries to hunt cows as well as bulls.

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