CONSIDERATIONS FOR INTENSIVE MANAGEMENT OF MOOSE IN ALASKA

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ABSTRACT: The Alaska Legislature recently passed a law directing the Alaska Board of Game to identify certain game populations that will be managed intensively. This mandate implies management for maximum sustained yield (MSY), yet managing populations for MSY is problematic. Over-harvest at MSY may cause populations to decrease to low levels, and in the presence of predation low-density equilibria can be established. We recommend maintaining intensively managed populations at densities above the actual point of MSY to avoid potential over-harvests caused by stochastic variation in recruitment. Managing intensively will require better information on factors that influence recruitment and corresponding rates of increase in moose populations, including: age at first reproduction; rates of pregnancy, twinning, age-specific survival, dispersal, and predation; as well as population sex ratios. Population modeling indicates that rate of increase is most sensitive to changes in adult survival, but under most circumstances in real moose populations, calf survival is very important. Factors affecting calf survival include habitat quality, weather, and predation, and the effects of these factors can be minimized by maintaining moose densities slightly above those which maximize recruitment. An intensive management strategy for moose populations in Alaska must include the ability to implement cow harvests, predator management, and habitat management. Aggressive monitoring of population parameters, cause-specific mortality rates, trends in habitat quality, and a knowledge of carrying capacity will be essential to selecting appropriate management strategies. Gaining this information will be expensive but the alternative is potential mismanagement and the risk of population declines.

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The State of Alaska recently enacted legislation instituting a policy of intensive management of selected ungulate populations. The Alaska Board of Game is charged with identifying populations of moose (*Alces alces*) and caribou (*Rangifer tarandus*) for which human consumptive use is the primary management objective. These populations are to be managed intensively to produce and maintain high levels of human harvest. A proposed amendment to this legislation defined harvestable surplus as the number of animals born less the number dying, excluding harvest and predation. At least 50% of this harvestable surplus was to be allocated to human harvest. This amendment was passed by the legislature in 1996 but was vetoed by the governor.

Although not stated specifically in the enabling legislation, this intensive management policy implies management for maximum sustained yield (MSY). In this paper, we review briefly the concept of MSY and the reasons why this is not a viable management objective, and we recommend an alternative for optimizing yields. We also review the factors affecting recruitment in moose populations and discuss strategies for managing these factors. While it is impossible to address comprehensive moose management strategies without considering the effect of habitat, we have purposely avoided detailed discussion of habitat evaluation and management. Knowledge of habitat stability (static or seral communities), plant species composition, site characteristics, and the effects of manipulations on non-target wildlife, among other factors is critical to proper habitat management, but these topics have been reviewed elsewhere (e.g., Eastman and Ritcey 1987, Joyal 1987, Oldemeyer and Regelin 1987). Here we only identify the density-dependent relationships between habitat productivity and population parameters.

MSY AND POPULATION REGULATION

Maximum sustained yield occurs when a population is managed at the point of maximum recruitment. Using a logistic growth equation, this point occurs at a population density one-half (K/2) that at nutritional carrying capacity (K). Population growth below this point is density-independent and recruitment increases with population size solely because of the increased number of breeders. Mortality from hunting and predation are largely additive at these low densities. Above MSY, density-dependent processes regulate population growth by reducing fecundity and juvenile survival. Mortality from hunting and predation are increasingly compensatory as densities increase.

Management of ungulate populations at MSY is not a new concept, as any density-dependent model of population growth can be used to estimate the density at which MSY is obtained (Caughley 1976). Modeling exercises of ungulate populations indicate that MSY occurs at densities greater than K/2, ranging from 56-72% of K (Caughley 1976, McCullough 1979, Crête *et al.* 1981), but we recommend caution in using these estimates. Crête *et al.* (1981) provided the only estimate of MSY for moose (64-72% of K) but they used a definition of K that is less than nutritional carrying capacity. Their estimate of MSY would decrease if expressed as a percentage of nutritional K. In the real world, however, management of ungulate populations at MSY is rarely achieved. The public ultimately decides the density at which ungulate populations will be managed and this often equates to the maximum number of adults that the habitat can support (McCullough 1979).

Management at MSY is fraught with risk (Larkin 1977, Holt and Talbot 1978, MacNab 1985). Although once a mainstay of fisheries management, MSY was found to be too difficult to achieve over the long term and often led to declining stocks (Larkin 1977). Setting a harvest level to maintain a population at MSY can result in over-harvest given stochastic variation in recruitment and nonharvest mortality. A model of moose population dynamics indicated that overharvests at MSY can result in drastic population declines (Van Ballenberghe and Dart 1982). Such an overharvest results in a smaller base population which produces fewer recruits the following year. An identical harvest accelerates the decline and continues the positive feedback loop. Current survey and inventory procedures are not likely to detect overharvests or decreasing densities unless they are extreme, at which point drastic management actions will be required to correct the problem. Crête *et al.* (1981) observed dramatically increased hunter effort at low moose densities in Quebec and suggested that this would serve to reduce harvests at low densities and consequently break the feedback loop. Their data indicate, however, that effort is a sensitive indicator of density only below a density of 0.2 moose/km^2, which is approximately equal to the density at which predation limits moose populations in Alaska and Yukon (Gasaway *et al.* 1992). Thus, this index would be unsuitable for moose management in Alaska.

Predation confounds the management of ungulate populations in many cases, as dynamics of moose and their predators can vary considerably among populations (Van Ballenberghe and Ballard 1994). Three forms of a general model of wolf (*Canis lupus*)-moose dynamics were proposed by Messier (1994) in which the degree of limitation of moose population growth by wolf predation varies. In general, wolf predation rate increases sharply with moose density at low densities (below approximately 0.65 moose/km^2) and becomes inversely density-dependent at moderate to high moose densities. The relative strengths of predation and habitat productivity determine whether predation will limit moose populations at some equilibrium level below K (Messier 1995).

Bear (*Ursus* spp.) predation differs from wolf predation in that it is largely independent of moose density (Ballard and Larsen 1987, Schwartz and Franzmann 1991). The combined effect of bear and wolf predation therefore can increase the potential for low-density equilibria compared with wolf/moose systems (Gasaway *et al.* 1992, Messier 1995). In systems with little human intervention and containing both bears and wolves, moose populations limited at low densities are to be expected (VanBallenberghe and Ballard 1994). These same density relationships, however, can be exploited in certain cases where reduction of predation is desired. As neither form of predation is regulatory at moderate moose densities, reduction of one predator will not trigger an increase in predation rate by the other (Dale *et al.* 1994), which can simplify predator management strategies.

Gasaway *et al.* (1992) demonstrated that predation is capable of limiting moose populations at low densities, and Messier and Crête (1985) provided evidence suggesting wolf predation may perhaps regulate moose densities. Therefore, managers attempting to generate harvests from moose populations must strive to maintain high moose densities and low predator:moose ratios. Yet as moose density approaches K, the adverse effects on population stability of density-independent factors such as severe winter weather increase (Skogland 1985), which can cause catastrophic population declines and re-establishment of low-density equilibria.

MANAGING POPULATION GROWTH FOR OPTIMUM YIELD

When maximum yields from moose populations are desired, we recommend a conservative approach that maintains population size somewhat higher than at MSY and optimizes, rather than maximizes, yield. McCullough (1979) defined such a population level as the fixed removal yield and defined it as "the maximum fixed number of animals that can be removed from a population with fluctuating recruitment without driving the population to extinction" (McCullough 1979:129). A management objective specifying a range of acceptable population densities is superior to an objective of one fixed density and we concur with Gasaway *et al.* (1992) that a range of optimum density with MSY as the lower limit of the range is desirable (Fig. 1). Determining the upper limit of this range is subjective and represents a trade-off between reduced annual yields and increased population stability in the face of stochastic variation in recruitment.

The relationship between recruitment and population density is complex; developing an understanding requires long-term research at varying population densities. Moreover, the definition of recruitment varies depending on the type of hunting allowed. In a system in which calves are harvested, recruitment can be estimated from pre-hunting season calf numbers adjusted for non-hunting mortality. If legally-harvested animals are older than calves, recruitment must be estimated from numbers of yearlings.

The intrinsic rate of increase (r_m) of a population, combined with the number of individuals in the population will determine recruitment. Caughley (1976) identified the factors that influence r_m in ungulate

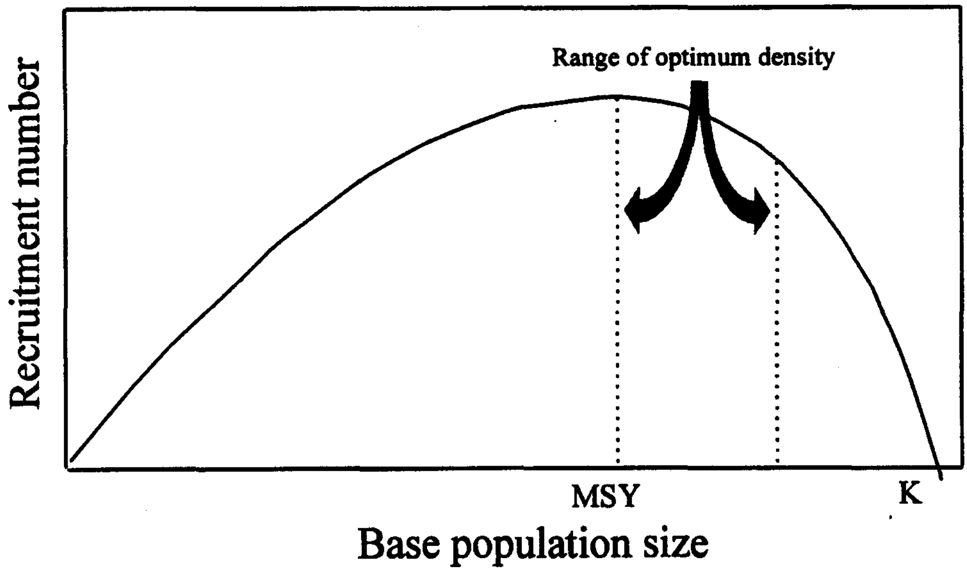

Fig. 1. A theoretical recruitment model illustrating the variability in recruitment number as population size changes. Note that the curve continues beyond nutritional carrying capacity (K), indicating negative recruitment beyond this point. MSY in this model occurs at approximately 0.65K. The range of densities within which moose populations should be managed to optimize yield is indicated (after Gasaway *et al.* 1992).

populations as age at first reproduction, litter size, first year survival, adult survival, sex ratio of young, and sex ratio of adults. We would add pregnancy rate and dispersal (immigration and emigration) to this list, although dispersal affects only recruitment, not r_m.

Reproduction

Age at first reproduction, pregnancy rate, and litter size (twinning rate) affect the number of young born. Age at first reproduction in moose populations is affected by climate and nutrition (Pimlott 1959, Markgren 1969, Schladweiler and Stevens 1973, Boer 1992), and in populations at or near K the first breeding event usually occurs at 2.5 years of age. In populations in which density is well below K, yearlings often breed as well (Gasaway *et al.* 1992, Boer 1992). In a declining population on the Kenai Peninsula that was at or above K, 22% of yearling moose were pregnant as opposed to 96% of cows aged 2-15 (Schwartz and Hundertmark 1993). Cows older than 15 exhibited a 14% pregnancy rate, which indicates the importance of age structure of a population on recruitment number. These data indicate that most "prime-aged" cows become pregnant even when nutrition is not maximized. Pimlott (1959), however, reported a pregnancy rate of 81% for cows older than yearlings from Newfoundland. When segregated by geographic area, pregnancy rates varied from 74-100%.

The environmental and biological factors that influence pregnancy rate and litter size in moose need to be addressed. Caribou exhibit reproductive pauses, with probability of pregnancy related directly to body weight (Cameron 1994). The energetic constraints imposed by poor habitat and nursing of the previous year's calf can thus influence the probability of pregnancy in the following year. Is such a phenomenon present in moose to some degree?

Twinning rate also is influenced by nutrition. Franzmann and Schwartz (1985) studied two adjacent populations, one of which inhabited highly productive habitat (1969 burn) whereas the other inhabited mature habitat (1947 burn). At the peak of habitat quality, the population inhabiting the 1969 burn exhibited a twinning rate of 70%, whereas the estimate for the 1947 burn population was 22%. Five years later, the habitat in the 1969 burn had declined in quality, and the twinning rate declined to 38% (Schwartz and Franzmann 1989). These data demonstrate that twinning rate responds to habitat quality and likely population density relative to K. Improving habitat quality or holding populations below K should successfully increase yield. The latter goal can be accomplished by harvesting cows as well as bulls, which has the added benefit of lowering the mean life expectancy of cows and thus removing relatively non-productive older cows from the population.

Survival

First year survival is related to predation, nutrition of the dam, habitat productivity, and winter weather. Predation by brown (*U. arctos*) and black bears (*U. americanus*) is the primary cause of calf mortality in many moose populations (Ballard *et al.* 1991, Ballard and Larsen 1987). There have been no rigorous field studies to test the notion that intensive bear harvest results in long-term increases in moose density or harvest. Experimental removal of bears, however, resulted in increased moose calf survivorship (Ballard and Miller 1990, Stewart *et al.* 1985). Additional research is needed to address this issue (Boutin 1992). At a minimum, the position of the population relative to K, the dynamics of the habitat (static, improving, or declining in quality), and the causes and extent of all causes of mortality must all be known before predator control is considered as a viable management option (Gasaway *et al.* 1983, Theberge and Gauthier 1985, Schwartz and Franzmann 1989).

Poor nutrition of the dam during pregnancy can lead to perinatal mortality due to lack of vigor in the calves (Schwartz and Hundertmark 1993), although little is known about the extent of this process in moose. Poor habitat productivity and severe weather, primarily deep snow, can cause decreased survival of calves during winter. Moose calves allocate most energy to growth and do not carry large or even moderate fat reserves into winter. Severe energy deficits caused either by poor nutrition or the increased energy expenditure of moving through and finding food in deep snow can increase calf mortality. Management options that would influence first year survival of moose are holding populations below K and aggressive bear management, although the efficacy of this latter strategy is problematic.

Survival of adults is related to nutrition and predation. Mytton and Keith (1981) reported adult survival rates of 0.84 in an unhunted and predator-free moose population in central Alberta, whereas Hauge and Keith (1981) reported a rate of 0.75 in a population in northeastern Alberta that experienced mortality from hunting and predation. Similarly, Gasaway *et al.* (1983) estimated annual survival of moose aged 6-10 at 0.67 in a population in interior Alaska experiencing heavy predation. After wolf control, this rate increased to 0.93. Pre- and post-control rates for moose aged >10 were 0.59 and 0.79, respectively. Gasaway *et al.* (1983) observed that wolf predation held moose populations at a low-density dynamic equilibrium, and that reduction of predation rates allowed the moose to escape the equilibrium. Conversely, Bangs *et al.* (1989) estimated a survival rate of 0.92 for adult females on the Kenai Peninsula, an area inhabited by wolves and bears, and noted that predation was no more common than hunting or automobile accidents as a cause of mortality. Larsen *et al.* (1989) determined that grizzly bears and wolves were the primary and secondary causes of moose mortality, respectively, in southwest Yukon, and that predation was limiting the growth of the population. Thus, reduction of wolf or bear predation in some areas can effectively increase adult survival, but the degree of limitation imposed by predation must be known before predator control can be considered. Even if predator management would be an effective strategy for enhancing certain moose populations, the political and social ramifications of such a policy can preclude its implementation (Franzmann 1993).

Sex ratios

Sex ratio variation among calves can affect population growth but is difficult to document. Schwartz and Hundertmark (1993) observed no deviation from a 1:1 sex ratio in moose fetuses in a wild population near K and cautioned that large sample sizes are needed before drawing conclusions regarding sex ratio variation. Reuterwall (1981) documented temporal and spatial variation in sex ratio of calves harvested in Sweden. The proportion of males in the harvest in any population varied from 51% to 69%. Reuterwall (1981) demonstrated the management implications of sex ratio variation via computer simulation. She estimated that a change in the proportion of male calves in a population from 50% to 55% would result in halving of the population size in less than 10 years if the management strategy sought to keep the population size constant based on an assumption of sex ratio parity. Reuterwall (1981) discussed a number of hypotheses attempting to explain variation in secondary sex ratios but was unable to identify the ultimate cause. Unfortunately, without a better understanding of the causes of sex ratio variation, it is difficult to propose a strategy for management.

The sex ratio of adults is important to population growth only to the extent that it is related to the total number of females in the population. McCullough (1979:141) modeled recruitment in the population of white-tailed deer (Odocoileus virginianus) on the George Reserve, Michigan using adult sex ratios varying from 20:80 to 80:20. All models produced the same number of recruits at MSY, albeit at different population densities. MSY was reached at lower densities when the sex ratio was skewed toward females.

Sex ratios of ungulate populations should be managed to achieve breeding synchrony (Schwartz and Hundertmark 1993). Child and Aitken (1989) and Aitken and Child (1992) documented changes in reproduction with changes in the adult sex ratio of a moose population in central British Columbia. Changes in hunting regulations in 1981 through 1985 resulted in an increase in the number of mature bulls in the population. Another regulation change in 1986 resulted in heavy hunting pressure on mature bulls and subsequently their numbers declined. Based on analysis of conception dates, the rut remained synchronous throughout the studies, but the variation about the mean date of conception increased with a decrease in abundance of mature bulls (Child and Aitken 1989). The proportion of cows bred during the second or subsequent estrus decreased from 17.5% to 7.7% as bull abundance increased. Additionally, the incidence of twinning was correlated with the bull:100 cow ratio (Aitken and Child 1992). Although these data were collected from *A. a. andersoni*, which exhibits a tending bond system of mating differing markedly from the harem mating of *A. a. gigas*, the concept applies equally to both subspecies, albeit at different scales. These data support the management strategies of Bubenik (1972) that not only is a high bull:100 cow ratio important for adequate and timely reproduction, but that the male component of the population must contain an adequate number of "prime-aged" bulls. Breeding synchrony is important from a management perspective because calves born to females bred after their first estrus have less time to grow during the summer and do not exhibit accelerated growth (Schwartz *et al.* 1994). Thus, these animals are at a greater risk of winter mortality than are other members of their cohort.

Dispersal

Dispersal to or from a population can bias attempts to determine population growth rates (Rolley and Keith 1980), which can confound attempts to determine appropriate densities for management. Additionally, moose exhibit limited dispersal, particularly among females (Gasaway *et al.* 1989, Ballard *et al.* 1991, which can affect recovery times of populations that are below MSY. Gasaway *et al.* (1989) demonstrated that creation of productive habitat will cause an increase in population size by increased reproduction of resident moose, but not always by attracting moose from adjacent areas.

Key factors

Modeling efforts have identified adult survival as the most important parameter in determining r_m (Nelson and Peek 1982, Eberhardt *et al.* 1982). For many moose populations in Alaska, however, first year survival clearly is a very important factor affecting recruitment. If populations are at or near K, however, production of large numbers of offspring will not increase recruitment due to the compensatory nature of mortality at high population densities. Bartmann *et al.* (1992) demonstrated a density-dependent relationship between fawn mortality and population density in mule deer (*O. hemionus*) in Colorado. In studies of enclosed populations, fawn mortality due to starvation was directly related to population density. Moreover, in a high-density wild population in which fawn mortality due to predation was reduced via removal of coyotes (*Canis latrans*), starvation mortality increased and total fawn mortality did not change. This compensation among mortality factors at high densities demonstrates that recruitment can be increased by reducing total population size, but not by predator removal.

RECOMMENDATIONS

Management strategies designed to optimize harvest (Table 1) must move a population toward a density that maximizes recruitment. For high-density populations this involves primarily the harvest of females, which will reduce the base population size and increase recruitment through density-dependent processes. For low-density populations a number of strategies are possible depending upon local conditions, all of which must enhance survival of adults and calves. Viable strategies include habitat and predator management, and should be determined through a step-down planning process similar to that developed by Theberge and Gauthier (1985). Population density objectives likely will fall within the range of 60-80% of K. Once a population goal is reached, managing harvest to optimize adult sex ratios and age structure is important. All of these strategies depend on the manager's ability to determine the position of the population relative to current carrying capacity and to MSY.

Strategies designed to achieve these goals may run contrary to prevailing public opinion and therefore can be highly controversial, and are not limited to predator control. For instance, in Alaska all management strategies involving the harvest of cow moose must be approved yearly by the Board of Game. Local citizen advisory committees have veto power over cow seasons within their jurisdiction, a power they hold for no other management strategy. Many communities associate cow seasons with precipitous population declines in the 1970s and are reluctant to approve new seasons.

To manage moose populations intensively, we must be permitted to implement cow

Table 1. A listing of factors influencing rate of increase (*r*) and recruitment in moose and potential management strategies to address these factors.

Factor	Strategy
Age at first reproduction	Hold population below K, habitat enhancement
Litter size	Hold population below K, habitat enhancement
Pregnancy rates	Young age structure
First year survival	
• Predation	Bear management
• Nutrition	Hold population below K, habitat enhancement
• Winter severity	Hold population below K, accept periodic die-offs
• Rut synchrony	Manage for prime bulls
Adult survival	
• Predation	Wolf management
• Nutrition	Hold population below K, habitat enhancement
• Winter severity	Hold population below K, accept periodic die-offs
Sex ratio of adults	Harvest management
Sex ratio of offspring	Unknown

harvests as well as efficient predator control programs when deemed necessary by the Board of Game. Additionally, our ability to implement habitat management within areas identified for intensive management must be increased. Currently, our ability to use these techniques is limited. Increasing the degree of human intervention in these systems will not be successful if managers are precluded from using effective tools.

Intensive management of moose populations will require collection of precise population-specific information concerning population dynamics and density, predator-prey relationships, harvest statistics, the carrying capacity of the habitat, and trends in habitat quality. Increased survey and inventory activities will be necessary in areas slated for intensive management. Research programs addressing the relationship between moose recruitment, predation rates, and habitat productivity, wherein prey and predator population densities are manipulated experimentally, would provide much needed information concerning proper approaches to intensive management. These programs will be labor and cost intensive; however, implementing intensive management programs without reliable information ultimately will lead to mismanagement and the risk of population declines.

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