MOOSE-PREDATOR RELATIONSHIPS: RESEARCH AND MANAGEMENT NEEDS

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ABSTRACT: Since the 1984 Swedish Moose Symposium our knowledge of moose (*Alces alces*)-predator relationships has substantially improved. Wolves (*Canis lupus*), brown or grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and recently, cougars (*Puma concolor*) have been identified as major predators of moose. During the past 2 decades, a number of studies have identified the role of predation as either limiting or regulating moose population growth. However, confusion over misuse-use of terminology has hindered our understanding of these relationships. Regulating factors are composed solely of density-dependent factors which keep populations in equilibrium or cause them to return to equilibrium. Whether a wolf functional response (i.e., per capita kill rate) is, in fact, related to moose density has come under scrutiny. There may be no biological justification for using a functional response in modeling exercises as wolf kill rates appear rather constant over a wide range of moose densities. Wolf numerical and functional responses are curvilinear relative to moose density and may be prey species specific. Knowledge of bear predation is inadequate to accurately model moose population trends. Whether predation regulates or limits moose population growth may be academic if reductions in predator numbers allow managers to increase moose populations and harvest yields. Managers currently have the biological tools to effectively manage moose-predator relationships.

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Ballard and Larsen (1987) and Van Ballenberghe (1987) reviewed the state of knowledge concerning moose-predator relationships at the 1984 Swedish Moose Symposium. At that time the major predators of moose were thought to be wolves and bears. Cougars or mountain lions, where they occur in association with moose, can now be added as significant predators of moose (Ross and Jalkotzy 1996). Our understanding of moose-predator relationships has increased greatly since that Symposium.

LIMITATION VERSUS REGULATION

Both Ballard and Larsen (1987) and Van Ballenberghe (1987) concluded that predation by bears and wolves could be a significant limiting factor of moose populations. Since that time a number of authors including Skogland (1991), Sinclair (1991), Messier (1991), Boutin (1992) and Dale *et al.* (1994) have concluded that misuse of terminology has greatly limited our understanding of predator-prey relationships because biologists were not communicating about the same causative factors.

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Indeed, Van Ballenberghe and Ballard (1994) concurred that terminology had been misused by many investigators and that whether or not predation on moose was a significant regulatory factor was not important to many management biologists. It was clear that predation was a significant limiting factor in many moose populations and could be regulatory. Boutin (1992) suggested that the evidence that predation was a significant limiting factor on many moose populations was "less than convincing." Van Ballenberghe and Ballard (1994) concluded, as had Gasaway *et al.* (1992), that predation by wolves and bears was a significant limiting factor when predator populations were lightly exploited. Otherwise, predation may or may not be a significant limiting or regulating factor depending on ecological conditions.

We utilize the terms limiting and regulating following definitions provided by Messier (1991). By definition, any factor which reduces the rate of population growth is a limiting factor. This definition can include both density-dependent and density-independent factors. However, the point when a moose population is in approximate equilibrium with its long-term natality and mortality factors is regulation, and this equilibrium depends on density-dependent factors. In other words, regulating factors (density-dependent) are a subset of limiting factors (both density-dependent and density-independent factors) (Messier 1991).

The above distinctions have caused confusion in the predator-prey literature. Biologists have not discriminated in the use of these terms and so it is unclear whether a particular moose population is regulated or limited by predation. Most discussion of moose-predator relationships has focused on the role of wolf predation. Identification of bears (both brown and black), and cougars, as major predators of moose has greatly complicated attempts to understand the relative importance of predation in the population dynamics of moose.

BEAR PREDATION

Nearly all authors have considered predation by bears to be a source of density-independent mortality (i.e., non-regulatory). However, the data for this assumption are based largely on several studies conducted in three areas of Alaska (i.e, Franzmann *et al.* 1980, Ballard *et al.* 1981, Boertje *et al.* 1988, Schwartz and Franzmann 1991, Ballard *et al.* 1991, Ballard 1992, Gasaway *et al.* 1992). The majority of this research has been based on two studies where both bear kill rates (i.e, functional response) and bear densities were similar, but moose densities were much different (several fold). Similarly, estimates of the impacts of black bear predation on moose have been greatly impeded as a result of small sample sizes.

Schwartz and Franzmann (1991) demonstrated that black bear productivity responded to increased moose densities and that moose inhabiting better habitats were better able to withstand such predation. Other than this study and that by Ballard *et al.* (1990) which estimated kill rates by sympatric black and grizzly bear populations, we found no estimates of black bear kill rates on moose in the literature.

Identification of bears as significant predators of moose has caused enormous public relations problems resulting in *defacto* bear reduction programs in several areas of Alaska and Canada. To some people, good moose management was equated with bear reduction (i.e, kill a bear and save a moose). Initially, such an approach appears justified because in many populations where sufficient densities of bears exist, bear predation is often a significant cause of both neonate and adult mortality (Ballard 1992). However, very little is known about bear predation, particularly whether compensatory relationships exist with predation caused by wolves. We simply don't know whether bear predation is density-dependent or density-independent nor do we know anything about possible compensatory relationships among individuals within a bear population, between bear species, or between wolf and bear populations. More importantly, we are not sure how to manage bear populations for the sake of perpetuating bears under sustained yield guidelines. Only four studies have attempted to evaluate the effects of bear reduction programs on moose populations.

Ballard and Miller (1990) evaluated the effects of a temporary grizzly bear translocation effort on neonate moose calf survival. Calf survival was significantly increased as a result of a temporary 60% reduction in bear densities, and subsequent yearling survival was high (Ballard *et al.* 1990, 1991). However, causes of moose calf mortality were similar before and after the bear translocation experiment which caused Boutin (1992) to surmise that results were equivocal and that the experiment failed to establish the condition of moose calves at parturition. Recently, Ballard *et al.* (1996) evaluated the condition of moose calves following different winter conditions and determined that indices of condition were similar following severe versus mild winters. It was clear that a temporary reduction in bear densities under the environmental conditions described by Ballard and Miller (1990) and Ballard *et al.* (1991, 1996) resulted in at least a temporary increase in the moose population. Whether such an increase could be sustained remains to be demonstrated.

Following the bear reduction experiment, the Alaska Board of Game liberalized bear hunting regulations over several areas of Alaska in an attempt to increase moose populations (Miller and Ballard 1992). Unfortunately, there was no formal research plan to evaluate the effects of this bear harvest strategy. Miller and Ballard (1992) attempted to evaluate this program and found no significant increase in moose calf survival as a result of an estimated 35% reduction in bear densities caused by liberalization of bear hunting regulations. However, this evaluation was wrought with problems because it was an uncontrolled experiment, and a number of other explanations existed for why moose populations did not respond to reduced bear densities (Miller and Ballard 1992, Ballard 1993).

Similar experiments have occurred in two black bear removal projects. Stewart *et al.* (1985) evaluated the effects of a short-term bear removal experiment in Saskatchewan and concluded that bear removal did not provide lasting effects on moose calf survival. However, Ballard and Van Ballenberghe (1997) concluded that the experiment was not conducted over a long enough period and that there may have been an increase in moose calf survival. In a second experiment, Crete and Jolicoeur (1987) evaluated bear removal and found no significant differences in calf survival among bear control areas, wolf control areas, and non-control areas. Although calf:cow ratios increased by about 38 % following bear removal, they attributed a lack of significant differences to small sample size, sampling variation, and the short-term nature of the experiment. In both cases, it appeared that reductions in black bear densities resulted in increased moose calf survival under a particular set of environmental conditions, but the short-term nature of these studies prevented unequivocal conclusions.

WOLF PREDATION

Several review papers have attempted to synthesize the effects of wolf predation on moose (Boutin 1992; Hayes 1995; Messier 1994, 1995; Van Ballenberghe and Ballard 1994). Research efforts have focused on determining the numerical and functional responses of wolves to estimate predation rates and whether predation regulates moose population growth.

Functional and Numerical Response

Boutin (1992:125) indicated that losses due to wolf predation were equal to or less than other sources of mortality and concluded that "evidence for predation acting as a major limiting factor in most moose populations is less than convincing." Gasaway *et al.* (1992) and Van Ballenberghe and Ballard (1994) concluded that predation was often a significant limiting factor when bear and wolf populations were naturally regulated. All authors subsequent to Boutin (1992) have agreed that further experimentation is necessary to test the hypothesis that wolf predation regulates moose population growth.

Messier (1994) analyzed wolf and moose data from 27 studies and concluded that there was evidence for significant wolf numerical and functional (i.e., per capita killing rate) responses, suggesting that wolf predation was density-dependent and a regulatory factor at low moose densities. He reported that wolf predation was density-dependent from 0 to 650 moose/1,000 km^2 and inversely density-dependent (i.e., non-regulatory) at higher moose densities. Moose populations at higher densities were regulated by food competition and not predation. He predicted that moose densities would stabilize at 2,000 moose/1,000 km^2 in the absence of predators and at about 1,300 moose/1,000 km^2 with only wolves present. When bears were also present he predicted a low moose density equilibrium ranging from 200 to 400 moose/1,000 km^2.

Dale *et al.* (1994) studied the effects of wolf predation on barren-ground caribou (*Rangifer tarandus granti*). They found little evidence of prey switching even at relatively low (i.e., <200 caribou/1,000 km^2) density, and little evidence for a functional response by wolves. Assuming wolves exhibited a linear numerical response to prey density, they concluded that the total predation response was inadequate to regulate caribou population density. They suggested that in multiple predator-prey systems the occurrence of more than one prey species may reduce the potential of wolf predation to regulate ungulate populations. Assuming that bear predation is also density-independent, such predation could negate any regulatory effects of wolf predation at low prey densities. When the predation effect of two predator species is density-independent, then reductions in one predator species at low ungulate densities may only result in small changes in total predation rate. At relatively high ungulate densities, the effect of the second predator species may be greatly reduced due to inversely density-dependent predation. Dale *et al.* (1994) suggested that such a scenario may have occurred in south-central Alaska when wolf reduction resulted in a moose population increase even though grizzly bear predation was the largest cause of neonate moose mortality (Ballard *et al.* 1991). Dale *et al.* (1994:650) concluded that "further knowledge of the occurrence and factors affecting prey switching, such as density-dependent changes in vulnerability within and between prey species, and further knowledge of wolf numerical response is needed to draw firm conclusions."

Recently, the entire concept of a wolf functional response has come under both qualitative and quantitative scrutiny. Mech (U.S. Geological Survey, *unpubl.*) has questioned whether the concept of functional response is even appropriate for large carnivores. The concept of a functional response was first proposed by Solomon (1949) and further expanded by Holling (1959), and Walters *et al.* (1981). Mech (U.S. Geological Survey, *unpubl.*) points out that the functional response concept proposed by Solomon (1949) appears to be quite different than that envisioned by current researchers. For example, Solomon (1949) and Holling (1959) conceived the concept based on experiments such as placing increasing numbers of immobile, indefensible dog biscuits or insect cocoons in front of predators. In these cases, per capita killing rate would obviously increase with prey density until predator appetite was satiated. Mech (U.S. Geological Survey, *unpubl.*) has suggested that prey vulnerability may have more to do with a perceived functional response than prey density. Mech has also suggested that there is no tight relationship between prey density and number of wolves, citing Isle Royale studies as prime examples. Both Keith (1983) and Messier (1995) also alluded to the importance of the functional response in terms of prey vulnerability. Mech (U.S. Geological Survey, *unpubl.*) has pointed out that it may be impossible to relate functional response to the density of vulnerable prey because this would be impossible to measure. Furthermore, most changes in prey vulnerability are usually related to density-independent effects such as weather, and not to changes in prey density. For example, Huggard (1993) found that wolf kill rates were correlated with snow depths, suggesting that vulnerability influences functional response.

A number of authors have suggested that wolf numerical responses are tightly controlled by prey availability (Packard and Mech 1980, Keith 1983, Messier and Crete 1985, Fuller 1989, Messier 1994, Hayes 1995). Hayes (1995) suggested that if wolf numerical response was not tightly controlled by prey availability in multiple predator-prey systems, then wolves could exceed densities predicted on the basis of ungulate biomass. Such populations could then exert high predation mortality and cause prey populations to decline to low densities based upon numerical response alone. If, on the other hand, wolf numerical response was tightly controlled by prey availability then wolves should stabilize at densities at or slightly below available prey biomass (Hayes 1995).

Most studies have concluded that wolf kill rates are negatively correlated with wolf pack size; smaller packs have higher kill rates per wolf than larger wolf packs (Peterson 1977; Messier and Crete 1985; Ballard *et al.* 1987, 1997; Sumanik 1987; Dale *et al.* 1995; Hayes 1995). This finding has significant implications for management. Hayes (1995) suggested that wolf pack number and size is an important factor in determining the impacts of predation on moose. Wolf pairs had relatively large but variable kill rates, thus estimates of the effects of wolf predation could be misleading based upon pack numbers alone. A number of investigators have questioned the use of wolf:prey ratios to assess the initial impacts of wolf predation (Ballard *et al.* 1987, 1997; Theberge 1990; Messier 1994; Hayes 1995).

Prey Switching

Prey switching can have a significant impact on calculating both numerical and functional responses. Several authors have concluded that at least under the conditions which they studied, wolves did not switch between moose and caribou even when the principal prey species was less abundant (Seip 1992, Hayes *et al.* 1991, Dale *et al.* 1994, Hayes 1995). However, wolves appear to prefer certain types of prey. Carbyn (1974) indicated that wolves preferred mule (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) over elk

(*Cervus elaphus*) while Ballard *et al.* (1987) and Dale *et al.* (1994) indicated that wolves preferred caribou over moose. Ballard *et al.* (1997) found that when caribou were unavailable, wolves switched to preying upon vulnerable moose rather than migrating with caribou. However, when moose densities reached very low levels, normally territorial wolves migrated and continued to prey upon caribou.

The relationship between numerical and functional response was summarized by Hayes (1995:91) who stated "A type II functional response rises at a decelerating rate and can not be regulatory without an accompanying density-dependent numerical response (Oaten and Murdoch 1975, Dale *et al.* 1994, Messier 1994). An exponential type III response can regulate prey without a corresponding numerical response because it has a rapidly accelerating phase that allows each wolf to kill an increasing proportion of prey as prey numbers increase." Hayes (1995) studied the kill rates of 21 wolf packs in the Yukon Territory during 1990-1994. Because of the large variation in kill rates among small wolf packs, Hayes (1995) evaluated the functional response for wolf packs >4 wolves and found that kill rates of moose were relatively constant (i.e., 2.2 to 3.4 moose/wolf/100 days) and were not related to moose densities which in his study ranged from 250 to 430 moose/1,000 km^2. By combining his data with Messier's (1994), Hayes concluded that if there was a wolf functional response it must occur rapidly below 200 moose/1,000 km^2. Hayes' (1995) analyses suggested that a low density equilibrium occurred at 70 to 120 moose/1,000 km^2 rather than at the 200 to 400 moose/1,000 km^2 suggested by Messier (1994). He suggested that at these lower moose densities wolf functional response could play a key role in regulating moose numbers to low densities regardless of the shape of the functional response curve. His model suggested that wolf predation would compensate for increased survival caused by reductions in bear predation. Short-term reductions in wolf numbers would result in moose population increases but for these increases to be sustained, on-going reductions would probably be necessary.

Hayes' (1995) model predicted that wolf predation could regulate moose populations in the absence of bears. Both Van Ballenberghe (1987) and Van Ballenberghe and Ballard (1994) suggested that the role of predation in regulating moose populations may be vastly different in ecosystems impacted by humans versus natural systems with minimal human impact. In Hayes' (1995) study the effects of a recovering wolf population following a severe control program may not represent what normally occurs in a natural system where wolf territories are relatively stable. In the latter, where bears also exist, bear predation may have a greater impact than wolf predation, and the presence of both predator species results in a low-density equilibrium (Van Ballenberghe and Ballard 1994). Also, the wolf kill rates reported by Hayes (1995) may have been inflated because calf moose composed a relatively high (i.e., 31%) proportion of the kills.

Person *et al.* (Univ. Alaska, *unpubl.*) concluded from their simulation models that functional response was not an important factor in determining equilibria between moose and wolves. Their analyses also indicated that functional response, if any, occurred only at very low prey densities and that such a response would be difficult to detect because of large variances associated with all estimates. They suggested that rate of prey population increase, the prey population's position in relation to ecological carrying capacity (K), and its position in relation to maximum sustained yield (MSY) dictate the number of wolves that can be supported at equilibrium.

Person *et al.* (Univ. Alaska, *unpubl.*) also suggested that differences in wolf densities were directly related to differences in densities of the primary prey species. Wolves exhibit prey selection regardless of availability of alternate prey and so total prey biomass may overestimate biomass available to support wolves. They suggested that wolf-prey ratios could be used to assess the effects of wolf predation so long as reasonably accurate estimates of annual rates of prey population increase could be obtained.

Most estimates of the relationships between prey and predator densities have assumed a linear relationship between these two variables (Keith 1983, Fuller 1989, Gasaway *et al.* 1992). However, where equilibrium occurs, the relationship and shape of the curve between prey biomass and predator density is probably not linear and may be species specific (Person *et al.*, Univ. Alaska, *unpubl.*).

Marshal (1997) recently argued that the relationships between wolf predation and moose populations may be poorly understood because previous analyses have focused on large scales rather than examining patch dynamics. He reanalyzed data presented by Messier (1994) and determined that linear models rather than curvilinear models explained more of the variation. Using linear functions he determined that at any moose density, wolf predation rates were greater than moose population growth rates. Consequently, wolf predation was anti-regulatory at low moose densities and increased exponentially at high moose densities due to the wolf numerical response. Using simulation modeling he attempted to examine the relationships between wolf predation rate and its effects on subpopulations of moose which migrated between patches and had different subpopulation growth rates based on habitat quality. Although these simulations made a number of questionable assumptions, they do demonstrate how heterogeneous habitat quality could affect the relationships between predation and prey populations.

Marshal (1997) hypothesized that moose could persist at low densities without wolf predation being density-dependent. His model seemed to best fit either the recurrent fluctuation or low-density equilibrium models currently thought to be the best models describing predator-prey relationships (Ballard and Van Ballenberghe 1997). However, he suggested that wolf kill rates (e.g., functional response) continued to increase even at high moose densities which is in conflict with the previously discussed studies in this paper. Marshal (1997) also suggested that there may not be an upper asymptote to the wolf numerical response which also conflicts with previously discussed studies. His model predicted that prey extinctions could occur. He concluded that if predation, and moose densities and dynamics were different over large landscapes, then modeling these situations may be inappropriate. He also suggested that wolf predation could be density-dependent or even regulatory at the patch scale and that current data do not support one theory of predation on moose.

Impact of Severe Winters on Predation Rate

During the past several years there has been considerable debate on the effects of severe winters versus predation on moose population dynamics. Mech *et al.* (1987) suggested that snow depths summed over 3 consecutive years influenced moose and white-tailed deer fecundity and calf or fawn survivability. Messier (1991) questioned these analyses based on an expected progressive impact each year in the population variables following a severe winter. Messier

(1991) suggested that fawn and calf survival were more influenced by moose food competition and wolf predation, rather than snow depths. McRoberts *et al.* (1995) challenged Messier's (1991) conclusions primarily because Messier had smoothed the data. Ballard *et al.* (1996) subsequently determined that there did not appear to be any measurable impact on neonate moose calf blood parameters or weights following a severe winter but adult cows did exhibit reduced parameters. C. C. Schwartz (Alaska Dep. Fish and Game, *pers. comm.*) indicated that adult cow moose within an experimental enclosure in Alaska continued to produce viable calves until after two consecutive winters when food stressed, at which time fecundity declined, partially supporting the conclusions of Mech *et al.* (1987). Both Adams *et al.* (1995) and Mech *et al.* (1995) have subsequently determined that caribou calves born following severe winters were more vulnerable to wolf predation during the first and subsequent years of life than those born following average or mild winter conditions.

RESEARCH NEEDS

Learning Through Modeling

The past two decades have greatly increased our knowledge of moose-predator relationships but much remains to be learned. With the advent of modern desktop computers, the availability of existing data sets, and financial constraints of field programs, modeling has become a common method of attempting to sort out numerical and functional responses, in addition to other complex aspects of predation. Although modeling is a valuable research tool, we must remember that it is just that and that the model is no better than its assumptions. We are aware of no models that have accurately predicted moose population changes in real-world ecosystems. Aside from a number of biological assumptions which may not be valid, and the relative imprecision of many of the parameters which we attempt to measure (Van Ballenberghe and Ballard 1994) there are also a number of statistical assumptions which may be invalid. For example, Messier (1994:482), and apparently Dale *et al.* (1994) used a Michaelis-Menton function which was similar to Holling's disk equation (Real 1977) to examine functional response and a "modified" Michaelis-Menton function to evaluate numerical response. Person *et al.* (Univ. Alaska, *unpubl.*) based their model on a modification of the theta-logistic equation (Gilpin and Ayala 1973). Few field biologists are familiar with these functions and consequently are unable to evaluate the credibility of inherent assumptions. They rarely have the time to critically evaluate all of the background literature on which the paper is based, in particular the statistical papers. Many mathematical approaches have a number of assumptions which are subject to justifiable criticism, and thus, modeling has its limitations in attempting to explain a unifying theory of predator-prey relationships. Models are an attempt to quantify our understanding of complicated phenomena, and in practice, few of these models are ever verified with field data. In this sense, we have made little progress since the earliest attempts to model moose-predator relationships (Van Ballenberghe 1980).

Our review of available literature suggests that the evidence that wolf predation is density-dependent is weak. Evidence suggests that a wolf functional response may exist at moose densities <200 moose/ 1,000 km^2 (Hayes 1995), if it exists at all. Mech (U.S. Geological Survey, *unpubl.*) has questioned whether it is even biologically reasonable for a functional response to exist. Both Dale *et al.* (1994) and Hayes (1995) provided evidence that prey switching by wolves did not occur under the circumstances that they studied. However, Ballard *et al.* (1997) demonstrated that when caribou were the preferred and most available prey, wolves preyed upon them until caribou densities reached very low levels as a result of their migration patterns, at which time wolves switched to moose. These findings could change our views of wolf functional response.

All modeling attempts of wolf-moose relationships in multiple predator-prey systems (e.g., brown bear, black bears, wolves, moose, caribou, deer, elk) have assumed that bear predation is a density-independent form of predation mortality. These assumptions are based upon relatively few studies and may be unwarranted. What if bear predation was density-dependent? To our knowledge no modeling simulations have investigated this possibility. Perhaps facultative carnivores may be more prone to respond to changes in prey density than obligate carnivores. When Ballard *et al.* (1986) modeled wolf-bear-moose relationships it was necessary to add density-dependence to kill rates. Without such an adjustment, moose populations quickly went extinct suggesting that either bear population data or kill rate estimates were grossly imprecise. Recent advancements in bear population estimation procedures (Miller *et al.* 1987, 1997) suggest that estimates of bear kill rates may be the most variable of the estimates. Although expensive, time consuming, and in many cases nearly logistically impossible, additional estimates of bear killing rates over a range of both bear and moose sex-age structures and densities are necessary before we can reasonably attempt to model real systems. Most modeling attempts have focused on wolf predation with only secondary thought to the importance of bear predation.

Another important component of predation that we poorly understand is the compensatory nature of predation among bears and among bears and other species. Gasaway *et al.* (1992) suggested that when both wolves and bears were present, both predator species should be manipulated because predation by one species may be compensated by predation from another. Miller and Ballard (1992) indicated that reductions in brown bears were unnecessary to allow moose population growth in a relatively high density moose population after wolves had been reduced. Failure to achieve increased moose calf survival following reductions in bear density may have been compensated by numerical increases in the wolf population (Ballard 1993). Clearly, if predation is compensatory within and between predator species this could affect the results of predator removal programs. Differences in moose densities and predator densities may dictate which predator species should be manipulated.

There is much debate in the literature concerning the limiting and regulating effects of predation. Identification of predation as a major limiting factor of many moose populations where natural assemblages of predators exist is a significant finding. Although predation may or may not be a regulatory factor it may not matter to wildlife managers attempting to provide additional moose for human consumption (Van Ballenberghe and Ballard 1994). Assuming that the principles of predation closely follow those of sustained yield management (McCullough 1979, 1984) then the benefits to be derived from predator management are strongly related to where a moose population exists in relation to carrying capacity (K) and maximum sustained yield (MSY). Predation to the left of MSY would be largely additive mortality, becoming increasingly compensatory as moose approach K.

Interpreting Predator-Prey Ratios

Wildlife managers currently have the

tools to assess when predation is a major moose mortality factor. Gasaway *et al.* (1983) proposed the use of simple moose-wolf ratios as a guide to interpretation of the importance of wolf predation. Although predator-prey ratios have been widely criticized because they do not incorporate a functional response, recent studies suggest this may not be necessary because either a functional response does not exist, or if it does it occurs at very low moose densities. Wildlife managers rarely rely on just one criterion to evaluate the effects of predation, and most have at least a conceptual model of where their particular moose population may be in relation to K. Wolves can be censused efficiently (Ballard *et al.* 1995), have high reproductive (Boertje and Stephenson 1992) and dispersal rates (Ballard *et al.* 1987, 1997; Hayes 1995), and can withstand relatively heavy rates of mortality (Keith 1983; Hayes 1995; Ballard *et al.* 1987, 1997). However, bear management is more complex (Miller 1990). In situations where moose-wolf ratios are low, multiple species of prey exist, and bear predation is a relatively minor factor, temporary reductions of wolves can elevate moose densities and allow for increased harvests of both moose and wolves (Boertje *et al.* 1996). When moose densities are relatively high and both bears and wolves are important predators, intensive wolf population manipulation may allow a moose population increase without reducing bear densities (Ballard *et al.* 1991, Miller and Ballard 1992). However, there are risks associated with allowing high density moose populations to continue to grow and approach K. When moose densities are relatively low and both wolves and bears are major causes of mortality, it may be necessary to reduce both wolves and bears to allow for a moose population increase (Gasaway *et al.* 1992). Although these management concepts are biologically based, we recognize that sociological and political factors (Stephenson *et al.* 1995) will often determine whether predator management is feasible.

Managing Moose for Human Harvests where Predators are Lightly Exploited

Periodic severe winter weather is relatively common within the range of moose. If predation is a regulating or major limiting factor, its effects can be greatly altered by severe winters. In many cases severe winters have precipitated moose population declines in North America (e.g., Gasaway *et al.* 1983, Ballard *et al.* 1991, Schwartz and Franzmann 1991). After one or several severe winters predation has appeared to accelerate moose population declines. In these cases wolf reduction appears to abate or reverse declining trends and may allow for increased populations of predators and prey, and their uses (Boertje *et al.* 1996). Modeling studies by Van Ballenberghe and Dart (1982) and Vales and Peek (1995), as well as empirical studies summarized by Gasaway *et al.* (1992) and Boertje *et al.* (1996) suggest that bull-only moose hunting can provide near-equivalent yields as either-sex hunting. However, an alternative viewpoint has been presented by Messier (1996) where antlerless hunting can be used to lower moose densities and associated predation rates, and thus stimulate moose population growth leading to increased sustained yields. However, Messier's (1996) results were based upon the observed wolf predation rate and moose density in Quebec which may not be representative of other predator-prey systems. How often predator control may be necessary in such situations depends on whether predation is regulatory or a major limiting factor. In the worse case scenario, periodic long-term wolf reductions may be necessary to maintain management goals, particularly following severe winters. If predation, particularly by wolves is a regulatory factor, available evidence in multiple prey-multiple predator systems suggests that the low-density equilibrium model has the best promise for explaining the role of predation in such systems while in single predator-moose systems the recurrent fluctuation model may be applicable (Ballard and Larsen 1987, Van Ballenberghe 1987, Van Ballenberghe and Ballard 1994, Ballard and Van Ballenberghe 1997).

Marshal's (1997) suggestion that the regulatory nature of predation may be explained by differences in patch dynamics and moose subpopulations warrants further consideration. However, biologists have been striving to manage ecosystems on a more holistic basis, inherently requiring that management occur on large scales. As pointed out by Caughley (1977), a population is a relatively arbitrary concept that depends on the area of interest. Even more confusion may exist when we attempt to define a subpopulation; a term used often to describe a subcomponent of a population. Determination of the regulatory effects of predation at the patch scale may be a useful endeavor for wildlife biologists to undertake because it may provide clues for the management of truly critical habitats (see White and Garrott [1990] for definition of criticalness) where moose are relatively invulnerable to predation.

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