THE ROLE OF PREDATION IN WILDLIFE POPULATION DYNAMICS

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Abstract: The role predation plays in the dynamics of prey populations is controversial. Our understandings of predator-prey relationships is complicated by a multitude of factors in the environment and a general lack of knowledge of most ecological systems. Various other factors, besides predation, may regulate or limit prey populations, and various factors influence the degree to which predation affects prey populations. Furthermore, some factors may create time lags, or even cause generational effects, that go unnoticed. Herein, we review the role of predation in wildlife population dynamics, some of the factors influencing predator-prey interactions, and attempt to indicate where the professional debate currently is focused and where it may need to go to enhance our understanding of predator-prey interactions.

Predation has been defined as individuals of one species eating living individuals of another species (Taylor 1984). The role of predators in the population dynamics of prey species has been investigated for decades, yet determining whether or not predators limit or regulate a prey population remains controversial within the scientific profession (e.g., Erlinge et al. 1984, Kidd and Lewis 1987, Newsome et al. 1989, Sinclair 1989, Sinclair et al. 1990, Messier 1991, 1994, Skogland 1991, Boutin 1992, Pech et al. 1992). Much of the debate results from the multitude of competing variables, including predation, that influence demographics of prey species and the difficulty of conducting large-scale, long-term studies with some degree of control or replication. In a review of studies involving predation on ungulates, Connolly (1978) reported that 45 studies suggested predation was a limiting factor, while 27 studies indicated predation was not a limiting factor on ungulate density. Assessments of the importance that wolf (*Canis lupus*) predation plays in regulating or limiting moose (*Alces alces*) populations varies among biologists. Interactions among moose, forage, and climate have been postulated to determine moose density (Peterson et al. 1984, Mech et al. 1987, Thompson and Peterson 1988). Bergerud et al. (1983), Bergerud and Snider (1988), and Van Ballenberghe and Ballard (1994) considered predation a major limiting factor of moose because moose density was generally below forage carrying capacity. Messier and Crête (1985) and Messier (1991) argued that moose and predator interactions were complex and that the effect of predation varied from density-dependent to inversely density-dependent over the range of moose densities resulting in population cycles, multiple stable states, and predator pits. Skogland (1991)

suggested that the existing data was inconclusive with regards to predation regulating moose, while Boutin (1992) argued that wolf predation as a limiting factor on moose populations was not supported.

In this paper, we will attempt to provide a foundation on predator-prey theory, describe some studies illustrating the roles that predators and other variables can play in the dynamics of wildlife populations (mainly from the carnivore-ungulate literature), and suggest reasons why the debate over the influence predators have on prey populations continues. It is not our intent to critically review all predator-prey studies, but to use certain studies to illustrate aspects of predator-prey relationships.

TERMINOLOGY

For our discussions of predator-prey relations to be fruitful, we need to clarify some terminology. We also should recognize that many of the initial terms and early theories concerning the role predators play in limiting or regulating prey populations were developed by entomologists examining relationships between numbers of parasites needed to regulate invertebrate pest species on agricultural crops. The terms regulating and limiting have often been used interchangeably, with regulation defined as "any density-dependent process that tends to stabilize population numbers over time. The process that causes the change(s) in population size is termed limitation" (Skogland 1991). We consider a limiting factor to be any mortality factor that reduces the rate of population growth (Ballard et al. 2001). We also will try to adhere to using the term 'kill' to denote the essential component of a predator's impact upon prey, rather than the ambiguous terms 'attack, capture, or consume' commonly found within the predation literature. The relationship between the kill rate by a predator and prey density is termed the "functional response." Lotka (1925) and Volterra (1926) provided initial mathematical descriptions of predator-prey interactions, which assumed that the number of prey captured increased in direct proportion to the number of predators. Nicholson and Bailey (1935) proposed the relationship was curvilinear with the kill rate decreasing as predator satiation sets an upper limit to food consumption. Subsequently, Holling (1959) described 3 types of functional responses (Fig. 1). A Type I functional response occurs when the kill rate per predator is directly proportional to prey density. In the Type II response, the kill rate is limited at higher prey densities by satiation of the predator, and is thus curvilinear. The Type III functional response is sigmoid in shape with a lag in kill rate at low prey density due to low hunting efficiency or absence of a search image and an upper limit set by predator satiation. Type II functional responses have been documented between wolves and moose (Messier 1994; Fig. 2), wolves and caribou (*Rangifer tarandus*) (Dale et al. 1994), as well as coyotes (*Canis latrans*) and black-tailed jackrabbits (*Lepus californicus*) (Stoddart et al. 2001). In addition to functional responses, Morris et al. (1958) demonstrated a "numerical response" in which predator numbers increase in response to increasing prey abundance. This numerical response may be from reproduction or immigration. Numerical responses of coyotes to changes in black-tailed jackrabbit (Knowlton and

Stoddart 1992) and snowshoe hare (*L. americanus*) abundance (O'Donoghue et al. 1997) have been documented. Messier (1994) found a numerical response of wolves to changes in moose density (Fig. 3). The combination of the functional and numerical responses represents the "total response." The total response may cause the predation rate to be density dependent at low prey density and inversely density dependent at high prey density (Holling 1959, Messier 1994). In a compilation of studies, Messier (1994) illustrated the total response of wolves to changing moose density.

Other terms commonly used when describing predator-prey relationships are "compensatory" and "additive" mortality. Ballard et al. (2001) defined additive mortality as occurring when the "additional risk of death does not cause reductions in other forms of mortality, but rather increases overall mortality rate." On the other hand, for compensatory mortality, the "additional risk of death causes a reduction in other forms of mortality so that overall mortality either does not change or is less than it would be if additive." Kunkel and Pletscher (1999) suggested that predation on cervids by several predatory species (mainly wolf and cougar, *Puma concolor*) was additive in northwestern Montana. Two terms also worthy of definition are "obligate" and "facultative" predator. An obligate predator is one that specializes on one primary prey species. Hence changes in the levels of the primary prey will generally influence a numerical change in the obligate predator. In contrast, a facultative predator is a dietary generalist that switches among prey species and is thus buffered by changes in abundance of any one prey species. A facultative predator in a multi-prey system

can limit one prey species to low levels because other prey maintain the predator population.

CONSTRAINTS OF PREDATOR AND PREY

Evolution has placed constraints of both predatory and prey species, with obvious implications for the relationships between them. In general, comparative body size, strength, speed, and agility dictate a predator's ability to kill particular prey, while similar constraints on prey define which predators pose a threat to them. For example, predation by swift foxes (*Vulpes velox*) on adult pronghorn antelope (*Antilocapra americana*) is highly improbable, even though both species occupy the same prairie habitat. Similarly, the body size and defensive capabilities of voles (*Microtus* spp.) are no match for the size and agility of coyotes, hence voles must rely upon other survival strategies. Such physical and behavioral characteristics, or constraints, have developed over extensive periods and represent an "evolutionary race" between predator and prey. Some physical abilities, e.g., the speed of pronghorn antelope, may even represent residual developments from interactions with predators now extinct (Byers 1997).

HUNTING STRATEGIES

The process within which predators seek and kill has important implications to their impact upon prey. In the case of obligate predators, relief from predatory pressures on the prey will certainly occur with the numerical decline in predators when prey become too scarce to support the predators. Among mammalian systems, this

is perhaps best exemplified by the patterns in abundance of lynx (*Lynx canadensis*) and snowshoe hare, or black-footed ferrets (*Mustela nigripes*) and prairie dogs (*Cynomys* spp.). When facultative predators, with their abilities to switch from one prey source to another or even from predacious to omnivorous diets, are involved, relief from predatory pressures may not be forthcoming. When a prey species comprises incidental portions of a predator's diet, the killing rate may be a matter of random encounter between predator and prey and be strictly a product of the numerical abundances of both predator and prey (Hollings' Type I functional response). This type of situation can be particularly hazardous to prey species that are scarce.

As the relative importance of a prey species increases in a predator's diet, or the effort needed to acquire the prey increases, the functional response assumes characteristics of a Type II functional response, with satiation placing an upper limit upon the killing rate by individual predators (for this discussion, we will ignore events like surplus killing, food caching, etc.). In this case, the killing rate of the prey is directly proportional to the number of predators but inversely proportional to the abundance of prey. This is perhaps best exemplified by Knowlton and Stoddart's (1992) hypothesis that predation upon black-tailed jackrabbit nestlings by coyotes may be a Type I functional response, being merely a matter of chance encounter because the frequency and size of reward is insufficient for coyotes to actively hunt for them. On the other hand, they suggest that predation upon adult jackrabbits is more likely a Type II functional response, with coyotes actively hunting jackrabbits as a dietary staple, but because it requires significant effort to capture adult jackrabbits, they are only hunted when coyotes are hungry. In this case, satiation of the coyotes places an upper limit upon the killing of adult jackrabbits. Hence the fraction of adult jackrabbits killed is related directly to the number of coyotes and inversely to the number of jackrabbits (the coyote-jackrabbit ratio). If these scenarios are correct, a transition from a Type I to a Type II functional response occurs as jackrabbits mature. In the relatively simple ecological situation studied by Knowlton and Stoddart (1992), there was an apparent feed-back mechanism with the numerical abundance of coyotes dictated by the abundance of their principle prey, adult jackrabbits. Thus they propose predatory mechanisms that might partially explain the cyclic nature of some predator-prey interactions.

In addition to a component of strict numerical abundance, the effect that facultative predators, which switch from one prey type to another, have on prey species probably reflects a complex integration of the relative abundance, efforts to capture, and the quantity and quality of reward associated with each prey species. Consequently, understanding the role of predation upon a prey species in this situation requires an understanding of the context within which it occurs. We acknowledge there also are components associated with habits, learning, and traditions, among individual predators, but those issues are beyond the scope we wish to present here.

FACTORS INFLUENCING PREY POPULATIONS

The role predation plays in wildlife population dynamics follows many of the constructs and theories established by earlier researchers working on insects. However, as in the entomological debates of decades past, the role of predation in the population dynamics of wildlife, particularly ungulates, is far from clear (Sinclair 1991, Skogland 1991, Messier 1991, 1994; Boutin 1992, Dale et al. 1994, Van Ballenberghe and Ballard 1994). Much of the confusion arises because predation is only one of many factors influencing prey populations. Growth rates (increasing or decreasing) of prey populations may be affected by habitat changes, severe weather (e.g., deep snow), starvation, diseases, predation, human hunting, competition with other ungulates (native and domestic), changes in sex and age structure, as well as interacting combinations of these factors (Ballard et al. 2001). For example, density-dependent food limitation and density-independent adverse weather have been implicated as factors regulating the numbers of reindeer in the arctic tundra (Skogland 1985, 1990). Gates et al. (1986) concluded that food limitation and snow conditions regulated barren-ground caribou (*R. t. groenlandicus*) in northern Canada. Mech et al. (1987) and McRoberts et al. (1995) reported the cumulative effect of snow depth over 3 winters influenced population parameters of moose on Isle Royale and white-tailed deer (*Odocoileus virginianus*) in Minnesota. In a counterpoint, Messier (1991) postulated that competition for food, not snow depth, had a regulatory effect on moose, and that deer density and deer population growth was inversely related to wolf density; with snow depth not a significant factor. Given the same information, various researchers provide differing interpretations of the data. It

seems unlikely the debate over the hierarchy of factors influencing ungulate population dynamics will soon be resolved.

Disease is another factor that may regulate some ungulate populations. The introduction of rinderpest to the Serengeti plains by domestic cattle caused high mortality among wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*) (Sinclair 1979). Once rinderpest was eradicated, the wildebeest population tripled in size from 1963 to 1974 (Sinclair 1979). Competition among ungulate species also may influence population levels. A theory currently proposed for the mule deer (*O. hemionus*) decline in some areas of the western United States is competition with elk (*Cervus elaphus*) and white-tailed deer. Equally disconcerting is the likelihood of hybridization between mule and white-tailed deer, particularly in areas where habitat modification increases the probability of interspecific hybridization (Hornbeck and Mahoney 2000). Competition with livestock also has been implicated as a result of cattle removing winter forage for mule deer and elk in the western United States. Increased urbanization has resulted in loss of suitable habitat, especially wintering ranges, for many ungulate populations, although land conversion to agriculture may benefit some white-tailed deer populations. Thus, while many factors affect prey population levels, for purposes of this paper, let us focus on the effect of predation.

FACTORS INFLUENCING PREDATION

Skogland (1991) identified 9 factors that may influence predation: habitat heterogeneity, prey refugia, nomadism

(temporal/spatial availability of prey), buffer zones for prey, synchrony of the birthing season and aggregation at birthing, prey size and age vulnerability, availability of alternate prey, the ratio between the dominant prey species and alternative (buffer) prey, and the effects of compensatory causes of mortality and the effects of alternative predator species. Several of these are related and interactions among factors may cloud our understanding of predator-prey systems. Food is often a limiting factor on ungulate populations (Sinclair 1979). Heterogeneity of habitat has been proposed to influence predation on prey populations. With increasing human modification of the landscape, prey populations become fragmented, or isolated, and more vulnerable to predators. Habitat degradation may increase predation of mink (*Mustela vison*) on water voles (*Arvicola terrestris*) in England (Barreto et al. 1999). Increased predation risk from habitat fragmentation has been implicated as cause for decline of game bird populations. In contrast, modification to urban landscapes may favor some prey species (i.e., white-tailed deer), yet dissuade large carnivores from these areas, forming a refuge from predatory pressures. In a more natural setting, Murie (1944) showed that Dall sheep (*Ovis dalli*) escaped wolf predation by using steep terrain and cliffs as refugia. Similarly, Ferguson et al. (1988) suggested that one population of woodland caribou reduced predation risk from wolves by residing on small islands.

The temporal and spatial availability of prey also influences predator-prey relationships. In northeastern Minnesota, white-tailed deer use buffer zones between wolf packs, which wolves avoid for fear of intraspecific strife with neighboring packs

(Mech 1977). Nelson and Mech (1981) suggest that wolf predation regulates deer numbers, but the buffer zones between wolf territories allow sufficient numbers of deer to survive and these deer can reoccupy wolf pack territories when wolf numbers are low. Subsequently, Nelson and Mech (1986*a*) reported that the effects of snow depth and vulnerability was the main factor regulating deer numbers, rather than wolf predation. Migratory behavior is another mechanism that reduces the effect of predation. In the Wells Gray caribou of British Columbia, Seip (1992) suggests that one caribou population was slowly increasing because its migratory behavior kept the caribou separated from wolves and moose throughout the year resulting in low wolf predation. Fryxell et al. (1988) postulated that migratory ungulates on the Serengeti may escape predatory regulation by their movements, while resident ungulate populations might be more vulnerable to the effects of predators. However, the seasonal migratory patterns observed for ungulates on the Serengeti are more likely due to changes in forage quality across the landscape (Fryxell 1995), than predator avoidance. Another antipredator strategy among ungulate species may result from reproductive synchrony and aggregation during and following the birthing process. Reproductive synchrony and aggregation during birthing can flood territorial predators to the point that only a small portion of the reproductive effort falls prey to predators (Estes 1976). Although, birthing synchrony is generally related to environmental seasonality and the plant growing season (Rutberg 1987). Perhaps an equally important effect may result from the territorial nature of most carnivores, which limits their ability to respond numerically to aggregations of prey, especially during

periods of heightened vulnerability, as in the case of yarding among white-tailed deer or winter concentrations of black-tailed jackrabbits (Smith 1987).

Prey vulnerability is regarded as a major factor in predator-prey interactions. Most predator-prey studies document how predators target young and old animals, individuals in poor nutritional condition, or prey that are weakened by disease or physical abnormalities. In a classic study in Alaska, Murie (1944) reported that wolves killed Dall sheep that were weak, diseased, or very old. Mech (1966) reported that moose with heavy infestations of hydatid cysts (*Echinococcus grandulosus*), calves, and very old individuals were at greatest risk of wolf predation on Isle Royale. In northeastern Minnesota, wolves killed a preponderance of fawns, old male deer, and individuals with abnormalities (Mech and Frenzel 1971, Mech and Karns 1977, Nelson and Mech 1986*b*). Even the nutritional condition of the mother and grandmother may influence the vulnerability of first and second generation fawns to wolf predation (Mech et al. 1991). In Yellowstone National Park, Gese and Grothe (1995) reported that adult elk killed by coyotes in winter were in poor nutritional condition, based upon femur marrow fat indices. Studies also have documented the high vulnerability of new born fawns and calves to predation by a suite of predators (e.g., Cook et al. 1971, Barrett 1984, Ballard et al. 1999). Vulnerability of a particular age group in the prey population can influence population dynamics. Predators may remove a high proportion of neonates annually which may or may not affect population levels (Linnell et al. 1995), or if predators remove a high portion of the reproductive cohort (e.g., prime-age does),

the repercussions to the prey population may be substantial.

Availability of alternate prey can influence predator-prey interactions by either diluting or exacerbating the effects of a predator on their primary prey (Kunkel and Pletscher 1999). Dilution could be expected when alternate prey becomes more vulnerable than the primary prey (Carbyn 1983, Potvin et al. 1988); in which case the 'new' prey may become the primary prey, buffering the former primary prey. In contrast, the abundance of one prey may cause a numerical response in the predator, which could exacerbate the interaction between a predator and another prey. In Montana, Hamlin et al. (1984) documented coyote predation as a major cause of mule deer fawn mortality. However, when microtine rodents were abundant, mule deer fawn mortality was low. They further concluded that vegetative production and winter snow cover may regulate microtine abundance, and thus fawn mortality rates. Kunkel and Pletscher (1999) reported that where deer were present, the wolf-caused mortality rate on moose was lower than in areas where deer were absent. In contrast, Fuller (1990) believed the effect of wolves on deer was exacerbated by the abundance of moose in north-central Minnesota. Stoddart et al. (2001) reported that coyotes responded numerically as black-tailed jackrabbits increased during their 10-11 year cycle. When the jackrabbit population began to decline, coyotes switched to domestic sheep and predation rates on lambs escalated.

The effects of alternative predators on a prey population can be substantial. In Alaska, Gasaway et al. (1992) identified wolf and bear (*Ursus arctos*) predation as a

major factor limiting moose at low densities. This multi predator system, with moose as the primary prey, held the moose population well below carrying capacity. Kunkel and Pletscher (1999) reported that with wolf recolonization in northwest Montana, the full compliment of predators (wolves, bears, and cougars) brought about changes in the abundance of some ungulate species. They postulated that the mortality rate by all predators on the cervid populations (elk, deer, and moose) was additive.

PREDATOR-PREY THEORIES

Previous sections identified many factors that may influence prey populations and predation rates. While these might add confusion to predator-prey interactions, scientists have developed several theoretical models that allow testing of specific hypotheses and predictions among competing models (e.g., Messier 1994). These models, examine the role of predation in ungulate population dynamics, are varied. Four models widely used in predator-ungulate dynamics include: low-density equilibria, multiple stable states, stable-limit cycles, and recurrent fluctuations (Boutin 1992, Van Ballenberghe and Ballard 1994, Ballard and Van Ballenberghe 1997, Ballard et al. 2001). Similar models are presented by Messier (1994) and Sinclair and Arcese (1995). Under the low-density equilibria model, prey populations are regulated at low densities for long periods. The prey population remains at a low density until either a natural phenomena or a decline in predator abundance (e.g., predator control) allows the population to grow. Limitation by food is not important because prey density never reaches carrying capacity. When predators recover from low numbers, the prey population returns to a low density (Ballard et al. 2001). This model generally persists in systems with multiple species of predators and prey where predators subsist primarily on other prey.

Under the multiple stable states model, a prey population is regulated by density-dependent predation at low prey density until either a natural phenomena or predator removal reduces the predator population, allowing the prey population to reach carrying capacity and become regulated by competition for food (Ballard et al. 2001). Food competition then regulates the prey population at this higher equilibria even after the predator population returns to its former level. This model led to the term "predator pit," which refers to the "narrow band of densities between upper and lower equilibrium points where ungulates can not increase because of density-dependent predation" (Ballard et al. 2001). The multiple stable states model may exist in multi-predator and multi-prey systems.

Under the stable-limit cycle model, prey populations may exhibit regular cycles of 30-40 years duration (Ballard et al. 2001). Ballard et al. (2001) reported that severe climate may influence the viability of young and the survival rates of young and adults. "Predation is density independent during population increases and inversely density-dependent during population declines" (Ballard et al. 2001). Forage, climate, and prey density all interact to regulate the prey population. The stable-limit cycle model typically exists in single predator and single prey systems.

Sometimes a prey population fluctuates and never reaches a state of equilibrium. Prey densities change in

14

response to changes in climate, forage quality and quantity, and human harvest, but the primary factor most often limiting prey density is predation (Ballard et al. 2001). At high prey density, predation is inversely density-dependent. Prey may escape the regulatory effect of predation and attain a higher density where ultimately food competition causes a population decline. Inversely density-dependent predation may accelerate or prolong the decline of the prey population. Perturbations cause the prey population to fluctuate without attaining a predictable density (Ballard et al. 2001). Both multi-predator and multi-prey systems and single predator-single prey systems may exhibit recurrent fluctuations.

It is unlikely that one of these models will describe any predator-prey system at all times. Habitat conditions, human populations, climatic events, and other factors are in constant flux. The acceptance of one model, without periodically reexamining the data on the entire system, would be foolish in light of the competing variables that influence both predators and prey. The relative merits of each model continues to be a source of debate within the scientific profession. Only through informative discussion, exchange of ideas, developing data sets, and testing of hypotheses will the debate prove fruitful.

EFFECT OF PREDATOR CONTROL ON PREY POPULATIONS

Predator control can enhance prey populations if prey is at low densities relative to carrying capacity. In Alaska, predator removal programs brought about irruptions of moose, which allowed for increased human harvest of moose (Gasaway et al. 1983, 1992, Ballard et al.

1991). In British Columbia, following reduction of wolf numbers, recruitment was enhanced 2-5 times for 4 ungulate species and all populations increased (Bergerud and Elliott 1998). Similarly, deer populations in south Texas increased following an intensive coyote removal program (Beasom 1974). Predator control may obtain an increase in ungulate numbers, but the addition of animals can have consequences not often anticipated. In a study conducted on the Welder Wildlife Refuge in south Texas, coyote predation on white-tailed deer fawns was substantial. To test if coyote predation was a factor limiting population growth, a 391-hectare exclosure was erected on the site and the coyote density reduced inside. Deer densities in the exclosure tripled compared to densities outside the exclosure, and remained stable for 2-3 years. At the elevated population level, forage became suboptimal within the exclosure and the general health of the deer declined. Parasite loads increased, deer conceived later, bucks retained velvet longer, males shed antlers later, and gross reproductive performance decreased (Kie et al. 1979, Kie and White 1985, Teer et al. 1991). Eventually, the population declined to levels comparable to outside the exclosure. Compensatory mortality occurred with higher mortality among fawns 6-12 months of age, rather than the mortality occurring among post-natal fawns (Knowlton and Stoddart 1992). Essentially, the addition of animals above carrying capacity required management action (e.g., increased harvest), or as in this case, compensatory mechanisms (i.e., malnutrition and parasitism) returned the deer population to levels as before predator removal, but in a less healthy condition (Knowlton and Stoddart 1992).

If predator control is considered for enhancing ungulate populations, several factors should be considered. In a study in Quebec, wolf reduction was conducted on 2 experimental areas while wolves were not reduced on 2 control areas (Potvin et al. 1992). They found that deer populations increased in all 4 areas as a consequence of mild winters and recommended that wolf reduction was not a viable management tool in this context. Thus it is important that managers determine whether or not predation is a limiting factor. Also, is the ungulate population below forage carrying capacity? Considerations of scale, timing, and method of removal need to be addressed (e.g., what size of area is needed, and can control be cost effective). As demonstrated throughout this paper, managers also need to consider what other factors may be limiting or influencing the ungulate population. In a recent review of the relationships between predators and mule and black-tailed (*O. h. columbianus*) deer, Ballard et al. (2001) concluded that (a) the relationship of a prey population to forage carrying capacity was critical to the impacts of predation, (b) prey populations do not respond to predator removal if prey is at or near carrying capacity, and (c) when prey populations are limited by predators and are far below carrying capacity, predator removal could enhance prey survival, but increased hunter harvest may be uncertain. Equally important is whether or not clear alternate values or objectives of the prey population are served.

WHITHER FROM HERE?

Assessing the impact of predation upon prey populations is one of the more daunting tasks facing the wildlife profession. If it were easy, we would already know the answers. Predation involves events towards the top of ecological trophic schemes, with events at lower trophic levels having repercussions manifested in higher levels. Consequently, attempting to unravel relationships at the top without accounting for those below becomes illogical. However, we would be remiss without identifying potential means of improving our understanding.

It now seems largely folly to attempt a comprehensive understanding of the role and impact of predation on prey populations independent of other ecological considerations. This may be less important in the case of obligate predators subsisting on relatively few prey types but it becomes increasingly important as the number and type of suitable prey and predators increases the complexity of the system (Table 1). Availability and abundance of alternate suitable prey constitutes a significant term in the predatory equation because they contribute to the base determining the numerical abundance of predators as well as provide buffers for the prey and stability for the predators. The balance between prey abundance and the resources upon which they depend is another integral part of understanding the interactions because as their resources (i.e. food, cover, etc.) become scarce, their vulnerability to predation typically increases.

One of the glaring lapses is an absence of long-term data sets with simultaneous measures of the abundances and demographic parameters of predators and prey within individual ecosystems. Such data sets provide the insights needed to generate the testable hypotheses that will help define predator-prey interactions. Ideally these data sets should include not

only routine measures of the abundances of predatory and prey species of primary interest, but also those of alternate predatory and prey species, as well as climatic conditions (especially deviant events), primary productivity, and cause-specific mortality among the age classes of each prey species. Unfortunately, the difficulty of establishing and maintaining the interest and resource stream required for such endeavors precludes many of us from such pursuits. It is indeed sobering to think that for some long-term fluctuations (e.g., the cyclic pattern in jackrabbit abundance in the intermountain west), it may take 10-20 years of data before we can generate the appropriate questions, yet alone provide the answers to them.

We must recognize that by managing predation, we may be merely sustaining prey populations in habitats that are marginal for other reasons. In our quest for numbers, we may be making choices between smaller but robust and healthy prey populations versus a more abundant but perhaps less thrifty ones. Ultimately, managers also must address the question of whether efforts to manipulate predation will result in extending the life of prey long enough to reap some alternate value from those animals. In doing so, we also need to recognize that 'alternate values' are more inclusive than harvest, and includes viewing, photographing, as well as simply preserving life forms for future generations.

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Table 1. Gradients of increasing complexity in predator-prey interactions.

Simpler predator-prey interactions	to	More complex predator-prey interactions
Single prey system		Multiple prey systems
Stationary prey		Mobile prey
Resident prey		Transient (migratory) prey
Carnivore		Omnivore
Obligate predator		Facultative predator
Single predator system		Multiple predator system
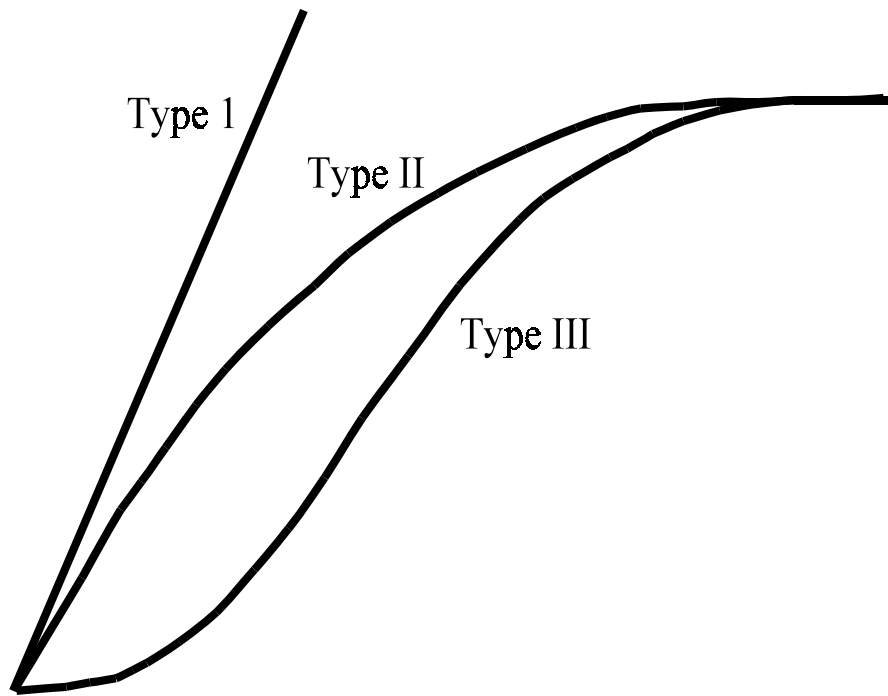
Figure 1. Types of functional responses of predators to increasing prey density: (Type I) predator kills a constant proportion of the prey population regardless of prey density; (Type II) predation rate decreases as predator satiation sets an upper limit; (Type III) predator kill rate lags at low prey density owing to low hunting efficiency or absence of search image (Holling 1959).
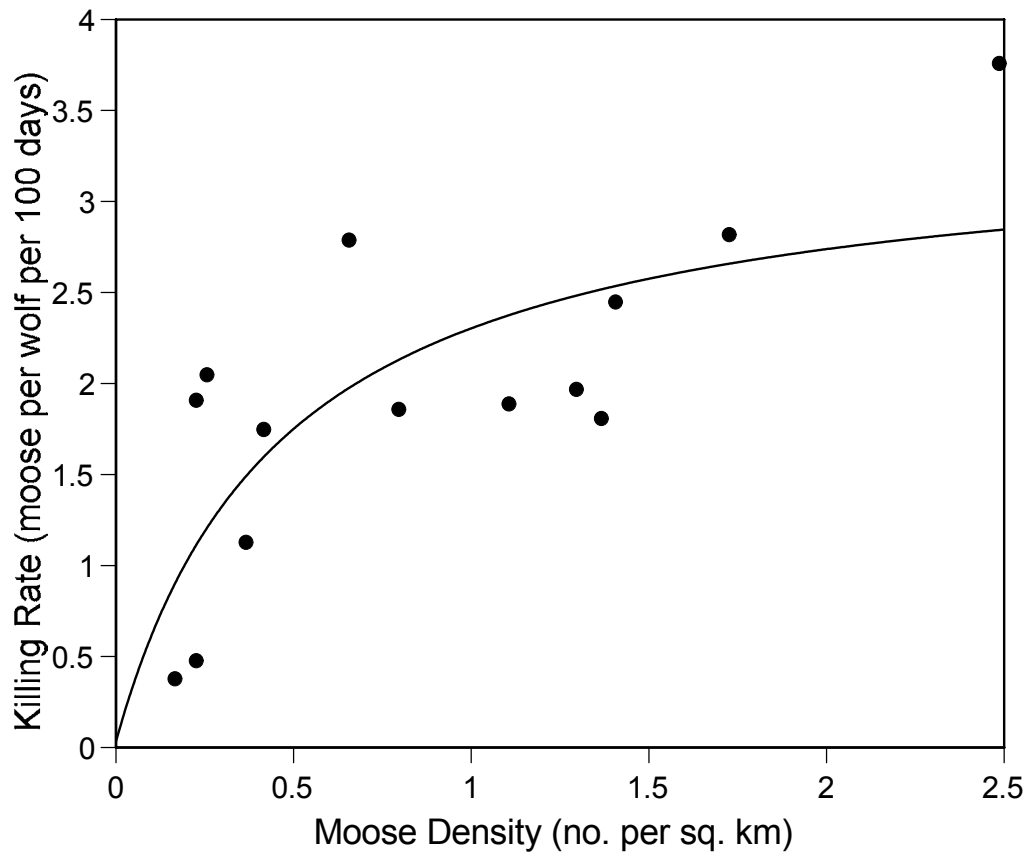
Figure 2. The functional response of wolves to changing moose density. Killing rate (number of moose killed per wolf per 100 days) was related to moose density (number/km^2) with a hyperbolic, Michaelis-Menton equation (data from Table 2 in Messier 1994).
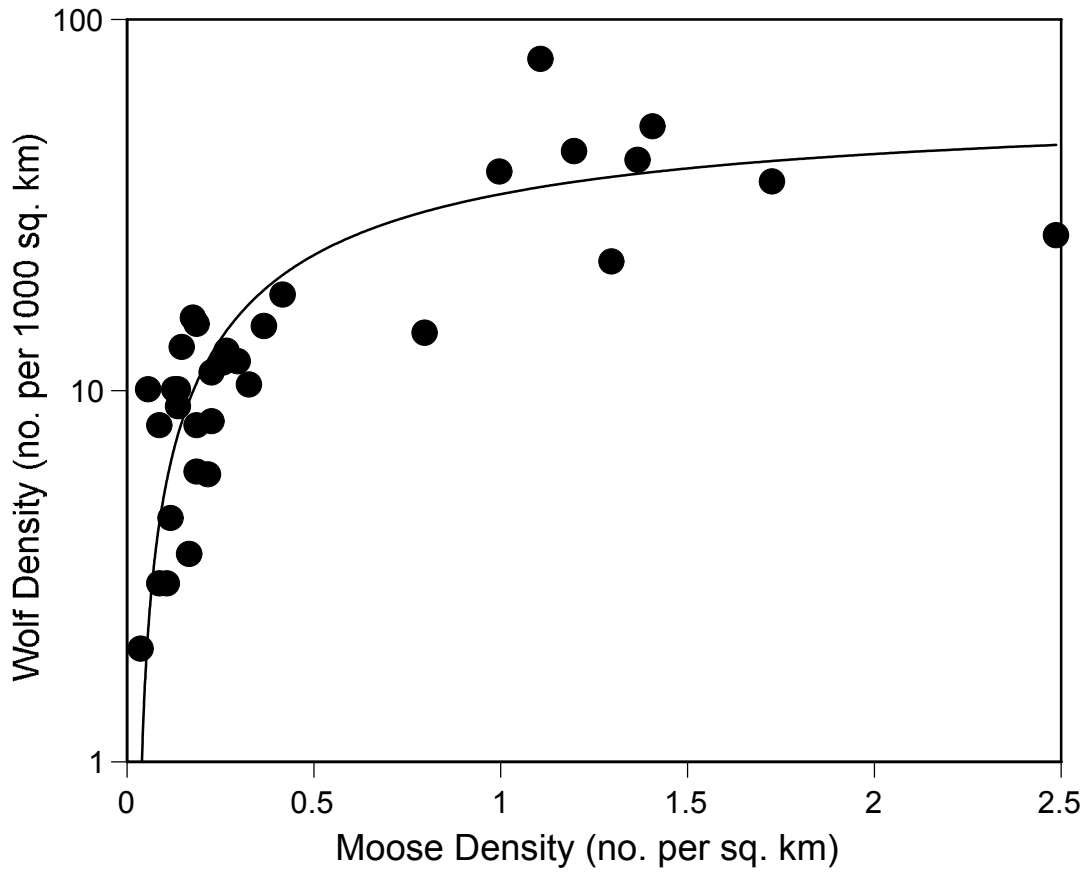
Figure 3. The numerical response of wolves to changing moose density. Wolf density (number/1,000 km^2 presented on a log$_{10}$ scale) was related to moose density (number/km^2) with a hyperbolic, Michaelis-Menton equation (data from Table 2 in Messier 1994).