Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer

Warren B. Ballard, Daryl Lutz, Thomas W. Keegan, Len H. Carpenter, and James C. deVos, Jr.

Abstract In recent years mule (*Odocoileus hemionus*) and black-tailed (*O. h. columbianus*) deer appear to have declined in many areas of the western United States and Canada, causing concern for population welfare and continued uses of the deer resource. Causes of the decline have not been identified, but predation by coyotes (*Canis latrans*), mountain lions (*Puma concolor*), and wolves (*Canis lupus*) has been proposed as one of many factors. We reviewed results of published studies conducted since the mid-1970s concerning predator–deer relationships to determine whether predation could be a factor in the apparent deer population declines and whether there was evidence that predator control could be a viable management tool to restore deer populations.

We reviewed 17 published studies concerning mule deer. We found only 4 published studies of the effects of predation on black-tailed deer. A larger database existed for white-tailed deer (*O. virginianus*), with 19 studies examining effects of predation on white-tailed deer.

Study results were confounded by numerous factors. A deer population's relationship to habitat carrying capacity was crucial to the impacts of predation. Deer populations at or near carrying capacity did not respond to predator removal experiments. When deer populations appeared limited by predation and such populations were well below forage carrying capacity, deer mortality was reduced significantly when predator populations were reduced. Only one study, however, demonstrated that deer population increases resulted in greater harvests, although considerable data indicated that wolf control resulted in greater harvests of moose (*Alces alces*) and caribou (*Rangifer tarandus*). The most convincing evidence for deer population increases occurred when small enclosures (2–39 km^2) were used.

Our review suggests that predation by coyotes, mountain lions, or wolves may be a significant mortality factor in some areas under certain conditions. Relation to habitat carrying capacity, weather, human use patterns, number and type of predator species, and habitat alterations all affect predator–prey relationships. Only through intensive radiotelemetry and manipulative studies can predation be identified as a major limiting factor. When it is identified, deer managers face crucial decisions.

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Reductions in predator densities have occurred only on relatively small study areas (2–180 km^2) where predators were identified as a major limiting factor and deer populations were well below forage carrying capacity (an important criterion). Thus a problem of scale, methods used to kill predators, benefit:cost ratios, results to hunters, and public acceptance are primary considerations. Methods of predator control available to deer managers have been severely restricted and current methods may not be feasible over large areas when and if predation becomes a problem. Public acceptance of predator reduction programs is essential for predator–prey management, but may not be achievable given current public attitudes toward predators. We identified several recommendations and research needs based on our review of the literature given current social and political limitations.

Key words black-tailed deer, carrying capacity, coyote, mountain lion, mule deer, population management, predation management, predators, wolf

Wildlife management agencies in the western United States and Canada are concerned about an apparent decline of mule deer (*Odocoileus hemionus*) and black-tailed deer (*O. h. columbianus*) populations over large portions of western North America (Western Association of Fish and Wildlife Agencies, Mule Deer Committee, 1998 unpublished report). Western deer populations have been described as very volatile, with major cycles of high and low populations (Denney 1976). Herds apparently began increasing in the 1920s, peaked in the late 1940s to early 1960s, declined during the 1960s to mid-1970s, increased during the 1980s, and then declined during the 1990s (Denney 1976, Hurley and Unsworth 1998). Some investigators indicated that deer populations in some areas have been declining since the 1960s (Workman and Low 1976, Schneegas and Bumstead 1977, Bleich and Taylor 1998).

Numerous factors could be responsible for deer declines, including habitat loss or change, severe weather (e.g., drought, deep snow), starvation, changes in age and sex structure, disease, predation, competition with livestock and wildlife species such as elk (*Cervus elaphus*), hunting, and interactions of these factors (Wallmo 1981, Halls 1984, Whittaker and Lindzey 1999). Recently, some members of the public (e.g., Barsness 1998) and some biologists (Gasaway et al. 1992) indicated that predation may be largely responsible for declines or lack of ungulate population recovery and that predator control may be necessary to restore some populations to greater levels. However, empirical evidence exists only for moose (*Alces alces*), caribou (*Rangifer tarandus*), and one black-tailed deer population, and this hypothesis has not been tested for mule deer.

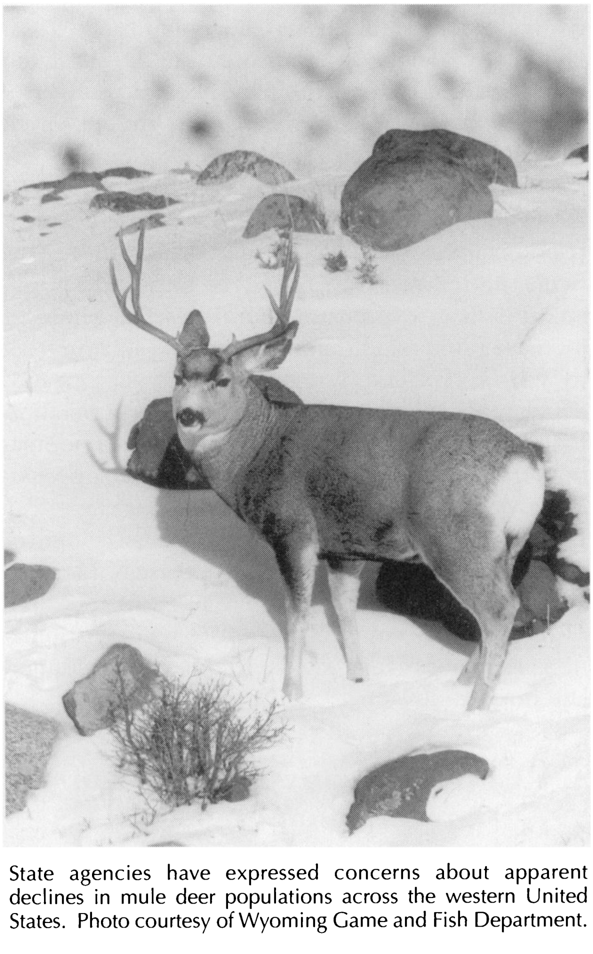
Connolly (1978), in his review of effects of predation on ungulates, indicated that a selective review of the literature could reinforce almost any view on the role of predation. He reviewed 31 studies that indicated predation was a limiting or regulating influence and 27 studies indicating that predation was not limiting (Connolly 1978). However, degree of documentation varied widely among studies. He concluded that predators acting in concert with weather, disease, and habitat changes could have important effects on prey numbers. Since Connolly's review, scientists have continued to debate whether predation is a significant regulating factor on ungulate populations (Messier 1991, Sinclair 1991, Skogland 1991, Boutin 1992, Van Ballenberghe and Ballard 1994). Because of increased interest in relationships between predation and deer populations, we reviewed available literature concerning deer-predator relationships and sought to draw conclusions regarding effects of predation on mule and black-tailed deer populations and, based upon our assessment, make appropriate recommendations for additional research and management.

Methods

We focused our review on studies conducted since the mid-1970s and, where applicable to deer, included some studies summarized by Connolly (1978, 1981). We used selected abstracting services and searched for literature pertaining to deer–predator relationships. We searched all major biological and wildlife journals and reviewed literature citations within articles for additional references. We purposefully excluded predator diet studies because these do not allow assessment of effects of predation on prey populations.

Several authors indicated that confusion exists in the predator–prey literature because biologists have used the terms regulation and limitation interchangeably and the role of predation in ungulate population dynamics was unclear (Messier 1991, Sinclair 1991, Skogland 1991, Boutin 1992, Dale et al. 1994, Van Ballenberghe and Ballard 1994). We use the terms limiting and regulating factors following definitions by Messier (1991). By definition, any mortality factor that reduces rate of population growth is a limiting factor. This definition can include density-dependent and density-independent factors. However, the point at which an ungulate population is in approximate equilibrium with its long-term natality and mortality factors is regulation and this equilibrium relies on density-dependent factors. In other words, the magnitude of impact depends upon density, more impact at greater density or vice versa (inversely density-dependent).

Bartmann et al. (1992) defined compensatory and additive mortality by explaining that an increase in one cause of mortality or introduction of a new cause may or may not increase total mortality rate depending upon whether there is additivity or compensation of mortality causes. For additive mortality, additional risk of death does not cause reductions in other forms of mortality but rather increases overall mortality rate. For compensatory mortality, 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. Generally, when an ungulate population is at habitat carrying capacity (*K*, Macnab 1985), mortality is thought to be entirely compensatory and becomes increasingly additive the farther below *K* the population is, until theoretically all mortality is additive. It is important to note that on some ranges in very variable environments, any mortality factor may shift from one end of the additive–compensatory scale to the other and back again (Mackie et al. 1998).



State agencies have expressed concerns about apparent declines in mule deer populations across the western United States. Photo courtesy of Wyoming Game and Fish Department.

Numerous studies have documented the following species as potential deer predators: gray wolf (*Canis lupus*), mountain lion (*Puma concolor*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), black bear (*Ursus americanus*), and grizzly bear (*U. arctos*). Wolves, mountain lions, and bobcats are obligate carnivores, meaning they must kill prey species to survive, whereas species such as coyotes, grizzly bears, and black bears are considered facultative carnivores in that, although they can and do kill prey, their diets consist of a diversity of items including mast and vegetation.

Introduction to deer population dynamics

Comprehension of annual population dynamics of a particular deer herd is essential to understanding the potential importance of limiting factors such as predation. Number of animals within a deer herd is a function of births, deaths, and factors that affect them. In theory, numbers of births and deaths and their impact on a deer herd depend on the herd's relationship to *K* (Macnab 1985). Because field biologists rarely are able to determine exactly what constitutes *K*, they use indices related to deer condition or browse utilization. A deer population at or above *K* should produce relatively fewer fawns than a population below *K*, and mortality from all factors should be relatively great, so the population essentially is stable. If a deer herd greatly exceeds *K* and over-utilizes forage resources, individuals should be in poor physical condition, birth rates should be low, and mortality rates should be greater. A deer herd that remains above *K* ultimately will damage its food resources, the deer population will decline, and when the herd recovers (i.e., to a lesser level than previously held), habitat carrying capacity will likely be reduced from previous levels.

Habitat carrying capacity is an important concept with many implications to evaluating predator-prey relationships. Prey population status in relation to *K* determines how mortality factors act on a population. When a deer herd is at *K*, deaths equal recruited offspring. The mortality cause (e.g., predation) is inconsequential, because once predation is removed or reduced, other mortality factors will replace it. However, the farther a population is below habitat carrying capacity, the more different mortality factors combine to retard population increases or even cause declines. In other words, at *K*, mortality factors are compensatory (i.e., they replace each other so that total mortality remains constant), but when populations are well below *K*, each mortality source adds to total mortality and mortality factors are termed additive. In reality, unless populations are well below *K*, these types of mortality are operating somewhere between complete additivity and complete compensation. Identification of additive or compensatory mortality is often difficult to determine in field situations.

Numerous biologists believe compensatory mortality is usually density-dependent. Deer birth rates remain relatively high over a wide range of densities, and only when densities become excessive are there density-dependent declines in reproduction. Therefore, as deer herds approach carrying capacity, reducing one form of mortality will only result in that mortality factor being replaced by another. For example, at relatively high deer densities where winter severity is the only major mortality factor, doe hunting before a harsh winter would be considered a compensatory form of mortality. Without hunting, losses to hunting would be replaced largely by the severe winter weather so that total mortality for the year would remain the same. On the other hand, if such hunting occurred before a mild winter, it could be additive mortality. However, deer herds also are affected by other factors.

Persistent drought appears to reduce habitat carrying capacity on summer and winter deer ranges and is reflected in poorer body condition (Kucera 1988, Taylor 1996) and lesser neonatal survival. On many deer ranges, individuals have improved physical condition during the growing season and then suffer declines in body condition during the non-growing season. If severe winters or droughts persist, then mortality from starvation increases and can cause a significant population decline. Also, drought results in lower-quality habitat (e.g., less fawning cover, poor nutrition, reductions in alternate prey species, lack of water), potentially exposing fawns and adults to increased mortality from predation. These effects can occur at any population density (i.e., they are density-independent) and affect rate of increase of a particular deer herd.

Most mortality in any ungulate population occurs among the youngest age classes. Most of these mortalities usually occur immediately following birth or during mid- to late winter, when deer are in relatively poor condition. Yearling deer (i.e., 1 to 2 years of age) probably experience mortality rates intermediate between those of fawns and adults, but some studies indicate that yearling survival can be similar to that of adults (White et al. 1987). Adult deer usually have low mortality rates, with mortality rates increasing among older animals. When number of deaths exceeds number of surviving young entering a herd, the herd declines; conversely, when number of surviving young exceeds total mortalities, the herd increases.

Predation is relevant to all of the above factors. If losses to predators are high, then the deer herd's relationship to *K* can dictate importance of this particular mortality factor. Therefore, if the deer population is near *K*, predator removal will do little to increase population numbers because such mortality will be replaced by other mortality factors and, if not replaced, will result in deer overpopulation that could harm habitat and may result in a population crash. In contrast, if predation were suppressing a deer population at low densities (i.e., deer population well below *K*), then predator control may allow a deer population to increase or increase at a greater rate until compensatory factors take over. Biologists continue to debate whether predation is a major regulatory or limiting factor of ungulate populations.

Current theories on effects of predation on ungulates

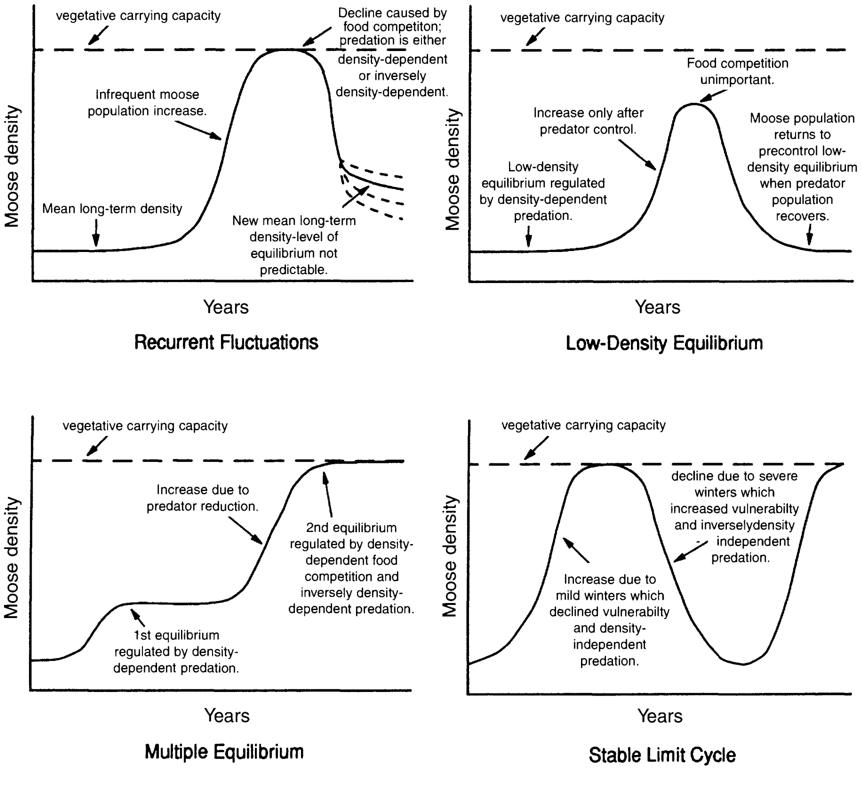
Current theories on the role of predation in the population dynamics of ungulates have focused on 4 models: low-density equilibria, multiple stable states, stable-limit cycles, and recurrent fluctuations (Boutin 1992, Van Ballenberghe and Ballard 1994, Ballard and Van Ballenberghe 1997). These theories have been the subject of intense debates focused on relationships among moose, wolves, grizzly bears, and black bears because these species continue to exist largely in ecosystems not impacted by humans. An understanding of predator-prey relationships under natural conditions is necessary before we can understand systems that have been affected by humans. Descriptions of the 4 models were provided by Ballard and Van Ballenberghe (1997), but as yet no model has been identified which explains ungulate-predator relationships under all conditions, and the models have not been tested on mule or black-tailed deer.

Low-density equilibria. Under this model, ungulate populations are regulated by density-dependent predation at low densities for long periods (Figure 1). Ungulates remain at low densities until either natural phenomena or predator control allows population growth. Food competition is not important because ungulate densities never reach *K*. When predators recover from low numbers, prey populations return to low densities. Such systems typically are characterized by multiple species of principal predators and principal prey.

Multiple stable states. Ungulate populations are regulated by density-dependent predation at low densities until either natural phenomena or predator control reduce predator populations, at which time ungulate densities reach *K* and prey become regulated by food competition (Figure 1). Food competition regulates ungulate population growth at the greater equilibrium even when predator populations return to former levels. Such systems also are characterized by multiple species of principal predators and prey. The term predator-pit, which is often misused, refers to a narrow band of densities between upper and lower equilibrium points where ungulates can not increase because of density-dependent predation.

Stable-limit cycles. Ungulate populations fitting this model exhibit regular cycles lasting from 30 to 40 years (Figure 1). Weather conditions (e.g., severe winters or drought) influence viability and survival of neonates and also influence adult survival. Predation is density-independent during population increases and inversely density-dependent during population declines. Ungulate density, weather, and forage interact to regulate populations. Such systems have been characterized as having one principal predator and one principal prey species.

Recurrent fluctuations. Ungulate populations are characterized by fluctuating densities that are not in equilibrium (Figure 1). Changes in ungulate densities occur because of changes in weather, food quality and quantity, and human harvest, but predation is the primary factor that most often limits ungulate density. Predation is inversely density-dependent at high



Recurrent Fluctuations **Low-Density Equilibrium**

Multiple Equilibrium **Stable Limit Cycle**

Figure 1. Conceptual models of ungulate population regulation by predation: low-density equilibria, multiple stable states, stable-limit cycles, and recurrent fluctuations (from Ballard and Van Ballenberghe 1997).

Table 1. Summary of case history studies where the effects of predation on mule, black-tailed, and white-tailed deer were studied in North America, 1977-1999. Note that for most studies assessment of whether predation was compensatory or additive, and a deer population's relation to *K* was based upon our evaluation unless specifically mentioned.

Deer species State/ province	Primary predator species	Size of study area	Length study of (yrs.)	Timing of fawn mortality				Predator reduction	Deer density (No./km^2)	Relation-ship to K	Type of mortality	Source
				Spr.	Sum.	Aut.	Win.					
Mule												
Ariz.	Coyote	2.43 km^2	6		X			Yes	4.5–18.5	Below	Additive	LeCount 1977, Smith and LeCount 1979
Calif.	Coyote	Kings River herd	5		X			No	?	At	Compensatory	Salwasser 1974, Salwasser et al. 1978
Calif. – Nev.	Mt. lion	5 herds	9				X[a]	No	?	Below	Additive	Bleich and Taylor 1998
Colo.	Coyote	3-140 km^2	7				X	Yes	61–80	At	Compensatory	Bartman et al. 1992
Colo. – Id.–Mont.	Mt. lion	Statewide	16				X[b]	No	14–70	?	?	Unsworth et al. 1999
Id.	Coyote	Statewide	16				X[b]	No	3–29	?	?	Unsworth et al. 1999
Mont.	Coyote	Statewide	16				X[b]	No	15–34	?	?	Unsworth et al. 1999
Mont.	Coyote	275 km^2	27		X		X	No	1.4–6.2	Below	Additive & Compensatory	Mackie et al. 1982, Hamlin and Mackie 1989, Mackie et al. 1998
Mont.	Coyote	250 km^2	6		X			No	?	?	Additive	Hamlin et al. 1984
N.M.	Coyote	20-26 km^2	6		X			No	?	?	Additive	Temple 1982
N.M.	Mt. lion	703 km^2	11		X		X	Yes	2–5	At	Compensatory	Logan et al. 1996
Oreg.	Coyote	194 km^2	12			X	X	Yes	11.6–15.2	Below	Additive	Trainer et al. 1981
Tex.	Coyote	?	1		X			No	41	At	Compensatory	Dickinson et al. 1980
Ut.	Coyote	30-40 km^2	4				X	Yes	6.0–19.0	Below	Additive	Austin et al. 1977
Wash.	Coyote	Small islands	1		X			No	1.7	At	Compensatory	Steigers et al. 1980
Black-tailed												
Alas.	Wolf	73 km^2	13		?			No	5.8–7.8	At	Additive	Klein 1995
B.C.	Mt. lion–wolf	2,400 km^2	10	X	X			Yes	2.8–14.8	Below	Additive	Hatter 1988, Hatter and Janz 1994, Atkinson and Janz 1994, McNay and Volley 1995

(*continued*)

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[a] Adult mortality.

[b] Fawn and adult mortality.

densities. Ungulates can occasionally escape constraints of predation and reach high densities where food competition causes population declines. Population declines are accelerated or extended by inversely density-dependent predation. Once an ungulate population is perturbed by any factor, it does not return to a predictable density. Although ungulate populations fitting this model appear characterized by systems with one principal predator and one principal prey species, such a scenario also can apply to multiple predator–prey systems.

Table 1 (*continued*). Summary of case history studies where the effects of predation on mule, black-tailed, and white-tailed deer were studied in North America, 1977-1999. Note that for most studies assessment of whether predation was compensatory or additive, and a deer population's relation to *K* was based upon our evaluation unless specifically mentioned.

Deer species State/ province	Primary predator species	Size of study area	Length study of (yrs.)	Timing of fawn mortality Spr.	Sum.	Aut.	Win.	Predator reduction	Deer density (No./km^2)	Relation-ship to K	Type of mortality	Source
White-tailed												
Okla.	Coyote	70-180 km^2	4		X			Yes	?	Below	Additive	Garner 1976, Garner et al. 1976, Bartush 1978, Stout 1982
Minn.	Wolf	2,000 km^2	11		X			No	2–5	Below	Compensatory	Mech and Karns 1977, Nelson and Mech 1986*a,b*; Kunkel and Mech 1994
N. B.	Coyote	Tobique-River Valley	4		X		X	No	?	Below	Additive	Whitlaw et al. 1998, Ballard et al. 1999
Tex.	Coyote	219 km^2	2		X^b			Yes	7.4–19.6	Below	Additive	Beasom 1974*a,b*
Tex.	Coyote	74-86 km^2	3				X^a	Yes	?	At	Compensatory	DeYoung 1989, Heffelfinger 1989, Heffelfinger et al. 1990
Tex.	Coyote-bobcat	32-89 km^2	3		X			?	9.9–41.1	Above	Compensatory	Carroll and Brown 1977
Tex.	Coyote	3.9 km^2	37		X			?	32	Below	Additive	Cook et al. 1971, Kie and White 1985, Teer et al. 1991

[a] Adult mortality.

[b] Fawn and adult mortality.

Synthesis of effects of predation on deer

When compared to other North American deer species, relatively few studies have been conducted on effects of predation on mule and black-tailed deer populations (Table 1). Unfortunately, inconsistencies and significant variations among studies because of relationships to habitat carrying capacity, differing weather patterns, and the short-term nature of most studies limit their usefulness in assessing overall importance of predation. Often small sample sizes limited usefulness of studies because of their low statistical power to actually detect significant differences. Also, many studies that simply determined causes of mortality with no additional information inform us only that predation may or may not be an important mortality factor, but say nothing about whether predation significantly limits or regulates population size. However, our review of case histories has uncovered some notable patterns.

Fetal rates/adult mule deer doe have been relatively high (1.0–1.9 fetuses/doe) over a wide distribution of deer densities that ranged from well below *K* to habitat carrying capacity. Most fawn mortality occurred immediately following parturition and during mid- to late winter, but in some studies substantial fawn mortality occurred in late summer. Coyote predation has been implicated as a significant cause of mortality in most mule deer studies that were based on either radiotelemetry or experimental manipulation of predator populations where predation was thought to be a problem. Although bobcats kill deer, no study has implicated them as a major source of deer mortality. However, our review focused on studies of predator–prey relationships in which the subject of predation was addressed or was a primary study objective. The literature is full of general ecological studies in which predation was not considered a problem and

Most mortality in ungulate populations occurs among the youngest age classes. Photo courtesy of George Andrejko, Arizona Game and Fish Department.

subsequently was not studied. We did not review these studies. No studies have implicated predation by mountain lions as a major mortality factor of neonatal fawns, but this may be because this aspect has not been studied with radiotelemetry. However, mountain lions have been implicated as major predators of adult deer.

Variable weather obviously changes impacts of predation through changes in forage and cover (Smith and LeCount 1979, Teer et al. 1991), changes in alternate prey densities (Hamlin et al. 1984), and impacts on deer physical condition that influence vulnerability to predation (Unsworth et al. 1999). However, it appears that effects of weather may be modified by predator densities, prey vulnerability, and by a deer population's relationship to *K*. Perhaps the best examples of this come from predator-free enclosure studies.

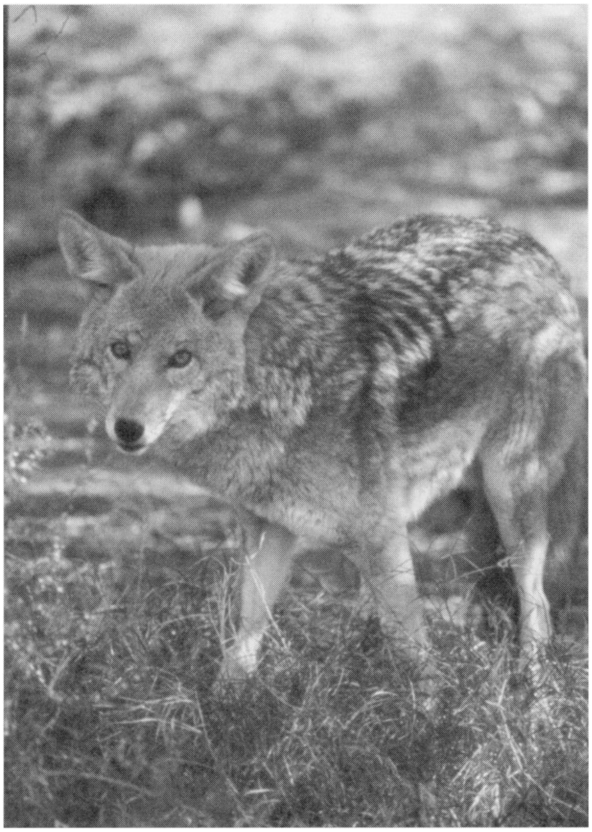
Smith and LeCount (1979) demonstrated that predation was a major limiting factor in their Arizona study as the deer population was well below *K* and the deer population in a predator-free enclosure increased from about 3-5 to 18 deer/km^2. Fawn survival was greater during wet years than dry years, but overall, the predator-free enclosure population averaged 30 fawns/100 does greater than populations outside. However, deer densities also increased outside the enclosure once favorable weather conditions returned. Teer et al. (1991) reported a similar experiment for white-tailed deer in south Texas with similar results. In both studies, protected deer populations increased to levels far greater inside than outside enclosures and then declined because deer numbers exceeded food supply. These authors did not know whether greater deer densities could have been sustained if the deer population had been cropped prior to exceeding *K*.

Bartmann et al. (1992) evaluated effects of coyote predation on mule deer fawn survival during winter where the population was at or near *K*. At this level, removal of coyotes resulted in fawns dying of starvation rather than predation. Predation mortality was compensatory at the reported mule deer densities and coyote removal had no impact on fawn survival. In other words, deer killed by coyotes were predisposed to die of other factors because the population was at or above *K*. Other studies where deer populations appeared to be well below *K* indicated that although neonates may have weighed less and may have been more vulnerable due to drought conditions, they appeared to not be predisposed to death.

Two studies have recently evaluated effects of mountain lion predation on mule deer populations, but only one of these involved experimental reduction of lion numbers to improve fawn survival. Logan et al. (1996) studied effects of a mountain lion translocation experiment on mule deer survival during a drought. Although the study lacked an untreated area, they compared deer survival before and after lion removal and concluded that lion predation was a compensatory form of mortality because of drought conditions. A concurrent evaluation of an untreated area may have shed additional light on effects of mountain lion predation. Bleich and Taylor (1998) suggested that mountain lion predation may have been regulating mule deer herds in the unpredictable environments of the western Great Basin of California and Nevada.

Effects of predation on black-tailed deer appear more pronounced because of the predator species involved. Wolves are the principal predator of black-tailed deer in British Columbia and Alaska. In these systems, wolves have effectively eliminated coyotes as serious predators of deer, whereas in northeastern portions of the continent where wolves have been eliminated, coyotes have replaced wolves as effective predators of white-tailed deer (Ballard et al. 1999). Two experiments evaluated effects of wolf predation on black-tailed deer on islands. Wolves introduced to a small island where they had not existed previously caused the deer population to decline to very low levels (Klein 1995). McNay and Voller (1995) found mountain lions and wolves to be significant predators of adult female deer on Vancouver Island. Atkinson and Janz (1994) experimentally reduced wolf numbers and documented large increases in fawn survival when the deer population was well below *K*. A relationship exists between presence of wolves and deer numbers on islands in southeast Alaska. On islands south of Frederick Sound where wolves occur, deer numbers are low; deer numbers are substantially greater on islands north of Frederick Sound, where wolves are absent (Smith et al. 1987). Smith et al. (1987) suggested that the prolonged recovery (i.e., 25 years) of deer south of Frederick Sound may be due to wolf predation. Numerous studies of white-tailed deer demonstrated that fawn survival on relatively small areas (2–194 km^2) can be increased with large budgets by removing predators when predation has been identified as a major limiting factor and when deer numbers are well below *K*.

Biologists continue to debate whether predation is a regulatory or a limiting factor (Sinclair 1991, Skogland 1991, Boutin 1992, Van Ballenberghe and Ballard 1994), but to wildlife managers who are responsible for managing deer populations to provide hunting and viewing opportunities, the distinction between these terms may not matter (Van Ballenberghe and Ballard 1994). If management of a significant limiting factor can result in increased deer harvest, then managers must be able to identify conditions under which such factors impact deer. Conditions that allow predation to become an important limiting factor are poorly understood in natural ecosystems with a full complement of predators. In very altered ecosystems, such as those where mule, black-tailed, and white-tailed deer exist, there is even more confusion about how and when predation can become an important mortality factor. Some insight can be gained by examining conditions under which predation has become an important factor on other species of ungulates.



Coyote predation has been implicated as a significant cause of mortality in most mule deer studies that were based on either radiotelemetry or experimental manipulation of predator populations where predation was thought to be a problem. Photo courtesy of George Andrejko, Arizona Game and Fish Department.

Numerous studies in arctic ecosystems, where presumably natural systems continue to function with minimal impacts by man, suggest that predation becomes an important mortality factor when severe weather or human over-harvest initially cause population declines and then mortality from predation either retards or prevents population recovery (Gasaway et al. 1983, 1992; Van Ballenberghe 1985; Ballard et al. 1987, 1997; Bergerud and Ballard 1988, 1989). Connolly (1978, 1981) and our review suggest that predation does not cause ungulate population declines, although some studies implicated predation as the causative factor for moose and caribou population declines (Gasaway et al. 1992, Seip 1992). In altered ecosystems such as those in the contiguous United States, and the Southwest in particular, prey populations may not respond or behave as those in unaltered or natural systems. In such systems Van Ballenberghe and Ballard (1994) concluded that predation may or may not be strongly limiting or regulatory, depending on degree of human influence on predators, prey, and habitat and on presence and relative densities of all species of predators. These conditions may explain why, in many deer populations, predation is not an important mortality factor or, where predation is the most important limiting factor, why population growth is not impacted. Elimination of major predators such as wolves and grizzly bears, livestock grazing, competition from livestock and other big game species, loss and fragmentation of habitats, and other major human influences alter relationships among predators, habitat, weather, and harvest by humans. Major changes in predator species composition also appear to alter how predators affect ungulate populations such as mule deer.

Biologists continue to argue whether predator kill rates depend on density of prey species or on other factors. Kill rates appear to depend on whether the predator species is an obligate or facultative carnivore. For obligate predators, kill rates appear fairly consistent over a wide range of prey densities (Ballard and Van Ballenberghe 1998). Kill rates of facultative carnivores such as bears and perhaps coyotes have been thought or assumed to be independent of prey densities. However, kill rates by facultative carnivores may actually be more dependent on prey density than kill rates of obligate carnivores, particularly for predation on neonates. Solomon (1949) and Holling (1959) first proposed the idea of a functional response of predators to prey densities. Holling (1965) experimented with consumption of nonmovable sawfly (*Neodiprion sertifer*) cocoons or dog biscuits by small mammals. Small mammals continued eating these items to the point of satiation. Predation on neonate ungulates may fit this pattern because they are largely stationary for several days, whereas predation on adults probably does not demonstrate a strong functional predator response. However, this may change when adults become vulnerable due to weather conditions. Predation by wolves and mountain lions fits the scenario of obligate carnivores, whereas predation by bears and coyotes may fit that of facultative carnivores.

Black bears appear to have greater reproductive rates and survival when neonate ungulates are available as prey (Schwartz and Franzmann 1991). Perhaps the same is true for facultative carnivores like coyotes. Like bears, coyotes appear to have the ability to switch to other food resources, such as fruits, and thus are not dependent on ungulates for survival. Such a system complicates attempts to make generalized statements about effects of predation on deer.

Several criteria exist that may help identify when predation has become an important mortality factor. First, predation must be identified as an important source of mortality. Seasonal or long-term changes in fawn:doe ratios can indicate when most losses are occurring, but can not be used to determine causes for changes. Simple changes in fawn:doe ratios can not be used to determine whether predation is a limiting factor. Only through intensive studies can predation be identified as a significant mortality factor. If predation has been identified, managers must estimate the deer population's relationship to habitat carrying capacity to determine whether predator control may be warranted.

Additional experimental long-term research, particularly on coyote, mountain lion, and black bear predation, is needed to clarify the role of predation on deer. Photo courtesy of Arizona Game and Fish Department.

As mentioned earlier, few managers know or can measure K, but several indices of relationship to K are available. Low natality rates, low fawn:doe ratios, poor body condition, high utilization of available forage, and high deer population densities should provide a reasonable indication that a deer population may be at, near, or above habitat carrying capacity. Unfavorable weather conditions may alter this relationship, and if predator reduction were conducted, then managers should expect a depressed prey response until weather conditions become more favorable. If predation has been identified as a major limiting factor and the deer population is well below K, other important factors must be considered before initiating predator reduction.

Costs and benefits of predator reduction programs

Historically, 3 methods were used to reduce predator populations: poisoning, trapping, and shooting from helicopters and fixed-wing aircraft. The toxicant Compound 1080 appeared to be relatively effective to reduce predator numbers, but its use on public lands was banned in 1972 (Connolly 1978) because of public distaste for government killing of predators and deaths of many nontarget species (Hamlin 1997).

Trapping also has been a popular method to reduce predator numbers. However, to significantly reduce predator numbers, trapping must extend well beyond the point of economic feasibility for most trappers. Further, trapping is effective only in small areas (Hamlin 1997). Small reductions in predator numbers are unlikely to have any lasting effect on predator populations. For example, Connolly and Longhurst (1975) estimated that coyotes could easily withstand annual harvests of 70%, and even with 75% harvest, coyote populations could persist for 50 years. Harvest levels for wolves must exceed 50% to cause significant population declines (Ballard et al. 1997).

Hamlin (1997) indicated that managers had used 2 approaches to reduce coyote numbers. The first was to reduce overall numbers over large areas and the second was to use selective control on individuals or small populations that likely accounted for most prey mortality. Trapping over large areas has been largely unsuccessful in achieving desired results of increasing game populations. Selective harvests immediately prior to denning may, however, reduce neonatal mortality in small areas (Hamlin 1997). He concluded that substantial knowledge of coyote territories and denning areas was essential for trapping to be effective and that intensive effort beyond levels resulting from fur price incentives was necessary to reduce losses of game to coyote predation. Aerial shooting is probably the most effective method to reduce predator numbers, but social acceptability is low (Boertje et al. 1996).

Relatively few data exist on benefit:cost ratios of predator control programs, and few studies have actually demonstrated that reductions in predators actually resulted in increased human harvests. Notable exceptions were provided by Boertje et al. (1996), who indicated that wolf control and mild weather conditions resulted in harvest of several thousand additional moose and caribou, as compared to harvests predicted without wolf control. Economic benefits were realized by Alaska and hunting-related businesses profited with increased game availability. Ballard and Stephenson (1982) indicated that an average of between $770 and $873, excluding personnel costs, was spent for each wolf harvested by aerial shooting in south-central Alaska, whereas Reid and Janz (1995) estimated that resident deer hunters on Vancouver Island, British Columbia, received a $5.90 benefit for every $1.00 spent on wolf control. Even fewer data exist concerning benefit:cost ratios for control programs involving mule or white-tailed deer.

The Western States and Provinces Deer and Elk Workshop (R. M. Lee, Arizona Game and Fish Department, unpublished data) surveyed western states and provinces to determine whether they practiced predator reduction to increase wild ungulate populations and determine annual expenditures. At the time of the survey, only British Columbia indicated wolves, mountain lions, and bears were important predators of mule deer and that they intended to provide more liberal predator hunting and trapping seasons in areas where predation was suppressing deer populations. They also indicated that wolf reduction may be essential to maintain ungulate populations at prescribed levels in some areas. Alaska, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Texas, and Washington reported they did not have predator reduction programs to benefit big-game species, but they did have programs for problem wildlife or depredation reduction for livestock or other agriculture programs. Arizona was one of the few states that had an active predator reduction program to reduce coyote populations to improve pronghorn (*Antilocapra americana*) fawn survival

Deep snow makes deer more vulnerable to predation. Photo by Len Carpenter.

in specific areas; annual expenditures were approximately $22,900. Only Colorado and Montana indicated annual costs for depredation reduction ($120,000 and $60,000, respectively). Since the 1997 survey, predator reduction programs have been initiated in Alaska, Nevada, New Mexico, and Utah.

Recently, Utah approved predator management plans for 15 management units to try to reduce mountain lions and coyotes and thus benefit mule deer populations (Bates and Welch 1999). Bodenchuk (United States Department of Agriculture [USDA], Animal Plant Health Inspection Service, Wildlife Services, unpublished letter to Mr. Jim Karpowitz dated 1 June 1999) summarized costs and benefits associated with predator control activities in 3 units (Henry Mountains, North Bookcliffs, and Pahvant). His analysis included several important assumptions: increases in fawn survival and deer herd numbers were entirely due to predator reduction, costs included all predator reduction for the deer program in addition to 50% of costs associated with domestic livestock depredation control, and the civil value of a deer in Utah was $300. Shooting from fixed-wing aircraft and helicopter in addition to ground shooting and trapping were used. Benefit:cost ratios for the 3 areas ranged from 11 to 23:1. However, Bates and Welch (1999) summarized the status of the 15 deer management areas after 3 years of predator control and found that treated and untreated areas increased or remained stable and that results were equivocal. Bodenchuk (USDA, Animal Plant Health Inspection Service, Wildlife Services, letter to Mr. Jim Karpowitz dated 1 June 1999) admitted that predator control activities were not entirely responsible for the increases in fawn survival because hunting pressure on bucks had decreased and that wet years had improved habitat and deer survival, but that "predator control projects have their place in wildlife management."

Human dimensions of predator management

Trapping as a method of harvesting furbearers for recreational use and for economic return appears to have become increasingly unpopular with the general public, particularly when leghold traps were involved. Recent ballot initiatives have banned or proposed banning trapping and using snares in Arizona, California, Colorado, and Massachusetts (Andelt et al. 1999). An initiative in Michigan attempted to ban spring bear hunting; in Oregon an initiative attempted to ban bear baiting and hounding for bears and mountain lions. Alaska voters banned use of aircraft to harvest wolves in 1998, but this initiative was recently overturned by the Alaska state legislature. Most individuals (75%) in the United States strongly or moderately approve of legal hunting and believe hunting should continue to be legal (Duda et al. 1998), particularly if hunting is for food, to manage game populations, or to control animal populations. Regardless, certain methods of and reasons for hunting or trapping are clearly not accepted by many members of the public. However, the public will apparently accept trapping and predator control under certain circumstances. For example, although most respondents to an Illinois survey disapproved of trapping, it received the most approval when involved with animal damage control (71%), animal population control (70%), or biological research (63%, Responsive Management 1994). In Utah, there was strong support for and strong opposition to use of predator control to protect game populations among the general populace (Krannich and Teel 1999). However, among hunting license buyers there was moderate support for controlling predators, whereas the general public was somewhat neutral on the issue (Krannich and Teel 1999). Messmer et al. (1999) measured public response to predator control of mid-sized carnivores to enhance avian recruitment. They found that the public was more prone to support predator reductions in avian populations if such control actions were surgical in nature rather than widespread. Clearly, wildlife managers need more information concerning public attitudes on large predator reductions to favor game species.

Conclusions

Numerous factors will dictate whether predator reduction may be warranted. These include public acceptance, scale, methodology, biological relevance, and relationship to habitat carrying capacity. Public acceptance of predator reduction has changed drastically during the past 4 decades. Public attitudes toward wildlife have changed along with changes in human population distribution, education, and economic status. A proportion of the human populace will not accept predator reduction, regardless of the reason (e.g., endangered species conservation and particularly for production of animals for sport harvest). Alaska probably has the best management data to support predator reduction in limited areas, but public controversy has stalled or canceled programs that were justified biologically (see Stephenson et al. 1995). Strong public support would be necessary to initiate predator reduction, even if biologically justified. Managers have a poor understanding of how the public views predator reduction programs and under what conditions such programs might be acceptable.

Scale of a predator removal program also will ultimately contribute to success of the program and must be addressed by wildlife managers. To date, all research (excluding that conducted on wolves) concerning predator removal programs to enhance deer populations has been conducted on small areas (i.e., <1,000 km^2). Although managers would like to affect ungulate populations over large areas, recent research suggests that the public is more likely to accept predator control if it is conducted in small areas.

Current bans on use of poisons restrict reduction methods to aerial shooting (from fixed-wing aircraft or helicopter), trapping, or ground shooting. Trapping and ground shooting are relatively ineffective by themselves to reduce predator densities. Thus, although aerial shooting is likely the most effective method, it also is the most expensive method. Aerial shooting in large areas to enhance ungulates at the population level will probably be cost-prohibitive unless specific areas are identified. For example, Smith et al. (1986) documented a 400% increase in a pronghorn population at Anderson Mesa, Arizona. Helicopter gunning was used during March through May to kill coyotes on a 490-km^2 area. Although they estimated that only 22–29% of the coyote population was removed each year, they speculated that removal of 30% of breeding females and disruption of denning activities may have had a disproportionate positive effect on the pronghorn population. They examined benefit:cost ratios and schedules for coyote reduction and found that the greatest benefit:cost ratio (1:92) occurred when reduction was conducted once every 2 years. If managers could identify similar types of areas, such as fawning concentration areas for mule or black-tailed deer, then intensive predator reduction could be feasible just prior to fawning, assuming that predation is a significant limiting factor and the prey population is below *K*. Available human dimensions research suggests that some predator reductions may be acceptable if such programs are viewed as focused, site-specific operations rather than broad-scale programs covering large areas.

Most studies we reviewed were relatively short-term and were conducted in relatively small areas, and only a few actually demonstrated increased fawn recruitment and subsequent larger harvests by humans (i.e., wolf reductions). Also, conditions that led to a particular deer population being limited by predation were poorly documented. Additional experimental long-term research, particularly on coyote, mountain lion, and black bear predation, is needed to clarify the role of predation on deer. An experimental approach is necessary whereby deer population performance in relation to predator removal is monitored in manipulated and unmanipulated areas. Such experiments should be conducted over sufficient time such that severe and favorable weather conditions occur. Confounding factors such as other predators, human harvests, and alternate prey species also must be measured to allow proper assessment.

Managers also need to document conditions under which predation becomes a significant limiting factor, identify conditions under which predator control should be implemented, and determine when control should be ended. Deer density in relation to *K* appears to be a key consideration. Deer densities vary widely over the range of deer distribution, but managers should qualitatively assess the relationship of individual deer herds to habitat carrying capacity. The lower a population in relation to *K*, the greater the likelihood that predator reduction would result in measurable increases in survival and herd numbers. Managers then need to determine when most mortalities occur and whether predation is an important cause. These types of information can be obtained by using methods varying from relatively inexpensive examination of autumn and winter fawn:doe ratios to expensive methods such as capturing and monitoring neonate fawns through a biological year to determine causes of mortality. Large losses immediately following parturition are usually indicative of populations experiencing high mortality due to predation. Managers then need to decide the scale of control in relation to resources available and public acceptance. However, determining when to halt predator control programs is equally important.

The literature has many examples in which predator reduction programs resulted in increased deer survival and populations quickly increased, only to exceed habitat carrying capacity. Managers should halt predator control well before deer populations reach these levels and ensure that harvests by hunters are adequate to stabilize deer numbers.

Perhaps one of the greatest needs is documentation of costs and benefits under varying levels of predator reduction. Although several studies demonstrated increases in deer survival in relatively small areas because of predator reduction, only a few studies on moose and caribou and one on black-tailed deer actually documented that increased survival was eventually passed on to hunters. The scale and level of predator management and public acceptance will likely determine whether predator control is a viable management tool. Lastly, managers need a better understanding of how the general public reacts to their programs; also needed is additional research on the human dimensions of predator control.

Recommendations

The relationship between predators and their prey is a very complex issue. The literature we reviewed is equivocal; in some cases predator control appeared to be useful in improving deer populations and in some cases it was not. Some similarities from cases in which predator control appeared to be effective are:

1) predator control was implemented when the deer populations were below habitat carrying capacity,
2) predation was identified as a limiting factor,
3) control efforts reduced predator populations enough to yield results (e.g., expected to be approximately 70% of a local coyote population),
4) control efforts were timed to be most effective (just prior to predator or prey reproduction), and
5) control occurred at a focused scale (generally <1,000 km2 [259 mi^2]).

Conversely, there were similarities where predator control was not effective or its effectiveness at improving mule deer populations could not be measured. These included:

1) when mule deer populations were at or near habitat carrying capacity,
2) when predation was not a key limiting factor,
3) where control failed to reduce predator populations sufficiently to be effective, and
4) where control efforts were on large-scale areas.

Numerous important factors must be considered prior to making a decision on whether to implement a predator control program. Minimally, the following steps should be in place:

1) a management plan that identifies the following: current status of mule deer populations and population objective desired from the predator control project, desired removal goals for the predator species, timing and method of removal efforts, scale of removal effort, and what other limiting factors may be playing a role in depressing mule deer populations;
2) an adaptive management plan that sets monitoring criteria that would result in evaluation of predator and prey populations and identifies thresholds at which predator control will be eliminated or modified.

One failure in much of the research that has been completed on the utility of predator control to improve mule deer populations is a lack of an adequate experimental design. Also, additional research is needed, particularly in social aspects related to predator control. To assist in improving the decision-making process related to predator management, we believe the following research is vitally needed:

1) Experimental, long-term research, particularly on coyote, mountain lion, and black bear predation, to clarify the role of predation on deer. An experimental approach is necessary whereby deer population performance in relation to predator removal is monitored in manipulated and unmanipulated areas. Such experiments should be conducted over a sufficient period of time that severe and favorable weather conditions occur. Confounding factors such as other predators, human harvests, buffer species densities, and habitat conditions also must be measured to allow appropriate interpretation of the study results.
2) Well-designed research to measure social attitudes toward various aspects of predator control programs. Minimally, we believe research should develop a better understanding of variation in public attitudes on methods of

predator control, timing of predator control, prey species thresholds that would call for implementation of a predator control program, and scale of a predator control program.

3) Research should include an analysis of cost:benefit ratios of any control efforts.

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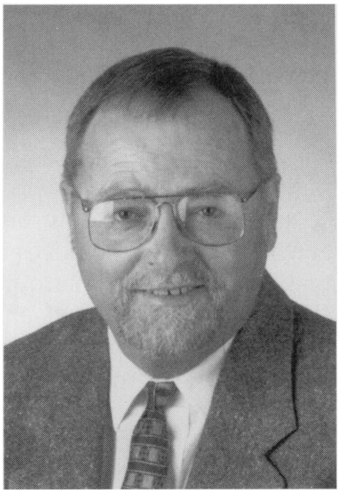

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