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ABSTRACT: Predation effects have been studied since the early days of wildlife management, with the goal of wildlife managers to balance wildlife populations with available habitat and management objectives. Still, research and public debate focuses on the degree to which vegetative carrying capacity (*K*) affects prey and the degree to which predation management could benefit prey species. *K*, to this point, has not generally considered the secondary effects that predators have on prey habitat availability. When setting wildlife management objectives, the relationship of predation impacts (i.e., factors that may cause mortality in a given species) to prey and available habitat and habitat availability must be examined carefully and understood. This paper discusses classic predator-prey relationships and the potential effects of secondary predation on prey. Managers must consider these effects and relationships to determine if, when, and how to implement an effective wildlife enhancement or predation management strategy.

KEY WORDS: carrying capacity, habitat availability, predation, predation risk, predator avoidance behavior, predator-prey relationships, prey behavioral shift, secondary impacts, secondary predation

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INTRODUCTION

Predation influences both predator and prey population sizes, behaviors and densities. In natural settings, predation "balances" with prey in some manner. However, numerous factors are responsible for wildlife population fluctuations, including habitat loss, weather, age and sex structure, disease, predation, predation risk, human interactions and competition with livestock and other wildlife (Wallmo 1981, Hall 1984, Whittaker and Lindzey 1999). At times, some prey suffer from excessive predation rates or risk and predation can drive prey populations below management objectives (Morse 1980, Edwards 1983, Lima et al. 1985, Ferguson et al. 1988, Hoban 1990, Lima and Dill 1990, Schmitz et al. 1997, Kie 1999, Hecht and Nickerson 1999, Creel et al. 2005). Professionals who manage wildlife populations for harvest may also have management objectives for wildlife populations other than population densities that exist in "balance." The reality is that without the intervention of an appropriate management strategy, we may be cheating ourselves into believing we are conserving natural communities (Hecht and Nickerson 1999).

Early detection and active management to reduce predation or predation risk may be important for prey population maintenance or recovery. For small or declining populations, the best hedge to increase numbers as quickly as possible is to reduce variability in productivity and survival (Hecht and Nickerson 1999). Predation or predation risks may affect adult survival, neonate survival, and recruitment or nesting success. Therefore, many wildlife management agencies have policies to: 1) protect critical wildlife habitats, 2) support reintroductions of native wildlife, and 3) protect seriously depressed wildlife populations. However, completely understanding predation, ecological factors, and predation effects is not an exact science, and in most cases, effects are inferred from observations of prey populations. Management strategies designed to protect resources may vary and may be solely related to prey species' populations and not habitat utilization. Wildlife managers must evaluate species populations and habitat utilization to most effectively reach management objectives or recovery goals.

PREDATOR-PREY RELATIONSHIPS

Vegetative carrying capacity (*K*) is an important concept with many implications for evaluating predation, predator-prey relationships and habitat utilization. For wildlife and range management, *K* is defined as the maximum number of a given species that can be supported in a defined habitat without permanently impairing the productivity of that habitat. Biological studies of population change suggest that once *K* is exceeded, a crash or collapse of the population follows. The population crash or collapse is normally associated with environmental degradation. *K*, to this point, has not generally considered the secondary effects that predators have on prey habitat utilization.

Ballard et al. (2001) described four predator-prey relationship models with emphasis on mule deer (*Odocoileus hemionus*). In brief, these models are: 1) low density equilibria, 2) multiple stable states, 3) stable-limit cycles, and 4) recurrent fluctuations. In each model, the relationship between predator and prey is examined in relation to prey and vegetative *K*, with predation being regulatory at low population levels[*] and non-regulatory as

[*] When populations are below *K*, predation and mortality factors are additive.

populations near $K^{\dagger}$. Less obvious, however, may be the behavior of prey to restrict their use of habitat due to predation risk (Hoban 1990). In theory, without the influence of predation, prey will occupy specific habitats because those are the habitats that best provide their bioenergetic requirements. However, if wildlife managers only evaluate vegetative K and do not consider the relationship of predation on prey utilization of available habitats or the landscape of the available habitat to allow for predator avoidance, their evaluations could be flawed.

In addition to the effects of primary predation, there is a growing body of evidence that points to significant secondary effects of predation (Wehausen 1996, Pitt 1999, Ripple and Larsen 2000, Ripple et al. 2001, Barber et al. 2004, Preisser et al. 2005). Secondary effects in this context are negative effects to prey because of "displacement" or antipredator behavior (i.e., adaptive shifts in prey behavior or habitat utilization) (Morse 1980, Edwards 1983, Risenhoover and Bailey 1985, Lima et al. 1985, Ferguson et al. 1988, Hoban 1990, Lima and Dill 1990, Schmitz et al. 1997, Kie 1999, Pitt 1999, Creel et al. 2005). Secondary predation effects result in trade-offs by prey to reduce predation or predation risks (Burk 1982, Lima and Dill 1990, Hecht and Nickerson 1999, Ballard et al. 2001, Preisser et al. 2005). An effect of secondary predation can be restricted range utilization by prey to areas adjacent to escape terrain/cover (Bergerud et al. 1983, Bergerud and Page 1987, Wehausen 1996, Bleich et al. 1997, Kunkel and Pletsher 2000, Creel and Winnie 2005, Creel et al. 2005), interspecific competition (Gill et al. 2001) and distribution of prey over their range (Messier and Barrette 1985, Molvar and Bowyer 1994). The prey behavioral response to predation or predation risk may result in reduced nutrient intake and lower offspring survival leading to a population decline or an animal in poor condition that may choose a foraging strategy more risky than an animal that is well fed (Skogland 1991, Bliech et al. 1997). Another consideration of secondary predation and the distribution of prey (e.g., large herbivores) is the movement of prey onto private lands (Gude and Garrott 2003) and the resultant foraging (Schmitz et al. 1997, Ripple and Larsen 2000, Ripple et al. 2001).

Morgantini and Hudson (1985) reported that undisturbed elk (*Cerrus elaphus canadensis*) preferred grazing to browsing but avoided open grasslands during hunting seasons (i.e., predation risk). Gray wolf (*Canis lupus*) restoration in Yellowstone National Park (YNP) has provided a unique opportunity to examine wolf predation and prey responses. For example, elk occupied riparian and aspen habitats in YNP prior to wolf reintroduction; however, following wolf reintroduction, increased aspen and willow regeneration in the Lamar Valley and Gallatin Range, Montana was noted, ostensibly because of reduced elk use of meadow habitat due to predation risk (Ripple and Larsen 2000, Ripple et al. 2001, Ripple and Beschta 2004).

To further bolster this observation, Gude and Garrott (2003), Creel and Winnie (2005), and Gude et al. (2006) reported that after a successful wolf predation event or human hunting, elk moved from the area or fewer elk occupied open areas. Gude and Garrott (2003), Creel and Winnie (2005) and Creel et al. (2005) reported elk were found in smaller groups and their distribution in available habitats was different following the re-introduction of wolves. Elk reduced their use of preferred grassland habitat when wolves were detected. Hunting success outside of YNP was also impacted because of behavioral changes in elk caused by wolves.

Hamlin and Cunningham (2009) reported that the combination of changed elk distribution and behavior because of predation risk caused "indirect" population-level effects. Morgantini and Hudson (1985) concluded that special winter elk hunting seasons caused a shift in the diet selection of elk to vegetation that was less digestible. It is reasonable to assume that during severe winters, when digestible energy is limiting, a decrease of digestible energy caused by either hunting or predation risk would have a negative impact on the welfare of elk. In addition, along with a possible impact on elk, competition between elk and mule deer for browse, particularly in winter, could have a negative impact on deer populations (Keegan and Wakeling 2003).

Wehausen (1996) and Hayes et al. (2000) examined mortality patterns of bighorn sheep (*Ovis canadensis*). Their results indicate that even a small number of mountain lions (*Puma concolor*) may effect bighorn sheep survival, and population-level impacts may be exacerbated if female sheep are heavily preyed upon or displaced into less optimal habitat (i.e., predator avoidance behavior). Wehausen (1996) believed mountain lion predation was responsible for behavioral changes and winter range abandonment and a subsequent population crash of bighorn sheep in the Sierra Nevada. The bighorn population declined from the indirect effects of mountain lion predation that changed the sheep's habitat selection. Thus, bighorn sheep distribution and the numbers that their ranges support are dependent on the predators that confine them to those ranges (Wishart 2000).

Edwards (1983), Ferguson et al. (1988), and Kie (1999) suggest that other ungulates modify their behavior and occupy habitats of poorer quality to avoid predators. Edwards (1983) states that, "Although a direct link between nutritional status and reproductive rate has not been demonstrated for moose, indirect evidence suggests that poor diet may increase mortality or lower reproductive success." Robinette et al. (1955) and Julander et al. (1961) reported reproductive success in mule deer is directly related to the quality of summer forage. Ferguson et al. (1988) suggested that caribou (*Rangifer tarandus*) sacrificed higher quality forage on a year-round basis to avoid a high risk environment even though, in some winters, the animals, especially calves, face starvation. West (2002) reported on predator exclusion fencing for waterfowl protection at Bear River Refuge in Utah. Prior to his investigations, waterfowl failed to nest on upland sites set aside for nesting. However, after installation of mammalian exclusions, ducks initiated nesting at a rate up to 1 nest/2 acres, indicating that the

† At K, density dependent mortality is compensatory (i.e., total mortality remains constant).

risk of predation affected nesting habitat selection by the birds. Thus, secondary predation impacts may exist for many predator-prey relationships. If prey are using lower quality habitat, the secondary effect of predation may cause a decline in the population (Hamlin and Cunningham 2009) and can affect prey distribution, habitat utilization, and abundance (Creel and Winnie 2005, Creel et al. 2005, Gude et al. 2006).

FACTORS AFFECTING PREDATION RATES

Within predator-prey relationships, a number of factors can influence predation rates and effects. In some cases, knowledge about prey population sizes, trends, and age structure are required to better understand the effects of predators on prey. There are different effects from predators removing a fixed number of prey from a small population than from a large population. Similarly, the removal of juveniles or males may not have the same population-level effects as removing reproductively viable females. Additionally, these factors can work together to affect prey and predator populations.

Habitat Factors

Habitat loss/degradation, disease, and other factors have resulted in declines in species throughout their ranges. To compound this, especially to threatened or endangered species, some predators have experienced unnatural population increases because of human development, elimination of natural predators, supplemental foods, and other factors. Further, components of habitat make prey more or less vulnerable to predation. Habitat may be linear, cover may be reduced or enhanced, or edge may be increased, which could make prey more easily detected and predators can more effectively search the habitat (Wilcove et al. 1986, Paton 1994). Linear habitat includes dikes, beaches, and riparian corridors that could be used for nesting, brood rearing, or fawning.

In deserts, limited access to water can concentrate predators and prey near water. Water sources, some built for wildlife, may increase the suitability of habitat for prey but also for predators. Such may be the case where desert bighorn sheep (*Ovis canadensis nelsoni*) existed at low densities prior to construction of water catchment devices. However, following the installation of water sources, predators may also be sustained in these areas and can impact prey populations (Hayes et al. 2000, O'Brien et al. 2006).

Burned areas or other open habitats, which may enhance habitat for some species, can increase predation impacts in the short term (Pierce et al. 2004). Possible impacts from wildfires include decreased cover for prey, concentration of predators in unburned areas, and the removal of rodents that serve as buffer prey.

There is also a correlation between drought and lower fawn survival for mule deer and pronghorn antelope (*Antilocapra americana*). Predation related impacts may include reduced fawn weights (extending the vulnerability of fawns), reduced cover for fawns, increased duration of feeding bouts (increasing predation risk), and/or decreased buffer prey. Regardless, drought is one recurring environmental factor that affects prey and habitat and can compound predation impacts.

While cover is essential for predator avoidance in some species (e.g., ring-necked pheasants *Phasianus colchicus*, ducks, deer fawns), excessive cover can be detrimental for other species that rely on vision to detect predators. Pronghorn antelope rely on sight to detect coyotes (*Canis latrans*) and other predators, and increased vegetation can increase predation risk (Goldsmith 1990). It has been reported that prairie dogs (*Cynomys* spp.) also rely on sight for predator detection, and increased vegetation can increase predation (King 1955, Koford 1958, Slobodchikoff and Coast 1980).

Perches, including power transmission lines, can also increase predation by raptors or ravens (*Corvus corax*) (Coates 2006). Both direct predation and nest predation by ravens may increase because of the presence of power lines. Powerlines can also provide nesting structures for ravens and fragment habitat (Rowland 2004, Coates 2006).

Finally, availability of escape cover can affect predation impacts. It is generally accepted that rugged terrain provides escape habitat for bighorn sheep (Wishart 1978). Thick cover, such as cattails (*Typha* spp.) and *Phragmites australis* provides escape habitat for pheasants. A lack of escape cover can either increase predation or cause otherwise suitable habitat to go unused (Risenhoover and Bailey 1985, Wehausen 1996, Frey et al. 2003). Thus, managers' evaluations must consider the species to be protected, their habitat preferences, and their habitat utilization.

Prey Factors

While predation helped form prey species evolution, certain aspects of prey populations make them more or less vulnerable to excessive predation impacts. Depressed prey populations can be more vulnerable to predation effects. It is generally accepted that predation effects are compensatory at or above K (Ballard et al. 2001) and additive at some point below K.

Breeding synchrony, and thus synchronized births, influence predation effects. "Flooding" predators with neonates is an evolutionary strategy to ensure that predators cannot kill all of the neonates before they outgrow their predation vulnerability (Geist 1982). However, at low population levels, predators can kill a larger percentage of the neonates, or if low male:female ratios exist, breeding can be extended and births spread over a longer time period, increasing the timeframe when neonates are vulnerable to predators.

Group size and composition also affect an individual's vulnerability to predation and may affect overall predation impacts if those individuals are crucial to the population. Hornocker (1970) noted that mule deer bucks were more vulnerable to predation by mountain lions. and theorized it was because of smaller groups and rugged terrain inhabited by older bucks and mountain lions. Mooring et al. (2004) noted similar risks for bighorn rams. Conversely, larger groups can increase the likelihood of predator detection and decrease the individual predation risk (Geist 1982).

The availability of alternate prey can affect predation in two opposing directions. Alternate prey may support increased predator populations and prevent decreases in predator numbers or attract predators to the area. Shaw (1989) and Cunningham et al. (1995) noted that mountain lion populations, supported by other prey, did not fluctuate with declines in mule deer populations. Cattle (*Bos* spp.) supported mountain lions in Arizona (Cunningham et al. 1995), and the availability of cattle increased mountain lion impacts on deer (Shaw 1977). Wagner and Stoddart (1972) and Clark (1972) noted that coyote populations increased with jackrabbit (*Lepus californicus*) abundance in northern Utah and southeastern Idaho, and livestock predation increased during downward cycles in jackrabbit populations. Conversely, when available, increased numbers of alternate prey can diminish predation impacts on any one species, mitigating some predation impacts (Connolly 1978).

Predator Factors

Just as habitat and prey affect predation, prey may be affected by characteristics in predator populations. In addition to simple numbers of predators, social structure of the predator population may affect predation rates. Established breeding pairs have extensive knowledge of their territories and may be able to affect prey to a greater extent than younger, newly established pairs. Wagner and Conover (1999) noted an apparent "residual effect" of livestock protection in the year following coyote removal, which may be explained by fewer experienced "alpha" coyotes and tenure on the territory.

In livestock predation, the vast majority of domestic lamb (*Ovis aries*) losses to coyotes are attributed to breeding (alpha) pairs (which represent <50% of coyote populations) (Connolly et al. 1976), and research suggests a similar relationship may exist in wildlife predation (Gese and Grothe 1995). Mule deer and pronghorn fawns and all ground-nesting birds are vulnerable, and may be impacted, during predator offspring rearing because of increased food requirements (Till and Knowlton 1983, Till 1992).

Predator population demographics are also critical to understanding predation impacts. In many cases, coyotes do not breed their first spring but form monogamous, territorial pairs and whelp during their second year (Bekoff 1978). Red fox (*Vulpes vulpes*), however, breed and whelp their first year (Creed 1960, Storm et al. 1976). Essentially, in most systems there are non-breeding coyotes in the population during the late winter and spring, while there are practically no non-breeding red fox (Strom et al. 1976), thus putting more pressure on breeding fox pairs to provision offspring.

Territoriality affects the density of predators and can affect predation rates through population regulation. Raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*) do not appear to be territorial and are more regulated by food availability (Urban 1970, Sonenshine and Winslow 1972, Hoffman and Gottschang 1977, Rivest and Bergeron 1981, Storm and Tzilkowski 1982, Rosatte 1987). Red fox are territorial during breeding, but can be compressed into very small territories if food is available (Harris 1977, MacDonald and Newdick 1982, Harris and Rayner 1986). Breeding coyotes are territorial, with non-breeders existing in spaces between territories or in "unoccupied territories" (Bekoff 1978). Mech (1977) suggested that wolves avoided the "buffer zones" between wolf packs to prevent intraspecific strife between neighboring packs. Thus, territoriality in predators may exist as a breeding strategy or to limit access to food resources, and the degree to which territories overlap can also influence overall predator abundance and predation rates.

Individual behavior cannot be discounted as an operative mechanism for predation impacts. Some mountain lions seem to specialize on bighorn sheep and horse foals (*Equus caballus*) as principal prey and appear to hunt them at disproportionally higher rates (Turner et al. 1992, Wehausen 1996, Kamler et al. 2002, Mooring et al. 2004). Mooring et al. (2004) also noted that some mountain lions concentrate on elk, especially in late winter and through the calving season. Likewise, black bear (*Ursus americanus*) appear to concentrate on cervid calving areas and specialize on preying on cervid calves and fawns during a short period of the year (Wilton 1984, Wilton et al. 1984).

Finally, the complex of predators may have an increased impact on a single resource. Predation or predation risk from bears, coyotes, wolves, mountain lions, or hunters singularly may not impact prey, but combined they may impact prey survival in some systems, particularly if prey are impacted at different stages. Red fox management for sage grouse (*Centrocercus urophasianus*) protection aided adult grouse survival in Strawberry Valley, Utah, but chick-to-hen ratios remained chronically low until raven removal was incorporated into the strategy (J. Flinders, Brigham Young University, pers. commun., 2005).

CONCLUSION

Biologists, researchers, and academia will continue to debate whether predation is regulatory or a limiting factor. Conditions that allow predation to become a factor limiting recruitment or survival are dynamic in natural ecosystems with a full complement of predators, which complicates management. Managers need to determine when most "mortalities" occur and whether primary predation, secondary predation, or other factors are an important cause.

Further studies may be required to determine if secondary predation is adversely affecting wildlife populations (Lima and Dill 1990), as the secondary effects of predation are often difficult to observe or understand. These studies may result in redefining "carrying capacity" as currently used, or better describe the role predators play in prey habitat utilization. While the models described by Ballard et al. (2001) can incorporate secondary predation, the secondary effects would lower *K* based on the prey populations' use of the habitat. Interspecies relationships between predators and prey certainly affect the utilization of food, water, cover, and space, and may make habitat availability more difficult for prey to use and for managers to interpret. If predators drastically influence prey behavior and displace those prey into less optimal habitats, managers have a more difficult job, and they must consider the secondary effects of predation to effectively manage wildlife populations under their responsibility.

Limited habitat may require management/enhancement, and habitat management is a process and should not solely be a goal for management agencies. Once habitat is manipulated, it progresses toward a climax vegetative community. Wildlife biologists and landowners must commit to habitat management on a sustained basis to meet the diverse needs of multiple species and humans. Because predation can affect prey habitat utilization, because predation management can benefit prey, and because habitat management is a process, it may be inappropriate to look at the issue as "habitat v. predators." Predation management can play a role in assisting species within the confines of existing habitat, and habitat management provides habitat for the future.

Managers are best served to approach *K* and predation management with an open mind, remembering that the objective is active wildlife management. Reducing predation is sometimes a necessary component of strategies to accomplish management or recovery objectives (Hecht and Nickerson 1999). The best overall predation management strategy is an adaptive approach that monitors many factors, considers a full range of management strategies, evaluates effectiveness, and makes appropriate adjustments (USDA 1997).

Predation management is a critical component of wildlife management, and when done in as targeted a manner as possible, it can be accomplished without negative environmental impacts. Predation management should be designed as a component of an adaptive management strategy, considering both non-lethal and lethal techniques, where populations are not meeting objectives or recovery goals. The predation management strategy must address the critical components (i.e., adult survival, recruitment, nest success) identified by managers as lacking in performance, so that management objectives can be reached or maintained as effectively as possible.

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