ECOSYSTEM IMPACTS OF PREDATORS: TO CONTROL OR NOT TO CONTROL, THAT IS THE QUESTION

SCOTT E. HENKE, Caesar Kleberg Wildlife Research Institute, MSC 218, Texas A&M University-Kingsville, Kingsville, TX 78363

Abstract: Wildlife managers often conduct predator control programs as a means to aid livestock and wildlife enterprises. The decision to initiate predator control typically is driven by single species management. I argue that biologists should consider the direct and indirect impacts of predator removal on ecosystems prior to the initiation of control programs. Predators may play a keystone role in the ecosystem, and removal of predators could have cascading detrimental effects at each trophic level.

"To keep every cog and wheel is the first precaution of intelligent tinkering."

Aldo Leopold

A long-held debate in ecology has been whether ecosystems are structured from the top-down (i.e., predator driven) or from the bottom-up (i.e., resource limited). The top-down theory states that the interactions between higher trophic level consumers and their prey influence the structure of the lower trophic community (Estes 1996). On the other hand, Hunter and Price (1992) argued that bottom-up influences were the driving force behind ecosystem stability because without primary production the remainder of the ecosystem would fail. However, Hunter and Price (1992) did recognize the benefits to the ecosystem that predators exert on their prey.

Examples can be found in the literature that will lend support to either theory. However, both theories have a component that suggests predators influence their environment, either as feedback mechanisms within the bottom-up model or as the main controlling factor within the top-down model.

Unfortunately, the impacts that predators have on ecosystems rarely have been considered by wildlife managers. Few researchers have looked beyond the impacts of predation on a single prey species, and usually only if the prey was a game species. Biologists should consider ecosystems rather than just the needs of a single species before making management decisions. For example, white-tailed deer (*Odocoileus virginianus*) are a profitable commodity in Texas and coyotes (*Canis latrans*) eat white-tailed deer fawns. On the surface it sounds reasonable to conduct coyote control to improve fawn recruitment. However, before such a program is initiated several questions should be answered, such as "will reducing the coyote population affect the dynamics of the ecosystem?" (i.e., Will other predators, such as skunks (*Mephitis* sp.) and raccoons (*Procyon lotor*), become more abundant and potentially affect other game species such as bobwhite quail (*Colinus virginianus*), and is this an acceptable consequence for additional fawn recruitment?)

The objectives of this paper are to 1) define terminology associated with predation to illustrate that all predators are

not necessarily alike, and 2) provide examples of predators in keystone roles within their respective ecosystems to illustrate the importance of the ecosystem approach to management decisions.

PREDATION TERMINOLOGY

The term "keystone" refers to a species that has a disproportionate effect on the persistence of other species and whose removal leads, often indirectly, to the loss of many other species in the community (Paine 1969). Keystone species are strong interactors and can affect the persistence, abundance, and distribution of other species, nutrient cycling rates, and ecosystem resiliency to perturbations (Vogt et al. 1997). Removal of keystone species typically results in loss of ecosystem diversity and stability (Paine 1969, Henke and Bryant 1999). Losing a keystone species can create a series of linked extinction events (i.e., extinction cascade) that result in a degraded ecosystem with biodiversity loss at each trophic level (Primack 1998). Therefore, biologists need to be aware of the presence of keystone species in order to make informed management decisions. One of the first examples of a predator as a keystone species involved intertidal ecosystems off the Washington coast (Paine 1969). Purple sea stars (*Pisaster ochraceus*) prey on several species of invertebrates, allowing many prey species to coexist. After sea stars were experimentally removed from some tide pools, the population of California mussels (*Mytilus californicus*) dominated those sites and reduced the diversity of invertebrates from 15 to 8 species. Reintroducing sea stars to the affected tidal pools did not restore the biodiversity of the ecosystem to pre-treatment levels.

Another concept often associated with predation is that of a numerical versus functional response of predators to their prey. A numerical response occurs when the numbers of predators increase with an increase in the density of the prey population. Coyotes and lynx (*Lynx canadensis*) have been documented to respond numerically to increased abundance of snowshoe hares (*Lepus americanus*) (O'Donoghue et al. 1997). However, the tendency of predators to switch their diets toward an abundant prey is considered a functional response. Holling (1959) described 3 basic types of functional responses (i.e., Type I, Type II, and Type III). A Type I functional response is one where the number of prey consumed is directly proportional to prey density. Such a response has been documented under laboratory conditions with invertebrates, but is considered rare for wildlife species. A Type II functional response, which is the response most frequently observed, occurs when the consumption rate of a predator rises with an increase in prey density, but then gradually decelerates until a plateau is reached at which consumption rate remains constant at increasing prey densities. Basically a plateau occurs because either the predator is at its maximum efficiency concerning handling time of prey and/or predators become satiated. Type II functional responses have been documented in single predator-prey ecosystems such as wolves (*Canis lupus*) and moose (*Alces alces*) on Isle Royale (Mech 1966) and coyotes and black-tailed jackrabbits (*Lepus californicus*) in Utah (F. C. Wagner, pers. comm.). A Type III response is a sigmoidal response of predators to their prey. A common way in which a Type III response is observed is when prey switching occurs on the part of the predator. Predators have

a low efficiency of consumption rate or a lack of search image when prey density is low. However, an increase in prey density leads to an increase in the predator's searching efficiency or a decrease in its handling time, thus the consumption rate rises faster than would be expected from an increase in prey density alone. Finally, the Type III curve plateaus as is seen in a Type II response. Such a response is observed in multi-prey ecosystems where predators are dietary generalists (e.g., coyotes in southern Texas; Henke 1992).

Finally, the terms facultative and obligate need to be defined. An obligate predator is a dietary specialist and focuses mainly on one prey. A facultative predator is a dietary generalist and typically prey switches (inclusive of vegetative matter). Although exceptions can occur, obligate predators typically exhibit Type II functional responses, whereas facultative predators, on average, exhibit Type III responses.

The importance of this component of discussion is to realize that not all predators are alike. The end result of predation may appear the same, but the process by which it occurred may have been quite different. Therefore, the influence a specific predator has on its ecosystem will depend on several factors including if the predator lives in a single or multi-prey system, a single or multi-predator system, if it's an obligate or facultative predator, and the abundance of prey and other predators.

EXAMPLES OF PREDATORS IN KEYSTONE ROLES

My viewpoint concerning predators and their impacts on ecosystems evolved during my dissertation work involving coyotes on short-grass prairies in western Texas. During this study, I evaluated the effects of removing coyotes on sympatric populations of rodents, lagomorphs, raptors, and mammalian mesopredators (Henke 1992). Faunal communities were examined on 4 5000-ha study sites for 1 year prior to coyote removal efforts (i.e., pretreatment period) and then for 2 years during which coyotes were taken from 2 sites (i.e., treatment sites) by aerial gunning every 3 months. A total of 354 coyotes were killed on treatment sites, which resulted in coyote density being reduced by about 50% (i.e., from 0.12 to 0.06 ± 0.01 coyotes/km^2). Coyote density remained stable on comparison sites. Faunal communities between the 4 sites were similar during the pretreatment period; however, within 9 months following the initiation of coyote removal on treatment sites rodent species richness and rodent diversity drastically decreased. Where once 12 rodent species could be found, only Ord's kangaroo rats (*Dipodomys ordii*) remained. Ord's kangaroo rats became the competitive dominant rodent species to the exclusion of all other species within grasslands and nearly so in shrublands; only southern woodrats (*Neotoma micropus*) were found to coexist with kangaroo rats in shrublands in the absence of coyote predation. Also, black-tailed jackrabbit populations increased 3-fold on treatment sites. Longland (1991) found that foraging by jackrabbits declined in areas >10 m from shrub cover. It was suggested that the foraging radius of jackrabbits would increase with a reduced risk of predation by coyotes. Consequently, increased foraging radius by jackrabbits also could intensify competition between jackrabbits and livestock. Therefore, due to a reduced risk

of predation by coyotes, jackrabbits exhibited a numerical response and potentially a functional response with regard to forage. Lastly, mesopredators, such as striped skunks (*M. mephitis*), gray foxes (*Urocyon cineroargenteus*), badgers (*Taxidea taxus*), and bobcats (*Felis rufus*) increased on treatment sites. Because mesopredators are known to consume eggs and young ground-nesting birds, an increased abundance of mesopredators could affect ground-nesting avian species. Overall, such findings were consistent with the predator-mediated coexistence hypothesis, which suggests that a keystone predator (i.e., coyote) can influence faunal community structure.

Other examples of coyotes playing keystone roles in ecosystems come from examples of mesopredator release (i.e., an increased abundance of small to mid-sized predators in the absence of a competitive dominate predator). The reduction or localized extinction of coyotes caused mesopredator populations to increase, which in turn, caused reductions or localized extinctions of prey species (Soulé et al. 1988, Vickery et al. 1992, Ball et al. 1995). Antagonistic behavior by coyotes has been suggested for reducing interspecific competition and may result in spatial segregation between potential competitors (Sargeant et al. 1987).

Another example of a predator as a keystone species is sea otters (*Enhydra lutris*) and their effect on kelp forests. Sea otters regulate herbivore populations, mainly sea urchins (*Strongylocentrotus* spp.), and thus protect kelp forests from overgrazing (Estes and Palmisano 1974). In the absence of otters, a trophic cascade of destructive events occur (i.e., greatly reduced kelp production, loss of available nutrients, loss of fish biodiversity, etc.).

An additional example of predatory mammals in keystone roles include the wolf-moose-balsam fir (*Abies balsamea*) system on Isle Royale (McLaren and Peterson 1994). The predator-prey cycles between moose and wolves have been well documented (Mech 1966, 1977). However, when wolf numbers are low and moose are abundant, growth rates of young firs are greatly reduced. Thus forest regeneration on Isle Royale is affected by wolf density.

CONCLUSIONS

Predators often are removed from areas due to their predatory nature, regardless of the effect such removal may have on the ecosystem. The debate continues; should predators be controlled? The answer is a human valued judgment. However, before biologists and wildlife managers answer that question, the ecosystem should be fully considered. Often undesirable indirect effects are the consequence of single species management decisions. Biologists need to remember that indirect effects are the rule rather than the exception in most ecosystems (Meyer 1996). Because biologists have such a limited understanding of ecosystem processes, perhaps it is best to heed the words of Aldo Leopold, *"To keep every cog and wheel is the first precaution of intelligent tinkering."*

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