Proceedings, Western Section, American Society of Animal Science
Vol. 40, 1989

PREDATOR BIOLOGY AND LIVESTOCK DEPREDATION MANAGEMENT

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Summary

Predators pose significant economic liabilities to some livestock grazing operations. Understanding predator biology and behavior can help improve the efficacy, efficiency, and selectivity of depredation control programs as well as reduce some undesirable consequences of predator removal. Current knowledge of coyote (Canis latrans) population processes and behavioral patterns illustrate ways of applying species biology to achieve management objectives. The need to understand natural patterns and to define depredation problems in biologic terms is an important aspect of developing the more intensive management programs dictated by controversial and multi-valued species.

Introduction

I want to start with several assumptions. First, the native eagles, bears, cats, and dogs of this country are equipped with claws, talons, or teeth so they can make at least part of their living by capturing, killing, and consuming other animals. Second, it is unreasonable to expect them to respect human claims about the ownership of domestic stock; hence depredations on sheep, cattle, and other domestic animals must be expected. Third, let's also accept the premise that depredations may be serious and some agricultural enterprises can be placed in economic jeopardy by losses to predators despite current depredation control programs. The reader is referred to U. S. Fish and Wildlife Service (1978, 1979), Wade and Connolly (1980), Wagner (1988), and others for further discussion of these assumptions.

Federally supervised depredation control programs currently rely primarily on removal or translocation of predators to reduce the risks to livestock. Such activities are not without controversy because various segments of society apply different values and priorities where predators are involved. In addition to depredation reduction, these include consumptive uses for sporting or economic purposes and non-consumptive aspects associated with aesthetic and "ecologic" goals. Agencies trying to meet the varied goals of the 3 major public interest groups are faced with more intense management concerns than when only single interests must be served. To strike some balance among the good and the bad, the desired and the undesired, the best biologic and behavioral information available should be incorporated into our management programs. Although frequently defined in economic terms, the most effective resolutions of the problem come from understanding the problem in biological terms.

Hence, I want to identify some of the biological patterns that have bearing on interactions between coyotes and livestock. While generalities seldom account for every case, understanding patterns provides predictability, and that creates a basis for achieving the desired and defending against the undesired. Although the following discussion centers on patterns related to coyotes, the species most familiar to me, depredations by other predator species certainly must be associated with patterns of their own.

Generalizations about Coyotes

The coyote is a medium-sized (25-30 pounds) wild canine native to North America. It is a versatile consumer, feeding on a wide variety of plant and animal matter (Sperry 1941, Andelt et al. 1987). Overall, rodents and lagomorphs (rabbits and their allies) are the principle prey of coyotes, but they can kill animals 6-8 times their own size under the appropriate circumstances. Depredation on livestock is not uncommon, and although coyotes sometimes kill calves, turkeys or other stock, their depredations on livestock are concentrated in the sheep and goat industries.

Patterns in Coyote Abundance

Geographic patterns. Originally, the coyote was considered an animal of the western plains and mountains. Now they occur from coast to coast and from the arctic to Costa Rica (Bekoff 1977). Based on data from the Westwide Survey of Predator Abundance conducted by the U. S. Fish and Wildlife Service between 1972 and 1981 (Bean and Roughton 1980, Bean 1982) Knowlton and Stoddart (1983) pointed out the mean index of coyote abundance increases nearly 2-fold from northern states to southern states. The same data also suggest that coyotes are moderately abundant in the Pacific coast states, much less abundant in the arid states of the Great Basin, and are most common on the prairies of middle America.

Although the foregoing suggests that coyote abundance reflects the general ecologic pattern of primary productivity, supporting documentation is meager. Knowlton and Stoddart (1983) suggested that the relative abundance of coyotes in various portions of Texas reflected the relative distribution of rodents. Similarly, Weaver (1987) noted that the summer distribution of coyotes within Jackson Hole, Wyoming, approximated the winter distribution of ungulates in the area. This leaves us with the impression that coyote densities reflect abundances of natural foods, especially those available in winter.

Inquiry about coyote numbers in areas where prey abundance fluctuates markedly over time is also instructive. In the northern portion of the Great Basin, jackrabbits (Lepus californicus) are the primary prey of coyotes (Clark 1972, Hoffman 1979), and they fluctuate in abundance in a cyclic manner. Peak jackrabbit numbers occur at about 10-year intervals with numbers 20 to 50 times higher than during troughs in the cycle (Gross et al. 1974, Stoddart 1987a,b, others). Trends in coyote numbers follow those of the jackrabbits, with perhaps a year or 2 delay, but thus far, only a 5- to 6-fold change in coyote abundance has been noted (Knowlton and Stoddart 1983, Stoddart 1987a,b).

Seasonal changes. The annual cycle in coyote abundance is particularly relevant when devising and implementing depredation management schemes. Coyotes are seasonal breeders; conception generally occurs in February, followed by whelping in April (Hamlett 1938). Populations typically double or triple at this time with numbers returning to pre-whelping levels prior to the next whelping season (Knowlton 1972). This results in an annual fluctuation in numbers, with increases and decreases occurring in a predictable fashion.

Coyote Demographics

Mechanics of coyote population change. Data on coyote demography from studies in northern Utah are instructive. Coyote reproductive rates change markedly. Mean litter sizes, as judged by placental scars in females, increase and decrease almost in synchrony with jackrabbit abundance. During the low phase of the jackrabbit cycle, coyote litters average less than 5 pups per pregnant female. As jackrabbits become abundant, coyote litters increase in size until the average exceeds 8. An apparent lag between jackrabbit abundance and mean litter size of coyotes is difficult to explain, unless it is associated with the relative ages of producing females.

Since each breeding pair of coyotes only needs to rear 2 pups to breeding age during their entire reproductive life in order to maintain a stable population, questions arise about other adjustments that must occur within coyote populations. To understand one aspect, we calculated an index to pup survival by comparing the number of juveniles to the number of placental scars among animals trapped in the fall. Interestingly, the index of pup survival declined dramatically through the mid-range of coyote abundance. Secondarily, pup survival also appeared to be influenced by the abundance of jackrabbits, the main food source for the coyotes in that area. While a precise cause for the changes in pup survival has not been identified, fetal resorption has been reported among transient and subordinate females (Knowlton et al. 1986), a loss of maternal behaviors noted among nutritionally deprived females (Sayles 1984), and apparent den-raiding by neighboring coyotes reported (Camenzind 1978).

Age structure of populations. Similar to populations of most wild animals, the majority of coyotes are in the younger age classes. Wild coyotes occasionally live to be over 10 or 12 years old, but among lightly exploited populations, typically about 60% are under one year of age and over 80% are under three years old (Knowlton 1972). This implies a relatively high mortality rate in the early years of life (Windberg et al. 1985). Interestingly, if the animals live to be 3 years old, their chances of living until 8, or longer, is reasonably good (Knowlton 1972).

Effects of exploitation. Effects of exploitation are usually assessed from a knowledge of characteristics of unexploited populations, but our information about the demography of unexploited coyote populations is very limited. Rather we must rely on insights acquired from less direct comparisons, extrapolations from other species, and a general understanding of population dynamics.

The degree to which populations are affected by the removal of animals depends upon which classes of individuals are removed, the timing, duration, and intensity of the removal, and the internal resilience of the population. The latter is a function of potential reproductive adjustments associated with the relative age structure of the population, the portion made up of subordinate members of territorial social units, the fraction of the population composed of transient individuals seeking territorial status, and movement patterns. Attempts to reduce coyote densities even on small areas frequently involves many more animals than might be expected solely from density estimates (Windberg and Knowlton 1988, Knowlton et al. in press).

Since efforts to reduce depredations on livestock generally rely on removal, a demographic equivalent of mortality, one primary expectation of such efforts should be alteration in the age structure of the population and decreased dispersal of young. This usually results in a reduction in the average age of surviving animals (Davison 1980), and secondarily may be reflected in reproductive performance, since younger animals are usually more productive than animals approaching senescence.

Another aspect of exploitation that may be more important than previously recognized is disruption of the social patterns and traditions of a population. Mills (1987) speculated that loss of continuity between generations could expedite realignment of territorial boundaries, allowing more rapid response to changes in environmental conditions than might occur if territories are "inherited" across generations.

Patterns in Behavior

Social hierarchies. Initial dominance relationships become established through a series of severe dyadic confrontations within litters when pups are only 3 to 7 weeks old (Brown 1973, Bekoff 1978, Knight 1978). The severe physical interactions gradually give way to more ritualistic displays and intimidations that eventually provide a basis for establishing and maintaining territorial status in later life.

Territoriality. Coyote societies consist primarily of social units, each composed of 2-7 adult coyotes, that partition the suitable habitat into territories. Each social unit defends it's territory from other coyotes (Camenzind 1978, Bowen 1982, Andelt 1985, Windberg and Knowlton 1988). To the extent that territories remain intact and are passed across generations, they also create stability in coyote populations. In addition to territorial groups, there are some non-territorial or semi-nomadic coyotes that spend most of their time within the interstices of the territories apparently trying to fit into territorial social orders. The latter are primarily younger individuals plus a few senescent older coyotes that are no longer able to maintain social dominance (Windberg and Knowlton 1988). Achieving dominant status within a territorial social group appears to facilitate (or is a prerequisite for) reproductive success (Knowlton et al. 1986).

"Geography" of vulnerability. Hibler (1977) and Knowlton et al. (1986) reported that the locations where individual coyotes were captured are commonly peripheral to, or outside the respective areas generally used by those coyotes. Windberg and Knowlton (Unpubl. ms.) have more deliberate analyses showing that among captures of territorial females, only 2 of 26 occurred near the centers of their ranges, where they spent over 60% of their time, while 18 were captured on the periphery or outside the apparent boundaries of their territories. Similarly, 9 of 12 non-territorial females were captured outside of the areas they normally used. In exploring some of the behavioral aspects linked to such observations, Harris (1983) estimated that it took 102, 12 and 5 exposures respectively before coyotes "scored" at artificial scent stations located inside, on the periphery, and outside their respective home ranges. This suggests coyotes may be 20 times more vulnerable to capture when they are outside their normal ranges compared to inside. While the foregoing is relevant for efforts to capture specific coyotes, Windberg and Knowlton (Unpubl. ms.) point out that traps set inside and outside territorial boundaries are equally apt to catch coyotes, but those set within the boundaries of a specific territory are appreciably less apt to catch the territorial coyotes that live there.

Motivations for depredations. It is easy to assume that all coyotes are equally prone to kill sheep. However, even given the opportunity, many do not. Based on pen studies, only 70 percent of wild-caught coyotes can reasonably be "trained" to kill sheep even though they are deprived of food (Connolly et al. 1976, U. S. Fish and Wildlife Service 1978).

Unfortunately, we know little of the specific experiences, circumstances, or motivations which lead coyotes to prey on livestock. One of the better illustrations of changing motivations is evident from the practice of "denning" (the process of locating coyote dens and removing pups) as a way of stopping depredations. Adult coyotes apparently respond to increased food requirements associated with feeding pups by seeking larger prey. Till and Knowlton (1983) demonstrated that this behavioral change can be reversed. When the pups of coyotes responsible for killing livestock were removed, depredations usually ceased within 1 to 2 days even though the coyotes actually responsible for depredations were still present. Typically, when "denning" is used to stop depredations, it must be repeated on an annual basis in association with the reproductive cycle. This, however, is also the case when the depredating adults are removed, because vacant territories are usually reoccupied quickly by other coyotes.

Patterns in Predation

Predation in natural populations is seldom random but a series of acts orchestrated by situations and circumstances; frequently with discernible patterns associated with locations, differing vulnerabilities, and other characteristics associated with differences among prey. As examples, moose (Alces americana) killed by wolves (Canis lupus) are primarily animals under 2 and over 6 years of age (Mech 1970); white-tailed deer (Odocoileus virginianus) living well within the territorial boundaries of wolves are more likely to be killed than those living near the boundaries (Mech et al. 1980); Jackson et al. (1972), noting that male white-tailed deer fawns were more active than female fawns and also sustained higher mortality, suggested the increased activity of males may have increased their vulnerability to coyotes; similarly, Bergerud (1971) suggested male caribou (Rangifer tarandus) calves might be more vulnerable to predation by lynx (Lynx lynx) than female calves because they explored more and wandered further from their dams; and Kruuk (1972) reported that wildebeest (Connochaetus taurinus) that appear different or behave abnormally tend to be selected by predators. The complexity of such events is illustrated by a study in southern Texas in which coyotes were the proximate cause of death for most white-tailed deer fawns. However, Knowlton (1976) identified a series of environmental factors, many related to rainfall in the preceding year, that appear to govern survival of the fawns. In such situations, to what causal agent should the deaths be attributed?

Differential vulnerability among livestock. Younger sheep and goats are more apt to be killed by coyotes than older animals. Although lambs compose only about half of the sheep exposed, and typically graze with the adult sheep less than half of the year, they constitute more than two thirds of the sheep reported killed by coyotes. The U. S. Fish and Wildlife Service (1983) provided more graphic data suggesting lambs may be almost 40 times more likely to be attacked than the ewes that grazed with them, and that kids, including some large enough to confuse the unpracticed eye, may be over 50 times more likely to be attacked than adult wethers in the same pastures.

Gluesing et al. (1980) and Blakesley and McGrew (1984) showed that lambs newly introduced into flocks of sheep were more vulnerable to attack than lambs with established social relationships with the rest of the flock. In addition, Gluesing et al. (1980) showed that lame lambs, lame ewes, as well as lambs of ewes that are lame and the more active sibling among twins were more likely to be killed than their counterparts. A common aspect among the foregoing seems to be that conditions or situations that place individuals at the edges of the flocks, either on the bedground or while grazing, are likely to increase the chances those individuals will be killed by predators.

Abundance of natural prey. On the basis of short-term studies, several authors (Kauffeld 1977, Gober 1979) have suggested that increases in the abundance of natural prey reduces predation on sheep and goats. On the other hand, Stoddart and Griffiths (Unpubl. ms.) indicated predation on sheep changed markedly in an area where changes in abundance of natural prey were accompanied by changes in the coyote abundance and sheep were grazed on a seasonal basis. Their data suggested that increased abundance of natural prey caused a numerical increase in the coyote population which resulted in greater predation on sheep. When densities of natural prey started to decline, but while coyote densities are still high, predation on sheep escalated sharply. Coyote numbers eventually declined to levels dictated by natural food supplies and depredation rates subsided. These authors also point out that the pattern of predation on lambs and ewes was different. While depredations on ewes appeared to be solely a function of coyote numbers, indicating a constant tendency for coyotes to kill ewes, predation on lambs was variable, with prey-switching and buffering occurring between lambs and jackrabbits. Lambs and jackrabbits essentially competed as contributors to the coyote diet.

Seasonal patterns in depredations. Coyote predation on livestock occurs during all seasons, but typically it is most frequent and persistent in the spring when the coyotes are rearing pups and when young livestock are available. In addition, field personnel from the Intermountain area suggest that depredations are frequently more common in late summer and early fall than at other times. This is sometimes attributed to pups learning to kill, but it also coincides with the season ground squirrels start to aestivate (Kauffeld 1977), which signals the seasonal disappearance of a major food source. Patterns in prey abundance do appear to influence the intensity of coyote predation on livestock.

Applying Biologic Patterns to Depredation Management

Depredation management involves (1) understanding the problems, (2) knowing the capabilities of available techniques, and (3) marshalling resources to resolve problems. Since resources are frequently meager, there is a premium on achieving goals effectively and efficiently.

Defining management objectives. Effective use of biological information in management programs begins by defining the problem in biological terms. This includes assessing problems in terms of seasons, events, and circumstances relevant to coyotes and livestock. The time(s) of year that problems occur is especially important as it relates to numbers, activity, motivation, and vulnerability of coyotes.

The information presented about coyote biology and behavior provides a rationale for suggesting that (1) coyotes vary with regard to the risk they pose to agricultural interests, (2) risks frequently change in predictable ways, and (3) the efficacy and efficiency of programs to manage depredation can be affected by the manner in which they are carried out. Since the federally supervised program to control predation on livestock currently relies primarily on removal or translocation of predators, many of the following comments will be directed in that regard.

Depredation control strategies. Depredation control activities are sometimes classed as "preventative" or "corrective" depending on whether they are conducted in anticipation of depredations or to stop losses that are already occurring. The latter are generally more narrowly focused in time and space as well as directed more toward specific animals. In practice, however, the two strategies frequently become intertwined, and clear distinctions are sometimes difficult to identify (Wagner 1988).

At the same time, the degree of relief needed to keep individual depredation problems within acceptable limits varies with the predatory species and the circumstances. In some situations, the risks of predation by coyotes can be a year-round concern, such as pastured sheep or goats, but when livestock are grazed on a seasonal basis or if vulnerability only lasts for a brief period, as in the case of calves, risks may be abbreviated. In the first case, predator removal may require a persistent year-round effort, while in the latter a temporary alteration in numbers or behavior of the predator may provide the relief needed.

Reductions in numbers of wild animals are usually transitory because populations of most predators are dynamic and self-regulated. Unfortunately, they frequently do not self-regulate at levels compatible with economically viable livestock production operations. As a result, they create problems. In trying to limit depredations by reducing predator numbers, we should expect persistent efforts will be required.

Timing of efforts. The importance of timing in the application of depredation control techniques is often overlooked. While some procedures are effective most of the time, others are not. Fencing to exclude predators (Dorrance and Bourne 1980, Linhart et al. 1982, Shelton 1984) and use of guard dogs (Linhart et al. 1979, Green and Tueller 1984, Black and Green 1985, Lorenz and Coppinger 1986) seemingly fall in the former, but some depredation control techniques are restricted to specific seasons or periods when relief is needed because of the aspects of coyote biology or behavior they wish to exploit. "Denning" can only be used in spring and early summer when whelping and pup-rearing normally occur. Aerial hunting from helicopters and fixed-wing aircraft, although helpful in corrective situations year-round, is more effective when foliage is reduced or snow cover provides a tracking medium and a contrasting background. On the other hand, use of frightening devices (Linhart 1984, Linhart et al. 1984) when depredations are not imminent could be counter-productive by allowing coyotes to acclimate to the stimuli, thus reducing the coyote's anxiety toward the unusual sights and sounds and thereby reducing their utility when they are really needed.

While depredation control personnel readily recognize seasonal variation in the utility of most coyote capture techniques, the relative merits of removing animals during various seasons is less obvious. If immediate relief is not an issue and local coyote population reduction is the management goal, removing individuals in late winter or early spring may be far more effective than doing so at other times (Knowlton 1972). Spring removals occur at the low point in the annual cycle of coyote abundance, thus additional losses at this time are added to normal attrition within the population. In addition, spring removal eliminates some of the reproductive capacity of the coyote population at a time when it is least capable of compensating.

Possibilities. As we gain understanding about the biological and behavioral aspects of predation on domestic stock, new or modified procedures for reducing depredations emerge. The efficiency of activities might be enhanced by improving the manner in which resources are allocated. Our ability to anticipate changes in predator abundance and to project needs for depredation relief are improving. The challenge may be in developing the administrative skills and mechanisms to respond adequately and appropriately, like moving resources across political "boundaries" (both geographic and temporal) to address uneven, but predictable, needs.

Interesting possibilities also exist for new depredation control procedures. Extending the behavioral studies of Gluesing et al. (1980) to improve predictions about which animals are most apt to be killed would enhance the use of the Livestock Protection Collar (McBride 1974, Connolly et al. 1978) so that coyote removal can be more directly applied to specific animals. Where "denning" is used annually to protect sheep on traditional lambing ranges, perhaps the period of depredation relief could be extended by capturing the adults, then sterilizing and releasing them so they will continue to defend their territories from other coyotes but without the predatory motivations associated with feeding pups. If this would work, what about chemosterilants to accomplish the same objective?

A more distant possibility involves a better definition of characteristics that distinguish coyotes that prey on livestock from those that do not. Utilizing this information along with knowledge about the relative efficiency of various tools and procedures in capturing the classes of animals that pose the greatest risks should help us promote increasingly efficient and selective programs for reducing depredations.

Most of the preceding focused on the biology and behavior of coyotes and how that relates to coyote predation on livestock, primarily sheep. I am confident that comparable patterns exist where other predators are involved in preying on livestock. Recognizing and understanding the patterns provides a measure of predictability, which in turn, allows us to anticipate conflicts and problems and permits us to develop strategies to keep them within acceptable bounds. This is particularly important in managing species with conflicting social values.

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