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M. M. Jaeger
Utah State University

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M.M. *Jaeger*

USDA Wildlife Services, National Wildlife Research Center, Utah State University, Logan, UT 84322-5295.

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Introduction

Research to find more effective and socially acceptable solutions of managing coyote (*Canis latrans*) depredation has been ongoing for many years. The primary objective is to develop strategies that effectively reduce losses, not simply reduce coyote numbers. An important step in solving such conflicts is to clearly define the problem. In this case, it is important to know which coyotes are most likely to kill sheep and when and where their depredation is greatest. For a control strategy to be effective, it must be appropriate to these three defining characteristics. The hardest of these questions to resolve has been determining if some coyotes are more likely to kill livestock than others and, if so, whether these animals can be relatively more difficult to remove than the others. While the conventional wisdom of trappers supports the existence of particular sheep-killing coyotes, it is another matter to demonstrate that they in fact occur and to explain why.

This paper is a review of our current state of knowledge about the coyotes that kill livestock, particularly sheep, and methods that can be used to target them. The important research findings upon which this is based will be discussed. The main thrust of the paper will deal with a series of studies done in California between 1993 and 2002. These were undertaken jointly by the National Wildlife Research Center (USDA/Wildlife Services) and the University of California at Berkeley. These studies represent the most intensive investigation to date of predation ecology of coyotes in the presence of sheep. In addition, future research needs will be discussed. This review will illustrate the importance of first developing an understanding of the problem before testing methods to alleviate it, that may be inappropriate.

Coyote Territoriality and Social Structure

It has long been recognized that removal of a single coyote from an area can stop depredation (Sampson and Nagel, 1948 from Gier, 1968). However, it was not known whether sheep-killing could be attributed to a particular class of coyotes. A key research finding that helped to better frame questions regarding sheep-killing coyotes was showing that coyotes are territorial (Camenzind, 1978; Windberg and Knowlton, 1988). Territories in an area are contiguous with little overlap (e.g., Windberg and Knowlton, 1988; Gese et al., 1996) and coyotes do not tend to occur where they cannot be territorial year-round (Ganz, 1990; Shivik et al., 1996). In addition, territoriality is maintained even in the presence of livestock (Sacks et al., 1999a). This implies that coyotes from surrounding territories do not concentrate where livestock are pastured (e.g., a sheep ranch), but rather that sheep-killing coyotes are likely to be residents in the territory where killing occurs. The basic social unit of coyotes occupying a territory is the alpha pair, who are the breeders. Other adult coyotes may also reside in a territory; they are referred to as betas and are usually offspring of the alpha pair from the previous year or two. Therefore, resident coyote packs are family groups controlled by the dominant alphas. Non-territorial coyotes, referred to as transients, have dispersed from their natal territories and are searching for opportunities to become alphas and to breed. Transients have relatively large home ranges that can encompass two or more territories, although they seem to avoid contact with alphas by moving in the corridors between territories. The question becomes: Are alphas, betas, and transients equally likely to kill sheep?

Alphas Implicated

In the inter-mountain west, where sheep are moved to summer grazing allotments, depredation coincides with the time coyotes are rearing pups. Conventional wisdom of government trappers is that coyotes kill lambs to feed their pups and that when pups are removed (referred to as denning) the killing stops. This was confirmed by Till and Knowlton (1983), and it implied that breeding coyotes were the principal killers in this situation. At the time of this study, it was thought that both alphas and betas could breed. Evidence now indicates that alphas are the principal breeders (e.g., Gese et al., 1996; Blejwas et al., 2002) and although beta females occasionally do give birth, their pups have a poor chance of surviving (Knowlton, personal communication). In addition, the primary feeders of pups seem to be the alphas; they can successfully rear pups with or without betas (Sacks and Neale, 2001). Where betas do occur, some of them do help with provisioning pups while others do not (Hatier, 1995). Therefore, denning provides indirect evidence that alphas with pups are the principal killers of lambs on summer grazing allotments. This is supported by the finding that depredation is less in territories with surgically sterilized adults that produced no pups (Bromley and Gese, 2001a,b).

The above findings suggest that provisioning pups is the driving force behind depredation. However, this maybe the case only where sheep are present at that time of year coyotes have pups such as the inter-mountain west. In large areas of California and Texas, sheep are present in the same areas year-round, and coyote depredation occurs throughout the year, including times when pups are not present. Generally, depredation peaks during the lambing season, which overlaps pup-rearing. In north-coastal California, however, the lambing season occurs in winter prior to whelping of pups. In this situation, depredation peaks during the lambing season before the presence of pups and the use of dens (e.g., Conner et al. 1998). As a consequence, it was not known whether betas and transients also killed lambs at this time of year, when naturally occurring prey can be relatively scarce.

Do All Coyotes Kill Livestock?

Attempts have been made to get at the question by looking at sheep-killing behavior of captive coyotes. Sterner (1997) tested whether observational learning (e.g., an inexperienced beta coyote watching its experienced alpha parent kill a sheep) was an important factor affecting whether coyotes kill sheep. The results, however, were ambivalent, and the sex, age and social status of test coyotes were not considered in the experimental design. Connolly et al. (1976) exposed captive coyotes to sheep in an enclosure to observe sheep-killing behavior. These coyotes had no previous experience killing sheep. The 2-year-old males and females paired with them (i.e. simulated alpha pair) attacked sheep more frequently than yearling males, while unpaired females did not attack. The conclusion was that most coyotes can kill sheep without previous experience but that some are more likely to do so than others. Another enclosure study found that 18 of 19 pen-raised coyotes killed sheep compared with 38 of 54 wild-caught adult coyotes (p.74, USFWS 1978). This result suggested that wild-caught coyotes may be more cautious of killing sheep, although other factors may account for this difference.

The first field study specifically addressing the question of which coyotes kill livestock was initiated in 1991 by scientists from the USDA Denver Wildlife Research Center (now known as USDA/WS/NWRC). The objective was to determine the age, sex, and territorial status of coyotes that kill livestock and to distinguish these coyotes from those that only feed on carcasses. Alpha coyotes were not distinguished from betas; both were classified as territorial and compared to the non-territorial transients. Goat-killing coyotes were to be determined by the use of radioactive markers in collars around the necks of the goats. Coyotes typically kill sheep and goats by suffocating them with a bite to the throat that crushes the trachea. No coyotes were subsequently found with the radioactive markers and, therefore, the study was unable to determine who the killers were. However, both territorial and non-territorial coyotes had fed on the carcasses of kid goats determined to have been killed by coyotes (Windberg et al., 1997). This does not mean that all of these coyotes had killed goats. Coyotes commonly feed on the carcasses of livestock or game that they did not themselves kill (e.g., Gier, 1968). It was unclear where in relation to territory boundaries the kills were made.

Hopland Studies

It remained to be determined whether alpha coyotes are more likely to kill livestock than betas or transients. This question was addressed in a series of studies undertaken at the UC-Hopland Research and Extension Center (Jaeger et al., 2001), which was the largest sheep ranch remaining in north-coastal California. Depredation had remained high at Hopland despite concerted efforts at control, including annual population reduction of coyotes with traps, snares, and M-44 cyanide ejectors and use of a variety of non-lethal methods (Timm and Connolly, 2001). Sheep were present year-round at Hopland; and coyotes, killed them throughout the year with peak losses during the lambing season (December to May). In general, the strategy for removal of coyotes was non-selective and based on the assumptions that all coyotes in the vicinity of sheep were equally likely to kill them and, if not, that the sheep-killers were as likely to be removed by control as were the non-killers. These assumptions were tested.

Several lines of evidence indicated that the principal killers at Hopland were the alphas whose territories overlapped sheep. First, radio-telemetry of coyotes of known social status located alphas near sheep kills within their own territories close to the time kills were made (Sacks et al., 1999a). While betas and transients were found at sheep carcasses hours or days after the kill had been made, they were not nearby around the time of the kill. Alphas, on the other hand, appeared to feed on sheep at the time they made the kill and did not later return to the carcass. Second, there was a single kill site within a territory during any one night suggesting that multiple, independent killers were not active in the same area (Sacks et al., 1999a). Third, killing within a territory stopped when a resident alpha was removed (Blejwas et al., 2002). Fourth, coyotes killed in the act of attacking a sheep were known alphas (Blejwas et al., 2002). One way that this was determined was to swab the site of the wound (i.e. throat) of a recent coyote-killed sheep and match the DNA from the saliva of the coyote that had made the wound to that from a tissue sample of the coyote taken at the time it was originally captured and radio-collared (Williams et al., 2003).

These findings are likely to be applicable to a wide set of circumstances and not unique to the Hopland study site. They are supported by evidence that alphas are the principal killers of wild ungulates (Gese and Grothe, 1995; Gese, 1999). As previously noted, coyotes have been found to be territorial virtually everywhere they have been studied. This implies that the territorial dominant animals (i.e. alphas) defend their space from intrusion by other coyotes and are the individuals most likely to kill sheep within its boundaries. But why betas in a territory do not seem to kill livestock, particularly small lambs, independently of alphas is unknown. Two factors may influence this. First, the energy demands of betas are probably less than those of alphas. Greater energy needed to maintain a pair of coyotes (i.e. alphas) as opposed to an individual (i.e. beta) and to provision pups may be the impetus for alphas to begin killing larger prey (e.g., Harrison and Harrison, 1984). Second, small mammals, such as rabbits and rodents are, in addition to carrion, the main prey-base of coyotes in many areas of the western United States where sheep and deer are common, suggesting a preference for this general size of prey (e.g., Sperry, 1941; Ferrel et al., 1953; Ellis, 1959; Gier, 1968; Wagner and Stoddart, 1972). This preference may be due, at least in part, to the difficulty in handling larger prey. Coyotes are known to prey principally upon lambs and fawns indicating that handling more fully grown animals may be difficult, particularly by individual coyotes. Furthermore, lambs are usually in the presence of their mothers, who may effectively deter betas. Connolly et al. (1976) noted that defensive behavior by ewes was often effective at deterring an attack, and coyotes, were never seen to attack rams. An alpha is more likely to be assisted by its mate who distracts the ewe while its lamb is killed. Blejwas et al. (2002) review the literature supporting the use of cooperative hunting by coyotes (alpha pairs or alphas and betas) for killing ungulates.

Efficacy of Selective Removal

Next it was important to determine whether a control strategy of selective removal of alphas effectively reduces depredation and, if so, for how long. Removal of one or both alphas from a territory could result in an influx of neighboring alphas and betas or transients and rapid resumption of the killing. This possibility was supported by radio-tracking data from Hopland showing movement into a territory by these other perspective territory holders within days following removal of the resident alphas (Blejwas, 2002). Nevertheless, when both alphas were removed from a territory, killing did not resume before a new alpha pair became established, which usually took three to four months (Blejwas et al., 2003; Gese, personal communication). In some cases, territories were divided among established alphas from surrounding territories (Blejwas et al., 2002). The time period over which this process occurred was not established. When only one alpha of a pair was removed, the average time to replace the mate was two months, which corresponded to the average time to resumption of killing. In a few cases, a lone alpha with pups resumed killing lambs within a few days or weeks of the removal of its mate. The presence of lambs in a territory affected a faster resumption of the killing than did the presence of ewes only, averaging 43 days as compared with 184 days (Blejwas et al., 2002). Notwithstanding, killing during the lambing season was significantly reduced or eliminated in a territory during the three-month period following removal of one or both alphas (Blejwas et al., 2002).The overall result of this control strategy (i.e. selective removal of alpha coyotes whose territories overlapped lambing pastures where depredation was occurring) was to effectively reduce depredation losses during the lambing season at Hopland. In contrast, non-selective removal was ineffective (Conner et al., 1998; Blejwas et al., 2002). This control strategy requires annual application.

Vulnerability of Alphas to Capture

The ineffectiveness of non-selective population reduction at Hopland suggests that either too few coyotes were being removed to show an effect or that the alpha coyotes were less vulnerable to the capture methods used than were other coyotes. Available evidence supports the second option. Sacks et al. (1999b) found that juvenile and yearling coyotes at Hopland were more vulnerable than were older coyotes (i.e. alphas) to capture by traps, snares, and M-44s. This was particularly true during the winter, prior to whelping, when lambs were present and depredation was at its annual peak. Following whelping, the need to provision pups likely requires that alphas take risks that make them more vulnerable to capture. Interestingly, alpha coyotes at Hopland were not vulnerable to M-44s at any time during the study. In contrast to these findings, Windberg and Knowlton (1990) reported no differences between juveniles and adults in vulnerability to capture with traps or M-44s. However, unlike Hopland, this study was done where coyotes had not been previously exposed to intensive removal. That coyotes, particularly alphas, can learn to avoid M-44s after brief exposure to their use is supported by the findings of Brand et al. (1995) with closely related black-backed jackals (*C. mesomeles*) in sheep producing areas of South Africa.

How can prior experience with control reduce a coyote's vulnerability to capture, particularly with a lethal method such as the M-44, which usually kills any coyote that activates the device? Would a coyote have to see another member of its pack killed in order to know to subsequently avoid the device? Probably not, as coyotes seem sensitive to missing pack members or neighbors (Blejwas, 2002) and may associate their removal with human activity in the area, and as a consequence become cautious toward any novel object associated with human odor.

Furthermore, alpha coyotes are harder to capture within their own territory than they are on its periphery or outside of it (Sacks et al., 1999b; Séquin et al., 2004). How are alpha coyotes better at avoiding capture? It has been argued that resident coyotes (i.e. alphas and betas) become very familiar with their territories as opposed to transients that range over much larger areas. As a consequence of this experience, residents are more likely to recognize unfamiliar objects or smells (e.g., trap set) when in their own familiar space than when outside of it and be cautious toward them (Lehner et al., 1976; Windberg, 1996; Harris and Knowlton, 2001). Alphas and betas, however, were not distinguished in these studies. Séquin et al. (2004) investigated the vulnerability of coyotes of different social status toward photo-capture and how this was affected by the location of camera stations relative to territorial boundaries. Alphas from five contiguous territories were exposed to cameras (two territories at a time) in eight, six-week sessions. Each territory was tested in at least two sessions at different times of year. All coyotes, except pups, avoided photo-capture during the day but at night the alphas were least vulnerable. They were never photo-captured within their own territories, whereas betas were. Transients were photo-captured along territorial boundaries. Radio-telemetry and direct observation indicated that the alphas avoided photo-capture within their territories by tracking human presence and evidently learning the locations of camera stations at the time they were set-up. This suggests that alphas are territorial while betas are simply resident within the territory and that there can be a fundamental difference between the two social classes in how each attends to the threat of capture.

Methods that Selectively Target Alphas

The Livestock Protection Collar (LPC) is the only method currently in use that targets a coyote that is in the act of killing a sheep (Burns et al., 1996). The collars contain the toxicant 1080, which the coyote ingests when it bites down on the sheep's throat and punctures the bladder containing the poison. Coyotes usually kill sheep in this way, although sometimes they avoid the collars. Despite its selectivity, the LPC is not widely used. One reason for this is that relatively few sheep in a flock can be collared. It is often necessary to substitute a smaller lure flock with collars.

Denning is another lethal method currently in use that is selective in that it targets alphas and/or their pups in the vicinity of depredation. The use of this method and its limitations were described previously.

Calling coyotes by imitating their vocalizations or those of injured prey has long been used as a way to attract coyotes within rifle range. "Calling-and-shooting" has the potential to be selective to alphas. This assumes that a particular type of call can be identified that imitates an intruder in a territory and will provoke a resident alpha to approach the source of the call. A study of responses of coyotes of different social status to a variety of playback calls, used at different times of year and at different times of night, has recently been completed and the data are now being analyzed (Mitchell, in prep.).

Traps and snares can also be used selectively by those with sufficient experience and the time to pursue individual coyotes. Other methods such as aerial gunning, while not selective to alpha coyotes, may be as likely to remove alphas as betas or transients. Aerial gunning may be more selective to alphas when used in combination with calling by ground crews. This should be tested.

Methods now exist that can be used to test whether particular methods are removing the problem coyotes. This is particularly true in the case of corrective control where coyotes are removed in response to depredation. Williams et al. (2003) demonstrated that coyote DNA can be swabbed from the throat area of a recently killed sheep and matched to that from tissue of coyotes removed by control. Initial findings from this work suggest that alpha males may be the principal killers of sheep. This needs further investigation. If true, the most effective methods should be those that take adult males, or at least, are not biased against them. This could be easily tested by collecting dead coyotes removed by a particular control method and determining their age, sex, and reproductive condition.

The one, non-lethal method that targets coyotes attempting to kill sheep is use of guard animals (e.g., Green et al., 1984; Andelt and Hopper, 2000). This is probably the most commonly used non-lethal method. However, coyotes are known to kill sheep in the presence of guard animals (e.g., Timm and Schmidt, 1989), although the relative incidence of this is unknown. This may reflect a flaw in the behavior of the guard animal (e.g., breed, age, training) or a lack of human supervision. Objective studies of the behavior of coyotes toward sheep, guard animals, and humans attending them is lacking. Do alpha coyotes learn to work around guard animals, and if so, under what conditions (e.g., dense cover together with rough terrain)? Non-lethal techniques are probably most effective when (1) they are interactive with the coyote, in other words respond when the coyote is present; and (2) are unpredictable in terms of when and where they are likely to be. This is to suggest that guard animals and shepherds are more effective deterrents when they are more interactive and less predictable. The article by Shivik in this issue addresses some of these concerns.

Surgical sterilization *in lieu* of denning has potential as a non-lethal means directed at alpha breeders (Bromley and Gese, 2001 a,b). This is not intended as a means of local population reduction but rather as a way to stop depredation by those alphas whose territories overlap sheep by affecting their motivation to kill for provisioning pups. A potential advantage of this approach is that a sterilized pair can remain together for years and defend their territory, thus eliminating the need for annual capture and sterilization. On the other hand, the major disadvantage is the difficulty in capturing and identifying the alphas. In the original study, the attempt was made to capture and surgically sterilize all adults in the area. This was facilitated by helicopter capture. Confirmation that alphas were in fact captured was done through subsequent radio-tracking. This process is impractical to do in a control operation. However, this method could be made more practical and cost-effective if a way was found to identify the likely alphas at the time of capture.

Conclusion

Alphas whose territories overlap sheep were the primary killers of sheep in a series of studies done in California. Betas and transients fed on sheep carcasses. These findings are supported by studies from elsewhere in the West. A control strategy that selectively targets alphas can be more effective at reducing depredation losses than a strategy of non-selective population reduction. Alphas were relatively less vulnerable to capture with traps, snares, and M-44s than were betas and transients. This was particularly true during winter prior to whelping and the need to provision pups. There is a need to develop additional control methods, both lethal and non-lethal, that selectively target alphas.

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