THE EFFECTIVENESS OF SELECTIVE REMOVAL OF BREEDING COYOTES IN REDUCING SHEEP PREDATION

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Abstract: We evaluated the effect on sheep losses of selectively removing breeding coyotes (*Canis latrans*) from territories experiencing depredations. Breeding pairs of coyotes were the primary predators of sheep, and they killed sheep only within or on the periphery of their territories. Removal of either or both members of a breeding pair reduced or eliminated predation in that territory during the subsequent 3-month period. Killing of sheep by coyotes resumed sooner in territories that overlapped lambing pastures than in those that did not. For territories with access to lambs, the average time interval until killing of lambs resumed (43 days) approximated the time for a replacement pair of coyotes to become established. Removals of breeding coyotes during the nonlambing season did not reduce losses during the following lambing season. Although <33% as many coyotes were removed per unit time during selective control as during nonselective control, lambing-season lamb losses were lowest during the selective removal period. During the nonlambing period (when predation on sheep was low) sheep losses were similar under selective, nonselective, and no control. These results suggest that selective targeting of breeding coyotes, which is more socially acceptable than nonselective population reduction, also can be more effective in reducing sheep losses.

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Coyotes are the major predator on domestic sheep in North America, accounting for 61% of all predator losses in the United States and 75% of predator losses in California in 1999 (National Agricultural Statistics Service 2000). The economic impacts of coyote depredations have contributed to the continuing decline of the sheep industry in the western United States (Wagner 1988, National Agricultural Statistics Service 2001). A mix of lethal and nonlethal coyote control techniques have been employed by producers of domestic sheep (Knowlton et al. 1999). Although lethal control is widespread among western producers, it is a source of controversy among the broader public (Wagner 1988, Andelt et al. 1999). Recently, ballot initiatives in several western states banned or restricted the use of several control devices, including leghold traps, snares, M-44 cyanide ejectors, and 1080 poison; similar initiatives are pending in other states (Minnis 1998). Opinion surveys indicate that public support for trapping predators is greatest when concerns about humaneness, effectiveness, and selectivity are addressed (Andelt et al. 1999, Messmer et al. 1999, Reiter et al. 1999). Selective removal of depredating individuals is more socially acceptable than nonselective control, but whether such an approach would be effective in reducing livestock losses has not been investigated.

There has long been support for the assertion that a few coyotes are responsible for most livestock depredations (Dixon 1920, Gier 1968), and recent evidence suggests that these individuals may be characterized more specifically as breeding adults (Sacks et al. 1999*b*). Field studies have implicated adult coyotes in predation on calves (Gilliland 1995) and breeding coyotes in losses of both poultry (Althoff and Gipson 1981) and domestic sheep (Till and Knowlton 1983, Sacks et al. 1999*b*). Till and Knowlton (1983) were able to stop predation on a spring lambing range in Wyoming by removing either the breeding pair or their pups. They attributed the preremoval depredations to increased energetic demands faced by pairs provisioning offspring. Sterilized packs also killed fewer sheep than packs with pups in a Utah study (Bromley and Gese 2001*b*). In northern California, where the winter lambing season precedes coyote pup-rearing, Sacks et al. (1999*b*) found no

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link between coyote pairs feeding pups and predation on lambs. Nonetheless, breeding adults were still responsible for most—if not all—lamb kills.

During spring 1993, an intensive field study of coyote predation on sheep was initiated at the Hopland Research and Extension Center (HREC) in northern California. The goal was to characterize coyotes that kill sheep to develop a more selective and effective approach to coyote control. Conner et al. (1998) analyzed records of sheep losses and nonselective coyote removals over a 13-year period at HREC and found no significant relationship between the number of coyotes removed and the number of subsequent sheep kills. Sacks et al. (1999*b*) determined that it was the breeding coyotes whose territories overlapped sheep that were responsible for most sheep kills. Most depredation losses were lambs killed during the winter lambing season, but breeding coyotes were relatively invulnerable to nonselective control at this time (Sacks et al. 1999*a*). Although their vulnerability increased during the spring–summer coyote pup-rearing season, the net effect was that nonselective control was not successful at targeting depredating breeding coyotes until after most of the predation on lambs had already occurred.

The above findings suggested that control would be most effective and efficient if it targeted only those breeding coyotes whose territories overlap pastures with lambs. Furthermore, if only known depredating pairs were targeted, other pairs in the area that do not kill sheep might help reduce predation by excluding sheep-killing coyotes from their territories (Boggess et al. 1980, Sacks et al. 1999*b*). To investigate these hypotheses, we monitored predation losses of sheep at HREC during periods of selective coyote control. Only breeding coyotes in territories where killing of sheep was occurring were removed (Timm 1999). Our objectives were to determine (1) whether breeding coyotes, particularly the males, continued to be the primary predators of sheep; (2) whether the removal of 1 or both breeding adults would stop predation in their territory and, if so, for how long; (3) whether selective removal of breeding coyotes was more effective at reducing sheep losses than nonselective control; and (4) whether nonkilling pairs would become established in removal territories and not kill sheep.

STUDY AREA

The HREC is a 21.7-km^2 University of California agricultural research facility located in the outer Coast Ranges of northern California in Mendocino County. It is situated in the eastern foothills of the Russian River valley at 150–905 m elevations. Four main habitat types exist: grassland, open oak woodland, dense woodlands, and chaparral; a more detailed description of the vegetation can be found in Murphy and Heady (1983). The climate is Mediterranean, with hot, dry summers and mild, wet winters. The fauna is diverse, and wild prey are abundant year-round (Neale 1996).

The HREC is the largest sheep operation in Mendocino County, with a year-round flock of 600–1,500 ewes, plus lambs. Originally, it was bordered on 3 sides by other sheep ranches. Now there are small sheep and cattle ranches to the west and south, vineyards and private hunting clubs to the south and east, and a Bureau of Land Management recreational area to the north. In much of the western United States, lambing takes place in late spring or summer. However, in north-coastal California, because of the Mediterranean climate, lambing season begins with the onset of the rainy season in late autumn. Most lambs at HREC are born in January or February. Lambs are pastured primarily on the southern half of HREC. After most of the lambs have been sold in late April or May, those retained as replacements are maintained in 1 or more of 3 different pastures (Fig. 1).

Predator losses on HREC, particularly to coyotes, have increased dramatically since the 1970s (Scrivner et al. 1985, Neale et al. 1998). Coyote densities at HREC are high, ranging from 0.5 to 0.7/km^2, but pack sizes tend to be small, with most packs having 2 or fewer associates (Sacks 1996). Coyote control, once practiced on a large scale throughout the region, is currently localized and intermittent. The rugged topography and dense vegetation preclude the use of aerial gunning in this part of California. Wildlife Services specialists have relied on traps, snares, M-44 cyanide ejectors, denning, and calling and shooting to remove coyotes (Coolahan 1990). An average of 334 coyotes (approximately 5% of the estimated coyote population) were killed annually in Mendocino County during the early 1970s (Connolly and Longhurst 1975); this number declined slightly to 315 during 1982–1989 (Coolahan 1990). Coyote control at HREC prior to the study was typical of the region; an average of 12 coyotes were removed from the property annually.

METHODS

Capture and Radiotelemetry.—Coyote capture and marking procedures during November 1995–July

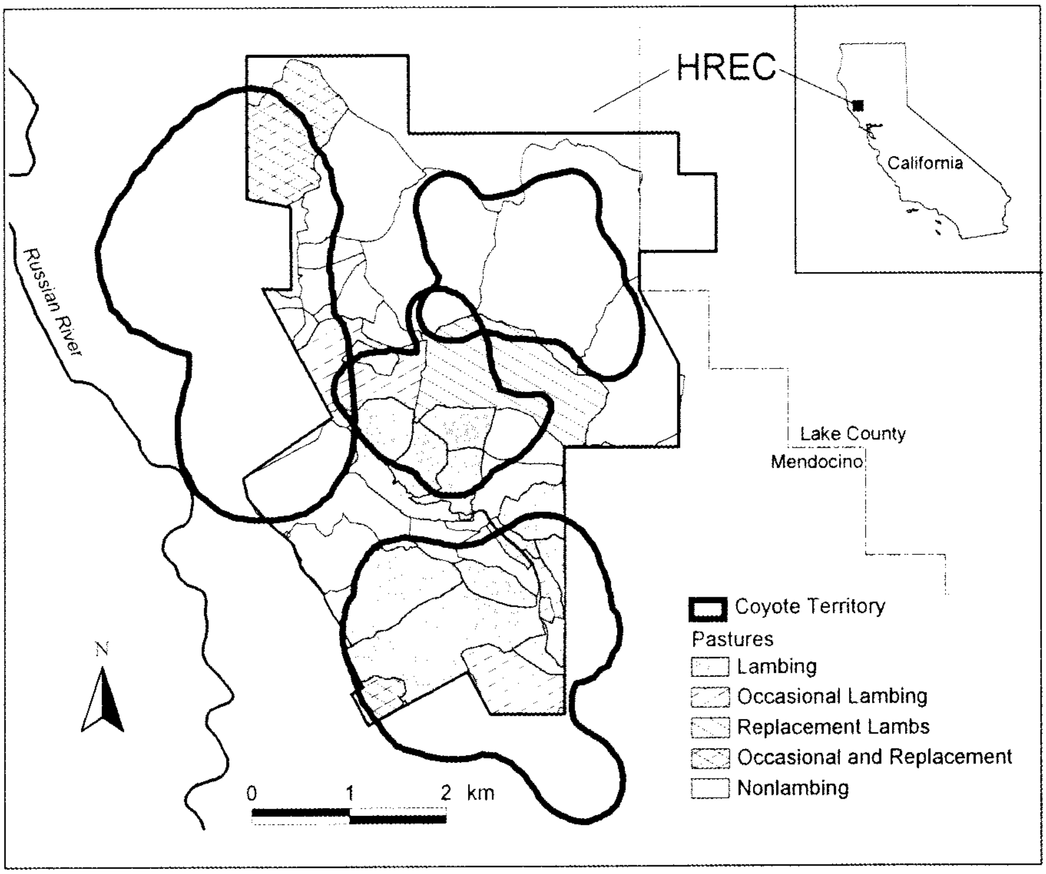

Fig. 1. Locations of lambing pastures and spring 1997 coyote territories on the Hopland Research and Extension Center, Mendocino County, California, USA. Shaded pastures contained lambs during the Jan–May lambing season most years, while striped pastures were used less frequently.

1998 were similar to those used during the previous study period (Sep 1993–Nov 1995) as described elsewhere (Neale et al. 1998, Sacks et al. 1999*b*). Beginning in November 1995, we fitted each coyote with a radiocollar equipped with activity and mortality sensors (ATS, Isanti, Minnesota, USA). After March 1996, we anesthetized coyotes with a mixture of ketamine hydrochloride and xylazine hydrochloride and extracted a premolar tooth for aging by cementum annuli. Teeth were sectioned and aged by Matson's Laboratory (Milltown, Montana, USA).

After November 1995, we located all coyotes on or immediately adjacent to HREC daily during each of 1–3 tracking shifts. Sacks (1996) found that coyotes killed sheep throughout the night and into the early morning; therefore, we obtained most locations during these times to maximize the probability of associating a coyote with a sheep kill. Telemetry error was estimated by the difference between global position system and telemetry locations of 11 test collars, each located by 1–3 observers ($\bar{x}$ = 126 m, SD = 91 m, n = 21).

We classified each coyote as a breeding resident, nonbreeding resident, or nonbreeding transient based on space use patterns, reproductive condition, association with a coyote of the opposite sex, and presence at a den with pups (Andelt 1985, Sacks et al. 1999*b*). We delineated resident territories by calculating the 90% adaptive kernel isopleth in program CALHOME (Kie et al. 1996). To avoid biasing the estimate toward weeks or months with greater numbers of daily fixes or toward areas where locations were more easily obtained, we used a maximum of 2 randomly selected, independent (>6 hr apart) locations per day.

Sheep Kills.—Station personnel helped us search pastures daily from the road for sheep kills. We also searched lambing pastures regularly on foot and investigated areas where circling turkey vultures (*Cathartes aura*) or low-flying golden eagles (*Aquila chrysaetos*) were seen. We skinned the head and neck region of all sheep carcasses found to examine the condition of the trachea and the location, size, and spacing of puncture wounds and hemorrhaging. This evidence, combined with feeding patterns on carcasses and the presence of tracks, scat, or other sign, was used to determine the species of predator responsible (Wade and Bowns 1985). The location and estimated date and time of each kill were recorded, and the locations were entered into ArcView geographic information system (version 3.1; Environmental Systems Research Institute, Redlands, California, USA).

To determine whether breeders continued to be the primary predators of sheep, we compared telemetry locations of all radiocollared coyotes to the locations of sheep kills. We assigned kills to individuals or coyote pairs based on their proximity to the kill, similarly to Sacks et al. (1999*b*). Kills were assigned with high confidence to nonbreeders or breeders from other territories only when the resident breeding pair could be excluded as suspects. For statistical analyses, we assigned all kills within the territory boundaries to the breeding pair unless radiotelemetry indicated another coyote was responsible. When the kill was located in an overlap or interstitial area and telemetry data were inconclusive, the kill was assigned to all pairs from adjoining territories. We investigated the hypothesis that breeding males were the primary killers of sheep (Sacks et al. 1999*b*) by comparing the number of male and female coyotes killed on livestock protection collars (LPC; see below).

Coyote Control.—The HREC employed 3 different control strategies during the course of the study: no control, nonselective control, and selective control (Table 1). During the no-control periods, animals on the periphery of HREC were still subject to control on adjacent ranches. During nonselective control, the local Wildlife Services specialist attempted to remove as many coyotes as possible from HREC. These activities were carried out independently of the ongoing coyote research and without benefit of radiotelemetry locations. During selective control, HREC personnel used LPC to target depredating coyotes. Once a pattern of coyote predation was established, all sheep were removed from the pasture except for a small target flock of 10–30 lambs or yearlings with LPC. Collared lambs were accompanied by uncollared ewes. A livestock protection collar consists of a pair of toxicant-filled rubber bladders attached to a velcro collar and placed around the neck of a lamb or small ewe (Burns et al. 1996). Coyotes typically puncture the collar while attacking the lamb's throat, thereby ingesting a lethal dose of the toxicant, sodium fluoroacetate (Compound 1080), or diphacinone (Timm 1999). In some cases, use of the LPC was impractical or unsuccessful, and HREC or Wildlife Services personnel used radiotelemetry to remove these depredating breeders by shooting.

Table 1. Numbers of coyotes removed under different control regimes at the Hopland Research and Extension Center, Mendocino County, California, USA, Apr 1993–Feb 1999.

Period	Control regime	Months	Number removed[a] Total	Breeders
Apr 1993–Jul 1994	None	16	0	0
Aug 1994–Mar 1995	Nonselective[b]	8	18	1–3
Apr 1995–Oct 1995	Nonselective[b]	7	10	7–8
Nov 1995	Selective	1	1	1
Dec 1995–Feb 1996	None	3	0	0
Mar 1996–Oct 1998	Selective	32	16	12–15
Nov 1998–Feb 1999	None	4	0	0

[a] Pups under the age of 6 months were excluded from the counts.
[b] The 1994–1995 nonselective control period was subdivided to reflect changes in vulnerability of breeding coyotes.

Statistical Analyses.—To test the hypothesis that selective removal of breeding coyotes would reduce predation within their territories, we used a paired *t*-test to compare availability of lambs and ewes, numbers of coyote-killed lambs and ewes, and lamb and ewe kill rates during 3-month periods before and after the removal of 1 or both members of the breeding pair. A selective removal was defined as the death of a breeding coyote (from any cause) in a territory where depredations were occurring. We calculated the average number of available lambs or ewes by summing the daily number of lambs or ewes in all pastures at least partially overlapped by that territory and dividing by the number of days in the period. We divided the number of lamb or ewe kills by availability to obtain kill rates for each pre- and postremoval period.

We used a 2-way analysis of variance (ANOVA) to test the effects of season of removal and access to lambs (i.e., spatial overlap of territories on lamb pastures) on the number of days until killing resumed within a removal territory, and we used

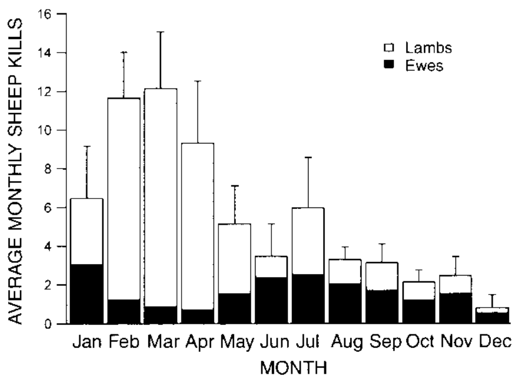

Fig. 2. Average (± SE) monthly sheep kills by age class at the Hopland Research and Extension Center, Mendocino County, California, USA, 1994–1999.

Tukey's HSD for pairwise comparisons. We defined 3 seasons based on events in the coyote annual cycle that were likely to affect predation on sheep: breeding–gestation–nursing (Jan–Apr), pup-provisioning (May–Aug), and pup independence–dispersal (Sep–Dec). We classified a territory as a lamb-access territory if ≥25% of its area overlapped lambing pastures, and as a no-lamb territory otherwise.

Most sheep losses were the result of lambs killed during the January–May lambing season (Fig. 2). Therefore, during the lambing season, we focused on lamb kill rates to compare control regimes. A relatively small number of lambs were retained each year as replacements, so we combined lamb and ewe kills and examined total sheep kill rates during the nonlambing period. Sheep were classified as lambs until November of their first year and as ewes or rams thereafter. Predation on the few rams retained for breeding purposes was negligible, and they were excluded from analyses. We used SYSTAT 9.0 to perform statistical analyses. Data were square-root transformed as needed to improve normality, and significance was set at $P < 0.05$.

RESULTS

We obtained >20,000 locations on 66 radiocollared coyotes during April 1993–August 1998. Twenty-three radiocollared coyotes eventually attained breeding status in 1 of the territories that overlapped HREC property (Fig. 1). At any point in time, most radiocollared coyotes were either breeding residents or nonbreeding transients; only 6 individuals spent time as nonbreeding resident associates.

We found 399 dead sheep during November 1995–August 1998; 125 were confirmed coyote kills, 67 were killed by other predators, 140 died of causes other than predation, and cause of death could not be determined for the remaining 67 sheep. Based on radiotelemetry data, we were able to assign 30 coyote kills with high confidence. Eight breeding pairs killed 22 sheep within their territory boundaries, and 4 of these pairs killed an additional 6 sheep on the periphery of their territories. Two nonbreeding transient males were implicated in 1 kill each; in both cases, the resident pair were excluded as suspects. We assigned another 28 kills with a lesser degree of confidence. Twenty-two of these kills were assigned to 9 breeding pairs, 18 within their territories and 4 on the periphery. Additionally, 1 breeding male was associated with 1 kill while on a foray within another pair's territory, 2 transient males and 1 transient female were associated with a total of 4 kills, and 1 nonbreeding resident male was associated with 1 kill. However, the resident pair could not be excluded as suspects in any of these kills. Finally, for 53 kills where no assignment could be made, all radiocollared coyotes except the resident breeding pair were excluded as suspects.

During August 1994–January 2000, 20 breeding coyotes were selectively removed. One nonbreeding transient male also was killed by an LPC, and 4 additional coyotes punctured LPC and were presumed dead, but their carcasses were never recovered. Both lamb and ewe kill rates declined following the removal of breeding coyotes ($P \leq 0.009$; Table 2). Likewise, the numbers of coyote-killed lambs and ewes also declined in postremoval periods ($P \leq 0.020$), although availability of lambs and ewes within a territory remained similar ($P \geq 0.336$). The number of sheep kills declined after 17 out of 20 removals (85%). Five out of 6 coyotes killed on LPC were breeders, and 2 out of the 6 were females. All breeding pairs in territories with access to sheep eventually killed sheep.

The mean interval between the date a breeding coyote was removed and the date of the first postremoval sheep kill in that territory was 105 days (range 4–398 days). The mean interval was significantly shorter for territories that overlapped lambing pastures ($\bar{x} = 43$, 95% CI = 22 to 73) than for those that did not ($\bar{x} = 184$, 95% CI = 51 to 401; $F_{1,\,13} = 12.7$, $P = 0.003$). The effect of season on the number of days until the first kill was also significant ($F_{2,\,13} = 5.1$, $P = 0.023$). The number of days to the first kill was significantly

Table 2. Pairwise comparison of within-territory availability of lambs[a] and ewes, predation losses (number of kills) and lamb and ewe kill rates (number of kills/1,000 available) for 3 months pre- and postremoval of breeding coyotes at the Hopland Research and Extension Center, Mendocino County, California, USA, May 1994–Apr 2000.

	Preremoval		Postremoval			
Variable	$\bar{x}$	95% CI	$\bar{x}$	95% CI	t	P[b]
Lambs	176	72–279	143	67–220	0.9985	0.336
Ewes	311	190–433	288	208–370	0.7285	0.475
Lamb kills	5.7	2.6–10.0	1.3	0.4–2.7	3.2998[c]	0.006
Ewe kills	1.6	0.6–2.8	0.4	0.0–0.8	2.5306[c]	0.020
Lamb kill rate	8.28	4.331–13.504	1.186	0.196–3.010	3.8931[c]	0.002
Ewe kill rate	0.81	0.232–1.737	0.045	0.002–0.141	2.8928[c]	0.009

[a] Lamb comparisons based on 14 territories that contained lambs during both the pre- and postremoval periods. Ewe comparisons based on 20 territories.
[b] Paired t-test.
[c] Test statistic based on square root-transformed response variable.

shorter during the pup-provisioning period than during dispersal ($P = 0.026$).

On average, 6.2 coyotes/year were removed during the selective control period, compared to 23.2/year during the nonselective period of the study (Table 1) and 11.7/year (SD = 5.1) during the nonselective control years prior to the study (1981–1992). During the lambing season, lamb kill rates were similarly high during 1994 (no control) and 1995 (nonselective control), declined slightly in 1996 (2 mo of no control followed by 3 mo of selective control), and were lowest during the selective control years 1997 and 1998 (Fig. 3A). During the nonlambing season, the average monthly sheep kill rate was relatively low and stable across all years except 1994, when it was double the rate in most other years (Fig. 3B). Overall, monthly lamb kill rates during the lambing period were lower under selective control ($\bar{x}$ = 0.007, 95% CI = 0.004 to 0.009) than either nonselective control ($\bar{x}$ = 0.018, 95% CI = 0.009 to 0.027) or no control ($\bar{x}$ = 0.017, 95% CI = 0.009 to 0.025; Fig. 4A). Monthly sheep kill rates generally were low during the nonlambing period and were similar among all control types (Fig. 4B).

DISCUSSION

These results corroborate previous findings that territorial breeding pairs are responsible for most coyote depredation on sheep (Till and Knowlton 1983, Sacks et al. 1999*b*). Radiotelemetry repeatedly associated breeding coyotes with sheep kills within their own territories or in the interstices between territories. Only 2 of the numerous nonbreeding coyotes present on

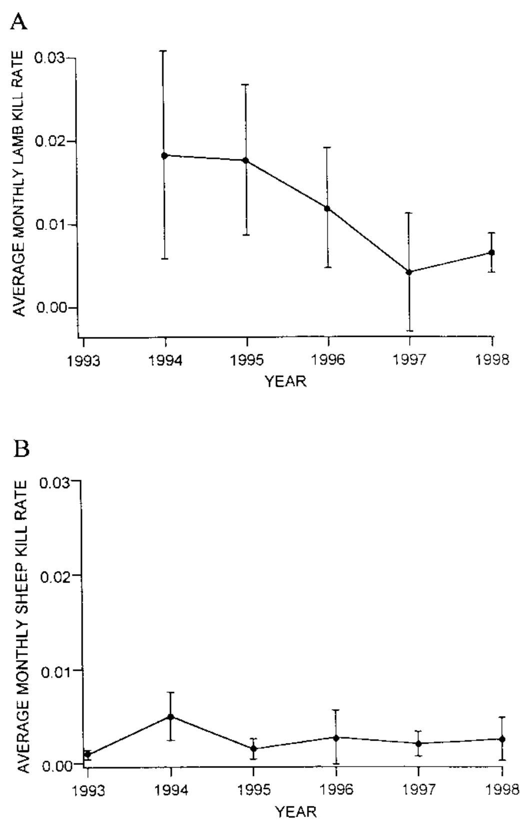

Fig. 3. Annual trends in the average (± 95% CI) monthly kill rates at the Hopland Research and Extension Center, Mendocino County, California, USA, relative to control strategies during Jun 1993–Dec 1998 (N = no control, NS = nonselective control, and S = selective control). Graphs depict (A) lamb kill rates during the lambing season (Jan–May) and (B) sheep (combined lamb and ewe) kill rates during the nonlambing season (Jun–Dec).

HREC throughout the study were conclusively linked to kills; 1 of these was subsequently killed by an LPC. The remaining 5 known-status coyotes killed by LPC were breeders. These results are consistent with observations of coyote attacks on wild ungulates in Yellowstone National Park, most of which involved the breeding pair (Gese and Grothe 1995). Most of those attacks were led by the breeding male, leading to speculation that breeding males also may be responsible for most sheep depredations. However, 2 out of 5 breeders killed on LPC were females, and a third female was believed to have been killed by an LPC after this study ended, suggesting that male and female breeders may be equally likely to kill sheep.

Selective Removal

Selective removal of breeding coyotes in territories experiencing depredations reduced subsequent sheep kills within those territories, although predation was completely eliminated only when no or very few lambs were available during the postremoval period. How quickly killing resumed following a removal depended on whether a territory overlapped lambing pastures. For those that did not, the interval between removal and the first subsequent kill averaged 7 months, compared with only 2 months for territories overlapping lambs. A slight seasonal effect occurred, with the 4 shortest intervals (4–9 days) during the pup-rearing period. However, this effect was not due to the presence of pups per se; pups were present in only half of those 4 territories, and in only 1 of the 3 territories with access to lambs (K. M. Blejwas, unpublished data). Pups may be a more important influence in territories without access to lambs. Predation resumed after only 4 days in the single no-lamb territory with a removal during the pup-rearing season (pups were present in this territory); this interval was substantially shorter than for the no-lamb territories with removals in other seasons (range 138–398 days).

There are 2 potential explanations for the effectiveness of selective removal of breeding coyotes in reducing losses: (1) only 1 member of a pair is killing sheep, and the killing stops because that coyote is successfully removed; or (2) both breeders kill sheep, but loss of a mate interrupts the sheep-killing behavior of the survivor. Several lines of evidence support the second hypothesis. First, a combination of radiotelemetry and LPC data indicated that both members of at least 2 pairs killed sheep. Second, the 15 non-LPC removals were essentially random with respect to which member of the pair was removed. It is unlikely that these removals would have repeatedly succeeded by chance alone in removing the depredating coyote if only 1 member of a pair was killing sheep. Third, the average 2-month interruption in killing observed for territories with access to lambs approximates the average time it took for 8 breeders to replace their mates. Furthermore, in 2 removal territories where the replacement process

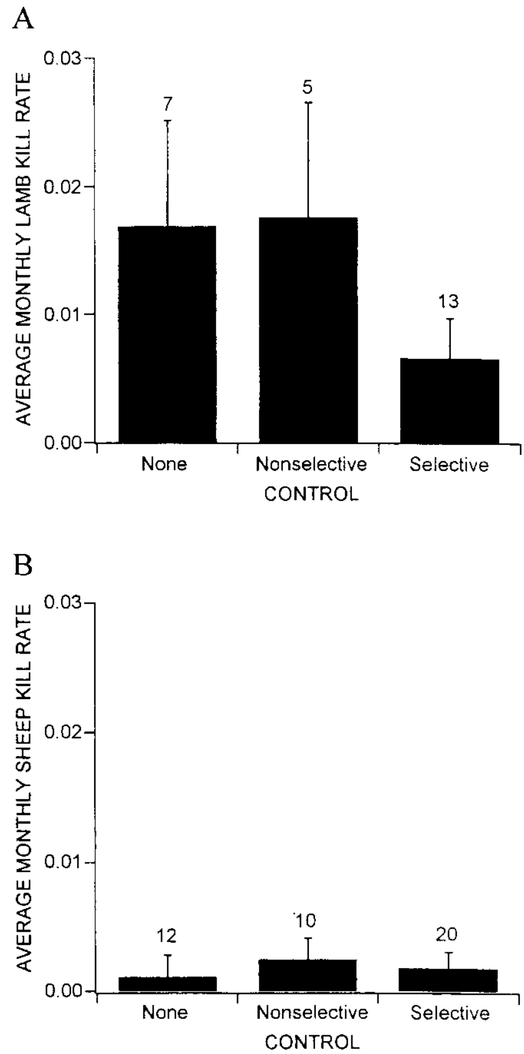

Fig. 4. Average (± 95% CI) monthly kill rates at the Hopland Research and Extension Center, Mendocino County, California, USA, 1994–1998, under 3 different control regimes. The number of months is given above the bars. Graphs depict (A) lamb kill rates during the lambing season (Jan–May) and (B) sheep (combined lamb and ewe) kill rates during the non-lambing season (Jun–Dec).

was monitored, predation resumed only after the new pair had formed (K. M. Blejwas, unpublished data). These data suggest that loss of a mate and the associated process of forming a new pair bond alters the behavior of the surviving breeder, temporarily interrupting predation on sheep.

Why Breeding Coyotes Kill Sheep

It is not surprising that breeding pairs are responsible for most depredations of ewes and large lambs. Most observations of coyotes attacking large ungulate prey indicate that these are cooperative endeavors involving more than 1 coyote (Cahalane 1947, Robinson 1952, Bowyer 1987, Gese and Grothe 1995, Lingle 2000). Most observations of coyotes attacking ungulate fawns also involve pairs or groups of coyotes (MacConnell-Yount and Smith 1978, Hamlin and Schweitzer 1979, Truett 1979, Bowyer 1987), and a pair may be present even when only 1 coyote is involved in the attack (Wenger 1981). In Alberta, adult coyotes hunted summer fawns in groups, although this apparently was not the most efficient means of obtaining food (Lingle 2000). There are several reasons that breeding pairs and packs might be more likely than lone coyotes to prey on ungulate fawns, including increased searching efficiency (Byers 1997), ability to decoy a defensive doe (Hamlin and Schweitzer 1979, Bowyer 1987), a greater incentive to hunt larger prey due to the increased energetic demands of provisioning pups (Harrison and Harrison 1984), and development or maintenance of social bonds through cooperative foraging (Messier and Barrette 1982, Gese et al. 1988).

Some or all of these explanations may apply to predation on domestic lambs as well. Increased searching or hunting efficiency are unlikely to be the incentive for breeding pairs of coyotes to prey on lambs, given that domestic sheep are more predictable than wild prey in their movements and behavior, and lack many antipredator defenses. Furthermore, even naive coyotes with no previous exposure to sheep successfully killed lambs in pen trials (Connolly et al. 1976). However, evidence supports the hypothesis that increased energetic demands faced by breeding pairs during pup-rearing drives predation on lambs, at least in the Intermountain West. In 1 study, packs with pups killed significantly more sheep than packs without pups (Bromley and Gese 2001*b*), and removal of either the breeding pair or their pups significantly reduced depredations in another (Till and Knowlton 1983). By contrast, at HREC, depredations occurred in all seasons, and breeding pairs killed sheep regardless of whether they successfully bred or whelped. Sacks et al. (1999*b*) suggested that even in the absence of pups, the high proportion of time breeding pairs spend together may require them to hunt larger prey, whereas nonbreeding coyotes that spend more time alone are under no such constraint. This hypothesis is consistent with both the pattern of year-round depredations at Hopland and the observation that removal of only 1 member of a sheep-killing pair stops predation.

The above explanations do not account for why nonbreeding transient coyotes do not kill lambs. Transients frequently were located near sheep and were suspected of scavenging sheep carcasses, indicating that they were familiar with sheep as a potential food resource. Sacks et al. (1999*b*) suggested that hunting within defended territories may pose a greater risk of confrontation with resident coyotes than scavenging. Confrontations with resident coyotes are potentially lethal; at least 1 nonbreeding female at HREC was killed by other coyotes (K. M. Blejwas, unpublished data). Because sheep are clumped together on the bedding grounds, it may be difficult for transient coyotes to kill lambs without attracting the attention of the resident pair, even on the periphery of a territory. Scavenging may represent an especially attractive alternative for transients at HREC because breeding pairs tended to make a fresh kill rather than return to an old one (K. M. Blejwas, personal observation). The 2 transient males implicated in killing lambs did so during periods of territorial instability, while new pairs were still becoming established.

Regional Differences in the Sheep-killing Behavior of Breeding Coyote Pairs

At HREC, all breeding pairs in lamb-access territories killed sheep regardless of whether they successfully whelped or not, whereas in the Intermountain West, breeding pairs with pups appear to be responsible for most depredations (Till and Knowlton 1983, Bromley and Gese 2001*b*). The reasons for this apparent regional difference in the sheep-killing behavior of breeding pairs are not well understood and deserve further study. The seasonal availability of sheep and the nature and abundance of alternate wild prey all are likely factors influencing coyote foraging behavior. Coyotes are known to be wary of novelty, and this caution extends to food. In 1995, HREC introduced a flock of Angora goats—a favorite prey of coyotes in Texas (Windberg et al. 1997)—in an attempt to divert predation from research sheep, but no goats were killed during the year they were present (J. Hays, HREC, Division of Agriculture and Natural Resources, University of California, personal communication). Similarly, coyotes in the Sierra Nevada mountains of northern California did not kill any sheep when a band was moved through the study area during 2 consecutive summers (Shivik et al. 1996). Lagomorphs—medium-sized prey that may be hunted by more than 1 coyote (Bowen 1981, Gese et al. 1988)—are the primary wild prey of coyotes in the Intermountain West, whereas sheep are only a seasonal and therefore a more novel resource (Kauffeld 1977, Gese et al. 1988, Mills and Knowlton 1991). Pairs accustomed to hunting lagomorphs for most of the year may need the added incentive of provisioning pups to switch to killing sheep. At HREC, lagomorphs are a minor component of the coyote diet, with deer and small rodents constituting the bulk of the wild-prey base (Neale 1996, Sacks 1996). Sheep, which are available year-round, may constitute an attractive and familiar alternative to deer for breeding pairs.

Selective versus Nonselective Control

Lamb kill rates during the lambing season were lower under selective control than either no control or nonselective control, and this reduction was achieved by removing nearly 4 times fewer coyotes on average than during the nonselective control period. Despite the large number of coyotes removed, lamb kill rates during the 1995 nonselective control period were comparable to the previous year, when there was no control at all (Fig. 3A). It is possible that the large number of removals during nonselective control contributed to the lower kill rates in 1996, the year in which selective control was initiated. However, kill rates actually were higher in 1996 than in subsequent selective control years. These results agree with the findings of Conner et al. (1998), based on 13 years of data from HREC, of no relationship between numbers of coyotes removed by nonselective control in 1 year with the number of sheep kills the following year. In a study of preventive aerial hunting of coyotes in Utah and Idaho, Wagner (1997) also found no consistent relationship between the extent and intensity of nonselective aerial hunting and summer lamb losses. The relatively higher lamb kill rates at HREC during the first year of selective control in 1996 likely were due in part to the timing of the removals that year. While control was selective, it was not initiated until halfway through the lambing season, and no breeding coyotes were removed from lambing pastures until April, a temporal pattern more typical of nonselective control.

During the nonlambing season, sheep kill rates were similarly low among all control types and among all years except 1994. During 1994, the relatively high losses suffered during the lambing season continued on through the summer. By this time, not only were pairs well established after a full year of no control, but nonselective control—when it resumed in late summer—removed primarily nonbreeding coyotes. By contrast, although lambing season losses in 1995 were similarly high, nonlambing losses were relatively low. Although breeders were not being exclusively targeted by nonselective control, their vulnerability increased at this time (Sacks et al. 1999*a*), and the ratio of breeders to nonbreeders removed changed from 1:6 during the fall and winter to 2:1 during the late spring and summer (Table 1).

Fall removals at HREC were ineffective at reducing losses during the subsequent lambing season. In 3 territories, a breeding coyote was removed during September–December, but predation resumed 3–17 days after lambs were put out to pasture the following winter. The benefit of selective control was brief relative to that reported by Wagner and Conover (1999) in Utah and Idaho, where nonselective, preventive aerial hunting 3–6 months before the introduction of lambs reduced losses on summer ranges. In that study, sheep were present only during June–September, and predation was likely confined to those breeding pairs with pups. If so, then removal of breeding pairs (especially breeding females) prior to whelping should have been effective at reducing depredations, as long as replacement pairs did not have time to breed. Furthermore, coyote densities in the Intermountain West probably are lower than at HREC (Sacks 1996:45), which may result in longer replacement times.

The Nonkilling Pairs Hypothesis

At HREC, all pairs with access to sheep eventually killed sheep, suggesting it is unlikely that there are nonkilling pairs where sheep are present year-round. Although individual differences among coyote individuals and pairs undoubtedly influence the extent to which they kill sheep, the availability of lambs within a territory appears to be the overriding factor. Coyotes with access to lambs killed substantially more sheep than coyotes without access to lambs. One male whose original territory did not overlap lambing pastures was implicated in only 2 sheep kills over the course of an entire year. After his mate died, he merged his territory with that of a widowed female in an adjacent lamb-access territory and was subsequently implicated in 2 kills within a month. Furthermore, at HREC, the same territorial pairs that have access to small lambs during the lambing season also have access to replacement lambs during the summer and fall (Fig. 1). Pairs in these territories killed sheep throughout the year, a pattern that may have been encouraged by the continuing presence of replacement lambs within the territory.

MANAGEMENT IMPLICATIONS

Previous studies have shown that breeding coyotes are responsible for most sheep depredations (Till and Knowlton 1983, Sacks et al. 1999*b*). Therefore, the finding of this study that selective removal of breeding coyotes is the most effective strategy of reducing sheep depredations should be widely applicable. Nevertheless, regional differences in the sheep-killing behavior of breeding pairs of coyotes can affect depredation patterns and therefore how selective control is best implemented.

We found that in north-coastal California, all breeding pairs of coyotes with access to lambs will kill sheep. Preventive control (i.e., the removal of coyotes prior to the lambing season) is unlikely to reduce losses because killing in lamb-access territories resumes quickly (typically within 2 mo) after a removal. Corrective, selective removal of breeders in response to depredations may be the only effective approach to coyote control in this region. Selectively removing breeding pairs in lambing territories only after they begin to kill will maximize the probability that the postremoval period will include the peak of the lambing season. By contrast, in the Intermountain West, not all packs whose territories overlap lambing range kill sheep (Bromley and Gese 2001*b*). In that region, the spring–summer lambing season coincides with coyote pup-rearing, and packs with pups are responsible for most depredations. Preventive, selective removal of breeding female coyotes prior to whelping, but too late for replacements to breed, may be the most effective lethal control strategy in this area (Knowlton 1972).

Contraceptive techniques, which create pairs that do not whelp and therefore do not kill sheep, have been proposed as an alternative to lethal control of coyotes. Our results suggest that in northern California, or wherever coyotes have year-round access to sheep, contraceptive techniques will be ineffective at reducing lambing season losses because breeding pairs kill sheep whether they whelp pups or not. However, in the Intermountain West, this could be a superior strategy in that the effect may last years as opposed to a single season. In a study from Utah, sterilized pairs in an unexploited coyote population killed fewer sheep than intact pairs, and the sterilized pairs remained together throughout the 3-year study period, despite failing to produce pups (Bromley and Gese 2001*a*). It is unknown whether sterilized pairs would remain together under different conditions. At HREC, 3 males switched mates following a reproductive failure (K. M. Blejwas, unpublished data). This response may be more typical of exploited populations, where breeders are younger, turnover is high, and pairs are less well established.

Livestock protection collars may be a good compromise between the need of domestic livestock producers for effective predator control and public concerns for minimizing the number of coyotes killed. However, in November 1998, California voters passed a ballot proposition banning the use of Compound 1080, the only toxicant registered for use in the LPC. The perception that LPC were used only after other lethal methods failed, combined with an aversion to poisoning predators (Arthur 1981, Reiter et al. 1999), may have contributed to public support for the ban. Social acceptance of LPC may be greater if they are used, as in this study, as a control tool of first resort, thereby maximizing selectivity and minimizing the number of coyotes removed by control.

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