

# WILEY

Effect of Coyote Removal on Sheep Depredation in Northern California Author(s): Mary M. Conner, Michael M. Jaeger, Theodore J. Weller and Dale R. McCullough Source: The Journal of Wildlife Management, Vol. 62, No. 2 (Apr., 1998), pp. 690-699 Published by: Wiley on behalf of the Wildlife Society Stable URL: https://www.jstor.org/stable/3802345 Accessed: 02-10-2019 00:51 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at https://about.jstor.org/terms



Wildlife Society, Wiley are collaborating with JSTOR to digitize, preserve and extend access to The Journal of Wildlife Management

## EFFECT OF COYOTE REMOVAL ON SHEEP DEPREDATION IN NORTHERN CALIFORNIA

MARY M. CONNER,<sup>12</sup> Department of Environmental Science, Policy, and Management, 151 Hilgard Hall, University of California at Berkeley, Berkeley, CA 94720, USA

MICHAEL M. JAEGER, U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, 151 Hilgard Hall, University of California at Berkeley, Berkeley, CA 94720, USA

THEODORE J. WELLER,<sup>3</sup> Hopland Research and Extension Center, 4070 University Road, Hopland, CA 95449, USA

DALE R. McCULLOUGH, Department of Environmental Science, Policy, and Management, 151 Hilgard Hall, University of California at Berkeley, Berkeley, CA 94720, USA

**Abstract:** We used 13 years of historical data to investigate effects of coyote (*Canis latrans*) removal on depredation of domestic sheep. The 2,168-ha study area maintained >1,000 breeding ewes that produced lambs yearly. Records from 1981 through 1994, which included numbers of sheep, numbers of sheep known killed by coyotes, known numbers of coyotes removed, and annual numbers of trapper hours were summarized and analyzed on a yearly, seasonal, and monthly basis. We used regression analysis and found that annual, seasonal, or monthly depredation losses were not correlated with number of coyotes removed. Both annual number of lambs killed and number of coyotes removed were positively correlated with number of trapper hours. We used a cross-correlation analysis to detect any relation between coyote removal and subsequent depredation losses at all monthly intervals from 0 to 24 months. We found a trend of low negative correlation between depredation losses and number of coyotes removed for lags of 2–12 months, suggesting some reduction of sheep killing due to control efforts. Low correlations within years may be due to inconsistent removal of depredating coyotes while removing primarily young, nondepredating coyotes. Lack of correlation between years may have occurred because past control efforts have not had a lasting reduction on coyote density due to immigration, the compensatory nature of control efforts on coyote mortality, reproductive compensation in the resident coyote population, or all 3 factors.

#### JOURNAL OF WILDLIFE MANAGEMENT 62(2):690-699

Key words: California, Canis latrans, coyote removal, depredation, domestic sheep, Ovis aries.

Coyote predation on domestic sheep remains a chronic problem in the western United States. A principal control strategy is perennial removal of coyotes from livestock operations (Andelt 1996). This local population reduction is selective with respect to the damage site but not necessarily selective to particular coyotes that kill sheep (Connolly 1978). Studies have been conducted on coyote predation at sheep operations in the presence and absence of removal (Klebenow and McAdoo 1976, Henne 1977, Nass 1977, Tigner and Larson 1977, McAdoo and Klebenow 1978). However, variation in annual predation rates between studies and variation in types and intensities of predator control produced inconclusive results (U.S. Department of the Interior 1978, Pearson 1986). Also, because

of the cost of direct field studies, only a small fraction of the sheep industry has been studied. Of 18 of the large coyote-sheep predation studies compiled by the U.S. Department of the Interior (1978) for their comprehensive review of predator damage in the West, 10 were field studies and 8 were questionnaire studies. Duration of the field studies was short: 1 field study was >5 years, while the remaining 7 studies were  $\leq 3$  years in duration. Also, the 8 questionnaire studies may be biased by overestimating losses to ensure federal aid for predator control (U.S. Department of the Interior 1978, Pearson 1986), making the effectiveness of control efforts difficult to evaluate.

This study was done on the Hopland Research and Extension Center (HREC), a sheep ranch in northern California where coyote depredation has been chronic (Scrivner et al. 1985, Timm 1990). The HREC offers a unique opportunity for study of coyote predation on sheep because (1) the dataset on coyote-killed sheep and coyote removals extends over a long period of time (13 yr); (2) daily records of coy-

<sup>&</sup>lt;sup>1</sup> Present address: Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA.

<sup>&</sup>lt;sup>2</sup> E-mail: mconner@cnr.colostate.edu

<sup>&</sup>lt;sup>3</sup> Present address: Department of Wildlife Management, Humboldt State University, Arcata, CA 95521, USA.

ote-killed sheep and coyote removals were kept for 13 years, allowing analyses of predation within and between years; (3) sheep were managed by university employees, which made records of coyote-killed sheep more accurate and unbiased; and (4) the HREC is similar to many sheep operations in the West, where over half of the feed supplied for commercial sheep comes from private land (U.S. Department of the Interior 1978), typically in pasture grazing. To add to the body of information on effectiveness of coyote control, we focus our analysis on long-term patterns of sheep depredation with respect to coyote removal efforts at 3 different time scales: yearly, seasonally, and monthly.

#### STUDY AREA

The University of California's HREC is a sheep research facility located in Mendocino County, California. Elevations ranged from 150 to 915 m. The HREC experienced a typical Mediterranean climate, with hot, dry summers, and mild, rainy winters. Average annual precipitation was 92 cm; summer rainfall was rare. Average temperatures ranged from 8°C in winter to 21°C in summer. The vegetation of HREC was a mosaic of 4 habitat types: grassland (27%), woodland-grass (33%), dense woodland (20%), and chaparral (19%; Murphy and Heady 1983). Common grassland species were wild oats (Avena barbata), ripgutt (Bromus diandrus), and foxtail (Festuca megalura). Woodland-grass patches were dominated by blue oak (Quercus douglasii), valley oak (Q. lobata), and interior live oak (Q. wislizenii); dense woodland was dominated by black oak (Q. kelloggii), madrone (Arbutus menziesii), and California bay (Umbellularia californica). Chaparral occurred mainly above 610 m and included chamise (Adenostoma fasciculatum), ceanothus (Ceanothus cuneatus), manzanita (Arctostaphylos spp.), and scrub oak (Q. durata).

The HREC maintained 900–1,500 ewes dispersed among 32 fenced pastures averaging 80 ha each. Sheep were rotated among pastures according to range quality and research needs. Typically, 8–12 of the pastures contained sheep at any time. Shepherds did not stay with the sheep in the pastures but checked pastures weekly. Between 700 and 1,300 lambs were born during 2 seasons between mid-November and March. Lambs were born in a main barn and held for at least 48 hr prior to placement in pastures.

Average annual predation rates of ewes (2.0%) and lambs (3.1%) at HREC were similar to those experienced in many operations in the West (U.S. Department of the Interior 1978, Pearson 1986). Coyote density over the entire study period is unknown. However, density estimates for the 21.68-km<sup>2</sup> study area, from preand postwhelping during 1994-95, were 0.59  $coyotes/km^2$  (95% CI = 0.41–0.95) for coyotes >5 months old, and 0.76 coyotes/km<sup>2</sup> (96% CI = 0.50-1.41) for covotes of all ages (Sacks 1996). Trapping, snaring, and, more recently, M-44s have been the primary coyote removal methods, but shooting and denning (Till and Knowlton 1983) also have been used. Coyote removal at HREC was similar to other western sheep operations (Gee et al. 1977, U.S. Department of the Interior 1978), particularly those in northcentral California. The HREC has records of sheep availability, sheep distribution, and dates and locations of predator kills from 1981 to 1994. Additionally, U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services program (WS; formally known as Animal Damage Control or ADC) records of coyote removals and annual trapper hours worked on HREC were available for the same period.

#### METHODS

We summarized 13 years of historical data from the HREC from 1981 to 1994 (1986 data were missing). Records were kept on a monthly basis and included number, age classification, and sex of sheep in each pasture, as well as age and sex of all coyote-killed sheep. Coyote kills were typically identified by hemorrhaging under the skin at the throat (Wade and Bowns 1985). The daily pattern of pasture searching was consistent from year-to-year, although search effort may have been less during 1991-92. Within years, pastures with sheep were visited most days, but pastures with lambs were searched more often. Numbers of coyote-killed sheep did not include the sheep missing in each pasture, because this number was not accurately recorded on a monthly basis. The same shepherd worked on the station from 1981 to 1994; hence, search effort and recording of missing animals were relatively consistent from year-toyear (J. Hays, HREC, personal communication). Annual records of missing lambs were available for 1977-79 and 1990-94. We excluded missing lambs from predation analyses because missing lambs were only recorded at weaning and sale, there was no relation between annual numbers of missing lambs and number of lambs killed or number of coyotes removed, and causes of missing sheep could not be determined (e.g., whether due to coyote, mountain lion [*Felis concolor*], black bear [*Urus americanus*], golden eagle [*Aquila chrysaetos*], disease, exposure, miscounts, etc.).

We also used WS records of date and number of coyotes 'removed and of annual trapper hours from September 1981 through August 1994. Annual number of coyotes removed by the WS represents a minimum because HREC personnel, neighbors, and seasonal hunters occasionally removed coyotes (typically by shooting), but these efforts were random and independent with respect to efforts of control personnel. Coyote pups were not included in the analyses. Thus, the population of interest was the total number of sheep killed by covotes and the total number of coyotes removed by WS personnel on HREC. All analyses in this study were done on a sample; that is, known coyote-killed sheep and known coyote removals are a sample of the total number killed and total number removed.

Depredation losses were represented by the known number of lambs or ewes killed, and lamb or ewe kill rates. Kill rates were the proportion of lambs and ewes killed per month or year, per number of lambs or ewes available. Lambs were present on HREC from November through mid-May, and only the months of this period were used in analyses involving lambs. To avoid confounding patterns of ewe and lamb killing, only months when lambs were absent (May-Oct) were used in analyses involving ewes. Removal of coyotes, which could take place during any month of the year, was regressed against only months when lambs were present. The HREC retained relatively small numbers of older lambs as replacements, and these were lambs were counted as ewes, beginning in May.

We examined annual patterns of predation through relations between the known number and rate of sheep killed, known number of coyotes removed, total number of trapper hours spent on HREC, and number of missing sheep. We determined effects of coyote removal on depredation losses by regressing annual number of lambs and ewes killed and kill rates against number of coyotes removed, with the null hypothesis that depredation losses were not correlated with the number of coyotes removed on a yearly basis. We regressed annual number of lambs and ewes killed and kill rates against annual trapper hours to evaluate if control on HREC, at least annually, was preventative or corrective. The null hypothesis was that number of kills or kill rates were not related to trapping effort. We regressed annual number of coyotes removed against annual trapper hours to evaluate if numbers removed were related to effort and not to changes in covote population densities. The null hypothesis was that trapping effort was not related to number of coyotes removed. Lastly, we regressed annual number of total kills (ewes plus lambs) against annual number of missing sheep to evaluate if missing sheep could be confounding the relation between number of kills and number of covote removals. The null hypothesis was that number of kills was not related to number of missing sheep.

We examined monthly patterns of predation by regressing number of lambs and ewes killed and kill rate against number of coyotes removed. The null hypothesis was that depredation losses were not related to the number of coyotes removed on a monthly basis. However, correlations between the number of lambs and ewes killed, or kill rate, and the number of coyotes removed could occur at intervals different than 1 month or year. For example, removing 3 coyotes in 1 month might not decrease the number of lambs and ewes killed until the following month, or the following year. Therefore, we used a cross-correlation analysis (Diggle 1990) to detect correlations at all monthly intervals from 0 to 24 months. Negative correlations between coyote depredation losses and number of coyotes removed would suggest that coyote removal was decreasing future depredation. Positive correlations may indicate a disruption in existing coyote territories, whereby more coyotes have access to sheep, which results in increased depredation. The null hypothesis was that depredation losses were not related to number of coyotes previously removed for lags of 0-24 months.

Seasonal analyses were conducted by partitioning time to examine the effects of lamb presence. Because coyote predation on sheep may be related to timing of lamb and sheep use and not related to calendar months, we performed an analysis based on seasonal changes in sheep production: lambing 1 = November,

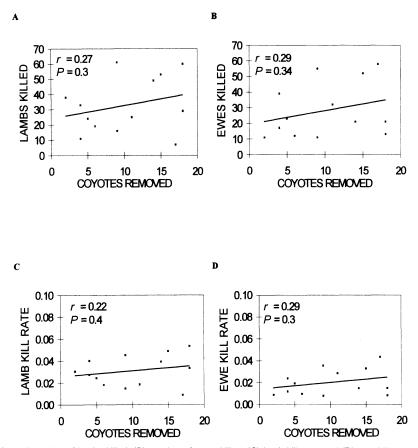


Fig. 1. (A) Annual number of lambs killed, (B) number of ewes killed, (C) lamb kill rate, and (D) ewe kill rate versus number of coyotes removed from Hopland Research and Extension Center, California, September 1981–August 1994.

December, and January; lambing 2 = February, March, and April; ewes 1 = May, June, and July; and ewes 2 = August, September, and October. Both number of kills and number of coyotes removed were grouped by these seasons. We regressed seasonal number of lambs and ewes killed and kill against number of coyotes removed. Because removal may reduce subsequent killing, numbers of coyotes removed were regressed at lags of 1–4 seasons. The null hypothesis was that depredation losses were not related to the number of coyotes removed on a seasonal basis.

Statistical analyses of the historical data were post hoc. We used  $\alpha = 0.05$  in all analyses. Power analyses on the correlation coefficients were based on a 1-sided alternative hypothesis (i.e.,  $H_0: \rho = 0$  vs.  $H_1: \rho < 0$ ). The relations between coyote removal and kill rates cannot be considered causal because of the observational nature of this study. We verified assumptions of nor-

mality, equal variance, and linearity of residuals for all regression analyses (Ott 1993).

#### RESULTS

Annual lamb and ewe kills and kill rates were not correlated with the number of coyotes removed (P > 0.05; Figs. 1A–D). There was a positive correlation between number of lambs killed per year and number of trapper hours worked on HREC per year  $(r_{12} = 0.68, P =$ 0.015), but lamb kill rate was not correlated to trapper hours ( $r_{12} = 0.50, P = 0.095, 1 - \beta =$ 0.64). There was also a positive correlation between number of coyotes removed per year and number of trapper hours worked on HREC per year  $(r_{12} = 0.75, P = 0.003)$ . Neither number of ewes killed nor ewe kill rate was correlated with number of trapper hours on an annual basis (ewes killed:  $r_{12} = 0.20$ , P = 0.530,  $1 - \beta =$ 0.19; kill rate:  $r_{12} = 0.14$ , P = 0.658,  $1 - \beta =$ 0.15). Post hoc power analyses (Zar 1984) in694

A

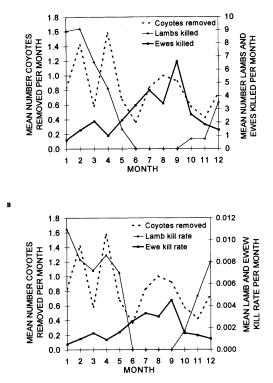


Fig. 2. (A) Mean monthly number of coyotes removed, number of lambs and ewes killed and (B) lamb and ewe kill rates on Hopland Research and Extension Center, California, September 1981–August 1994.

dicated an effect size of r = 0.76 was needed to ensure 90% power for annual regression analyses. Annual mean number of coyotes removed was 10.8 (SE = 1.6, n = 13). Annual mean number of missing sheep was 177 (SE = 8.9, n = 8), which was an average of 11.8% (SE = 0.5, n = 8) of the HREC flock. Annual number of missing sheep was not correlated with annual number of kills ( $r_7 = 0.55, P = 0.205, 1$  $-\beta = 0.49$ ).

Plots of mean monthly sheep kills and coyotes removed showed highest lamb kills and lamb kill rates occurred during January through April, while ewe kills and kill rates were highest during July through September (Figs. 2A,B). Coyote removals occurred over the entire year, with peaks in February, April, and September (Figs. 2A,B). Neither monthly number of lambs killed nor lamb kill rate was correlated with number of coyotes removed (lambs killed:  $r_{71}$ = 0.19, P = 0.117,  $1 - \beta = 0.47$ ; kill rate:  $r_{71}$ = 0.20, P = 0.093,  $1 - \beta = 0.51$ ). Similarly, neither monthly number of ewes killed nor ewe kill rate was correlated with number of coyotes removed (ewes killed:  $r_{71} = 0.16$ , P = 0.196,  $1 - \beta = 0.48$ ; kill rate  $r_{71} = 0.22$ , P = 0.071,  $1 - \beta = 0.56$ ). Post hoc power analyses (Zar 1984) indicated an effect size of r = 0.37 was needed to ensure 90% power for monthly regression analyses.

Monthly effects of coyote removal on number of lambs and ewes subsequently killed and proportion of lambs and ewes subsequently killed were determined via cross-correlation plots for lags of 0-24 months (Figs. 3A-D). Most correlations for lambs were low, nonsignificant, and negative. An annual pattern of negative correlations for ewe kills and kill rate versus number of coyotes removed appeared for lags of 3–11 months. Correlations were all low; 97% of all confidence intervals contained zero. However, there were more negative correlations than expected at random for lags of 1-12 months (P < 0.001 for all independent variables) and lags of 13–24 months (P < 0.006 for)all independent variables). Post hoc power ranged from 0.17 to 0.72 for the cross-correlation regression coefficients. Post hoc power analyses (Zar 1984) indicated effect sizes from r = 0.37 for no lag to r = 0.41 for a 24-month lag were needed to ensure 90% power.

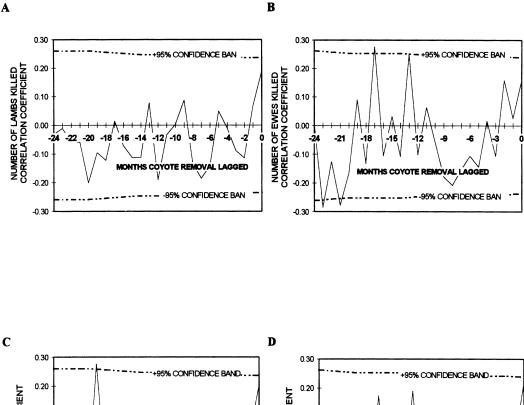
All of the highest correlations were negative; that is, the numbers of sheep killed and kill rates decreased with increasing numbers of coyotes removed (Table 1). The 12-month lag of the number of coyotes removed had the highest correlation coefficient for number of lambs killed (Fig. 3A) and lamb kill rate (Fig. 3C). The 7–9-, 21-, and 23-month lags of number of coyotes removed had the highest correlation coefficients for number of ewes killed (Fig. 3B) and ewe kill rate (Fig. 3D).

Two of the seasonal correlations were borderline significant. These were for ewe kills and kill rates during ewes 1, when coyotes were removed during lambing 2 (ewes killed:  $r_{19} =$ -0.51, P = 0.074; kill rate:  $r_{19} = -0.51$ , P =0.063).

#### DISCUSSION

#### Temporal Patterns

On an annual scale, there were significant positive correlations between the number of lambs killed and number of trapper hours worked and number of coyotes removed and number of trapper hours worked. However,



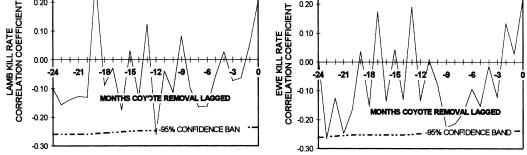


Fig. 3. (A) Plot of correlation and 95% confidence intervals for monthly numbers of lambs killed, (B) numbers of ewes killed, (C) lamb kill rate, and (D) ewe kill rate versus the numbers of coyotes removed monthly for intervals lagged from 0–24 months (previous to analyzed month) on Hopland Research and Extension Center, California, September 1981–August 1994. Correlations for lamb kills were done for November–April (lambs and ewes present), while correlations for ewe kills were done May– October (only ewes present). Correlations were significantly different from zero when they cross the 95% confidence band.

Table 1. Regression statistics for best significant lags between number of coyotes removed per month and number of sheep killed per month, Hopland Research and Extension Center, California, 1981–94. The year 1986 is excluded from analysis, because of missing data.

Response variable	Lag <sup>a</sup> (months)	Regression equation	Sample size	Slope P-value	$r^2$
Lamb kill rate	-12	$\hat{Y} = 0.0084 - 0.0014x$	66	0.034	0.068
Ewe kill rate	-9	$\hat{Y} = 0.0032 - 0.0009x$	68	0.064	0.051
No. of lambs killed	-12	$\hat{Y} = 5.90 - 0.77x$	66	0.124	0.039
No. of ewes killed	-8	$\hat{Y} = 4.17 - 0.97x$	69	0.085	0.043

<sup>a</sup> Lag of 12 months expresses the relation between known number of lambs killed in the present month versus known number of coyotes removed 12 months earlier.

there was no relation between number of lambs killed and number of coyotes removed. If only certain coyotes kill sheep, increasing numbers of coyotes removed will have no effect on number of sheep killed unless the problem coyote is removed. Thus, the lack of relation between number of lambs killed and number of coyotes removed may be because most of the coyotes removed were not killing sheep. Superficially, low power appears the culprit in failure to find a relation between sheep killing and coyote removals, but low power was an artifact of low effect sizes.

Nonlagged monthly patterns of coyote removal suggest that coyote control at HREC tended to be more corrective than preventative in that peaks of removals occurred in February and April, when lamb killing was greatest, and in July through September, when ewe killing was greatest (Fig. 1). All response variables for ewe and lamb killing were positively correlated with numbers of coyotes removed on a yearly and monthly basis. Although none of the correlations were significant, the consistent pattern of positive correlations was evidence there was a corrective element of coyote removal practiced at HREC.

Alternatively, increased coyote population densities on HREC could result in high numbers of kills and coyote removals. Whether high depredation losses and high numbers of coyote removals were positively correlated with high coyote population densities is unknown. However, annual number of coyotes removed was positively correlated with annual number of trapper hours worked at HREC, suggesting that years with higher coyote removals were years with more trapping effort. Also, annual number of lambs killed was positively correlated with annual trapper hours, suggesting that the corrective responses focused on number of lambs killed. If number of lambs killed and coyotes removed were not positively correlated to trapper hours, then fluctuations in coyote density as the underlying cause of higher depredation would be a likely conclusion. Hence, number of coyotes removed at HREC likely was determined by number of lambs killed rather than vice versa.

Coyote removal during the second lambing season reduced ewe depredation during the following 3-month season. Coyote removal may reduce ewe depredation more than lamb depredation because the corrective nature of control with respect to lambs leads to a preventative strategy with respect to ewes. However, the majority of negative correlations at all lags suggests some preventative effect of coyote removal for both lambs and ewes. However, preventative effects were low; the highest negative coefficient of determination was 0.08, indicating that only about 8.4% of the variability in kill rates can be explained by the removal of coyotes. Low effect sizes and correlations between kills and number of coyotes removed within years may be explained by the lack of consistency in removing the offending coyotes.

There was no indication that removal of coyotes reduced predation the following year (i.e., lagged intervals >12 months), suggesting that covote density was not being reduced by removal efforts. Thus, 1 year later, territories of removed coyotes were replaced. There are at least 3 explanations for this result. First, immigration may be density dependent, thus enabling coyote densities to remain at or near saturation levels (Knowlton and Stoddart 1983). For coyote density to be decreased, there must be geographical isolation from other covotes within a dispersible distance, or there must be methods available, such as aerial gunning, whereby high numbers of coyotes can be consistently removed. The HREC is a relatively small area (2,168 ha). Aerial gunning was not an option, and control efforts could not prevent immigration from adjacent areas, including 30,000 ha of land with no coyote control. Second, control moralities may be only compensatory (Gese et al. 1989). Third, coyote reproductive flexibility may make it extremely difficult to reduce coyote density, even within HREC boundaries. Pregnancy rates (Gier 1968), litter size, and pup survival (Knowlton 1972, Gier 1975, Connolly 1978, Knowlton and Stoddart 1983, Sterling et al. 1983) are inversely correlated to coyote population density, which allows a coyote population to maintain itself except at very high levels of control (Clark 1972, Connolly and Longhurst 1975). Thus, if lamb and ewe losses were positively correlated with coyote population levels, then extremely high levels of coyote removal on HREC and surrounding areas would be required annually to decrease depredation losses.

The relation between number of coyotes removed and subsequent sheep kills was irregular and highly variable among months. This variability may be due, in part, to factors other than inconsistent removals of problem coyotes. For example, the effect of trapper-removed coyotes may have been confounded by additional coyote removals by HREC personnel, hunters, or neighboring ranches, but there was no reason to suspect such removals. In general, very few additional coyotes (0-3) were likely removed from the immediate study area each year, and these removals were opportunistic and random in relation to when and where depredation occurred. Also, variation among trappers could confound the results. However, only 2 trappers were in charge during the study period; the same trapper worked from 1981 to 1988, and a second trapper worked from 1989 to 1992. We feel trapper effort was a response to depredation and was directed to when and where losses were occurring. If trapper removals were effective, then there should be reduced losses at some monthly lag, irrespective of other occasional and temporally scattered removals.

### Factors Influencing Efficacy of Coyote Removal

Coyote removals on the HREC have had a limited effect on reducing sheep losses, which suggests depredating coyotes were not being removed, but our result may not apply to other sheep operations where coyotes are removed. However, a number of factors likely influence the efficacy of coyote removal that is not selective to the offending animal, and these factors vary among situations. First, the vulnerability of offending coyotes to removal may vary between fixed grazing and range operation. Adult, breeding territorial coyotes are thought the principal killers of livestock (Till and Knowlton 1983, Windberg and Knowlton 1990, Sacks 1996) and may be difficult to remove by conventional means of control (Windberg and Knowlton 1988, 1990; Sacks 1996) in areas where animals have prior exposure to capture efforts. The control techniques used on HREC were primarily snaring, trapping, and M-44s. Windberg and Knowlton (1990) found no difference between adults and juveniles in relative vulnerability to M-44s and leghold traps. This finding contrasts to Sacks (1996) who reported that M-44s were effective against juvenile and yearling coyotes but were ineffective against adults. The principal difference between these studies was the long history of control at HREC, where capture efforts had been intensive. The Windberg and Knowlton (1990) study was done where prior

exposure to capture efforts was unlikely. Coyotes exposed to control may become wary and harder to remove. This interpretation is consistent with the findings of Brand et al. (1995) in southern Africa who found that adult blackbacked jackals (Canis mesomelas) avoided coyote-getters when exposure duration increased and resulted in high proportions of young jackals taken. Thus, in areas where coyotes are naive with respect to control efforts, removal of the problem territorial animals may be more successful. At HREC or other pasture operations with consistent coyote control, typical removal efforts may differentially remove young coyotes and only occasionally remove problem coyotes, resulting in weak negative correlations between total coyotes removed and subsequent sheep kills.

Second, there may be seasonal differences in the vulnerability of coyotes to removal. Adult territorial coyotes become more vulnerable to trapping and M-44s during pup rearing season (Till and Knowlton 1983, Sacks 1996). If the peak of lamb killing occurs simultaneously with pup rearing, then removal of problem animals may be more successful than at HREC, where pup rearing begins 2 months after the peak of lambing season and lamb killing. Removing denning coyotes or their pups can stop nearby depredation (Till and Knowlton 1983). In situations such as north-coastal California, where lambing occurs during winter and is out-ofphase with pup rearing, it may be more difficult to remove the territorial animals responsible for most of the killing versus removals in range or pasture operations where pup rearing and lambing coincide.

Third, prey availability may buffer depredation (Hamlin et al. 1984, Mech 1988) or curtail the length of high predation rates. Other studies have found 2 peaks in sheep losses to coyote predation similar to those on HREC: 1 in spring during lambing season, and another in late summer and fall (Rosko 1948, Klebenow and Mc-Adoo 1976, Tigner and Larsen 1977, McAdoo and Klebenow 1978). The abundance of food during early summer, in the form of mule deer (Odocoileus hemionus) fawns or small mammals, possibly can replace sheep as the preferred coyote prey. Thus, for range or pasture operations, there may be a similarity in temporal fluctuations in coyote predation. Timing of removal efforts may vary among operations, but timing removal to occur just prior to know peaks of predation should be the strategy on all types of operations.

#### MANAGEMENT IMPLICATIONS

Results of the analyses presented here suggest the need for more selective targeting of coyotes. Situations similar to the HREC are likely common among sheep grazed on private land and where local population reduction is perennial and nonselective. A method that is selective for sheep-killing coyotes is the 1080 Livestock Protection Collar, which is limited in availability by restrictions necessary for its safe use. Denning (i.e., killing pups in dens) and shooting of territorial animals located in areas of high killing may be a practical selective strategy. Timing of control should occur just before annual peaks in losses, such as just prior to lambing, otherwise the removal of a problem coyote can result in its replacement before peak killing times. Real effects of coyote removal will not be fully known unless a proper experiment with a treatment (coyote removal) and control site with no coyote removal is examined for effects on predation rates. Monitoring the effect of coyote removals on subsequent livestock depredation is also a necessary component of effective management.

#### ACKNOWLEDGMENTS

We thank S. A. Ardley, V. Bolshov, C. M. Mogel, M. S. Murphey, A. Peet, and E. Ruddick for hours spent in the field and behind the computer. Also, a special thanks to R. M. Timm and the HREC personnel who made the project possible. W. F. Andelt, F. F. Knowlton, J. A. Shivik, and G. C. White were most helpful in reviewing earlier drafts of this manuscript. We also thank Fisher Consultants for all their support. This study was funded primarily by USDA/APHIS/WS/Denver Wildlife Research Center through cooperative agreement 12-34-74-0235-CA with the Environmental Science, Policy and Management Department of the University of California at Berkeley. Other support was provided by the University of California, Berkeley, from Wildlife Graduate Student Funds.

#### LITERATURE CITED

ANDELT, W. F. 1996. Carnivores. Pages 133–155 in P. R. Krausman, editor. Rangeland wildlife. Society for Rangeland Management, Denver, Colorado, USA.

- BRAND, D. J., N. FAIRALL, AND W. M. SCOTT. 1995. The influence of regular removal of black-backed jackals on the efficiency of coyote getters. South African Journal of Wildlife Resources 25:44–48.
- CLARK, F. W. 1972. Influence of jackrabbit density on coyote population change. Journal of Wildlife Management 36:343–356.
- CONNOLLY, G. E. 1978. Predator control and coyote populations: a review of simulation models. Pages 327–345 in M. Bekoff, editor. Coyotes: biology, behavior, and management. Academic Press, New York, New York, USA.
- , AND W. M. LONGHURST. 1975. The effects of control on coyote populations: a simulation model. University of California-Davis, Division of Agriculture Bulletin 1872.
- DIGGLE, P. J. 1990. Time series: a biostatistical introduction. Oxford University Press, Oxford, United Kingdom.
- GEE, C. K., R. S. MAGLEBY, W. R. BAILEY, R. L. GUM, AND L. M. ARTHUR. 1977. Sheep and lamb losses to predators and other causes in the western United States. U.S. Department of Agriculture Economic Resource Services Publication 369.
- GESE, E. M., O. J. RONGSTAD, AND W. R. MYTTON. 1989. Population dynamics of coyotes in southeastern Colorado. Journal of Wildlife Mangement 53:174–181.
- GIER, H. T. 1968. Coyotes in Kansas. Kansas State College Agricultural Experiment Station Bulletin 393.
- . 1975. Ecology and social behavior of the coyote (*Canis latrans*). Pages 247–262 in M. W. Fox, editor. The wild canids: their systematics, behavior, ecology, and evolution. Van Nostrand Reinhold, New York, New York, USA.
- HAMLIN, K. L., S. J. RILEY, D. PYRAH, A. R. DOOD, AND R. J. MACKIE. 1984. Relationships among deer fawn mortality, coyotes, and alternative prey species during summer. Journal of Wildlife Management 48:489–499.
- HENNE, F. R. 1977. Domestic sheep mortality on a western Montana ranch. Pages 133–146 in R. L. Phillips and C. Jonkel, editors. Proceedings of the 1975 Predator Symposium. Montana Forest and Conservation Experiment Station, School of Forestry, University of Montana, Missoula, Montana, USA.
- KLEBENOW D. A., AND J. K. MCADOO. 1976. Predation on domestic sheep in northwest Nevada. Journal of Range Management 29:96–100.
- KNOWLTON, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. Journal of Wildlife Management 36:369–382.
- AND L. C. STODDART. 1983. Coyote population mechanics: another look. Pages 93–108 in F. L. Bunnell, D. S. Eastman, and J. M. Peek, editors. Natural regulation of wildlife populations. Proceeding 14. Forestry, Wildlife, and Range Experiment Station, University of Idaho-Moscow, Moscow, Idaho, USA.
- MCADOO, J. K., AND D. A. KLEBENOW. 1978. Predation on range sheep with no predator control. Journal of Range Management 31:111–114.

J. Wildl. Manage. 62(2):1998

- MECH, L. D. 1988. The arctic wolf: living with the pack. Voyageur Press, Stillwater, Minnesota, USA.
- MURPHY A. H., AND H. F. HEADY. 1983. Vascular plants at the Hopland Field Station, Mendocino County, California. Wasmann Journal of Biology 41:53–95.
- NASS, R. D. 1977. Mortality associated with sheep operations in Idaho. Journal of Range Management 30:253–258.
- OTT, R. L. 1993. An introduction to statistical methods and data analysis. Fourth edition. Wadsworth, Belmont, California, USA.
- PEARSON, E. W. 1986. A literature review of livestock losses to predators in the western U.S. U.S. Fish and Wildlife Service Final Report, Denver, Colorado, USA.
- ROSKO, L. 1948. Losses of sheep from predatory animals on summer ranges in Iron County, Utah. Special Report. Utah Cooperative Wildlife Resource Unit and Range Department, Utah Experimental Station, Logan, Utah, USA.
- SACKS, B. N. 1996. Ecology and behavior of coyotes in relation to depredation and control on a California sheep ranch. Thesis, University of California-Berkeley, Berkeley, California, USA.
- SCRIVNER, J. H., W. E. HÓWARD, A. H. MURPHY, AND J. R. HAYS. 1985. Sheep losses to predators on a California range, 1973–1983. Journal of Range Management 38:418–421.
- STERLING, B., W. CONLEY, AND M. R. CONLEY. 1983. Simulations of demographic compensation in coyote populations. Journal of Wildlife Management 47:1177–1181.
- TIGNER, D. S., AND J. P. LARSON. 1977. Sheep losses

on selected ranches in southwestern Wyoming. Journal of Range Management 30:244–252.

- TILL, J. A., AND F. F. KNOWLTON. 1983. Efficacy of denning in alleviating coyote depredations upon domestic sheep. Journal of Wildlife Management 47:1018–1025.
- TIMM, R. M. 1990. Predator damage and research at Hopland Field Station, University of California. Pages 3–9 in G. A. Gusti, R. M. Timm, and R. H. Schmidt, editors. Predator management in north coastal California. University of California, Hopland Field Station Publication 101.
- U.S. DEPARTMENT OF THE INTERIOR. 1978. Predator damage in the West: a study of coyote management alternatives. U.S. Fish and Wildlife Service, Washington, D.C., USA.
- WADE, D. A., AND J. E. BOWNS. 1985. Procedures for evaluating predation on livestock and wildlife. Texas Agricultural Extension Service, and Texas Agricultural Experiment Station of the Texas A&M University, and U.S. Fish and Wildlife Services Cooperative Publication B-1429.
- WINDBERG, L. A., AND F. F. KNOWLTON. 1988. Management implications of coyote spacing patterns in southern Texas. Journal of Wildlife Management 52:632–640.
- —, AND —, 1990. Relative vulnerability of coyotes to some capture procedures. Wildlife Society Bulletin 18:282–290.
- ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Received 13 January 1997. Accepted 15 September 1997. Associate Editor: Sinclair.