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RELATIVE VULNERABILITY OF COYOTES TO REMOVAL METHODS ON A NORTHERN CALIFORNIA RANCH

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Abstract: Evidence suggests that predation on domestic sheep by coyotes (*Canis latrans*) is caused primarily by breeding pairs with territories overlapping sheep. Accordingly, we investigated vulnerability of coyotes to removal methods relative to factors associated with reproduction and territoriality. We collected live and lethal coyote capture data during April 1993–February 1998 on a north-coastal California sheep ranch. Routine coyote removal was conducted in response to sheep depredation before and during (part of) the study. Younger (nonbreeding) coyotes generally were more vulnerable to capture than older (potentially breeding) individuals, although age bias varied among removal methods. Recaptures of radiocollared coyotes in foothold traps and snares indicated a bias toward progressively younger individuals (juv > yearling > ad; $P = 0.002$). Proportionally more juvenile and yearling coyotes were removed by M-44s (sodium cyanide ejectors) than by traps and snares ($P = 0.016$). We found no difference between traps and snares in the ages of coyotes taken ($P = 0.50$). Vulnerability of younger coyotes was likely elevated by lack of experience and more time spent in unfamiliar areas where they were least able to avoid capture devices. Coyotes were caught more often than expected outside of core areas of their territories with both traps ($P = 0.001$) and snares ($P = 0.02$). Older coyotes were most vulnerable in spring and summer when rearing pups, after most depredation occurred. Radiocollared breeders ($P = 0.012$) and uncollared coyotes of breeding age ($P = 0.052$) were captured less often during the non-pup-rearing period than the pup-rearing period. These results suggest conventional control in northern California is poorly suited to the segment of the coyote population killing the most sheep, particularly during the time of year when most sheep depredation occurs. Efficacy of control methods might be improved by conservative use of conventional devices to minimize learned avoidance by coyotes, and by greater reliance on methods such as livestock protection collars that are specific to depredating individuals throughout the year.

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Coyote predation on domestic sheep is a serious problem for sheep producers and has been identified as an important factor in the decline of the U.S. sheep industry (Wagner 1988, National Agricultural Statistics Service 1995). Depredation management historically centered on efforts to greatly reduce or extirpate coyote populations (Nunley 1995). Due to changing attitudes in recent decades toward such strategies (Dunlap 1988, Schmidt 1990, Reiter et al. 1995) and the shrinking spatial scale and fragmentation of sheep production in many regions (Hackett 1990), these goals are no longer realistic. Since the early 1970s, removal efforts have been restricted to sheep production sites where depredation occurs (Connolly 1978). Current strategies are either (1) preventive, aimed at reducing coyote numbers locally before introduction of sheep; or (2) corrective, removing individuals in response to sheep depredation (Connolly 1978, U.S. Department of Agriculture 1994, Wagner 1997). The methods most commonly used for corrective removal are foothold traps (hereafter, "traps"), snares, M-44s, and shooting (U.S. Department of Agriculture 1994, Andelt 1996). The corrective approach is used throughout the western United States, sometimes in conjunction with preventive removal (Wagner 1997). Control specialists usually have extensive field experience and are highly skilled at using available techniques to remove coyotes. However, depredation levels remain unacceptable to many producers, indicating a need for more information on which to base removal strategies.

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Conventional corrective removal efforts are aimed at specific areas where depredation has occurred (Connolly 1978), but techniques remain nonselective to depredating versus nondepredating individuals using those areas. The degree to which conventional methods alleviate sheep depredation is difficult to assess but seems to vary throughout the western United States (McAdoo and Klebenow 1978, O'Gara et al. 1983). Recently, Conner et al. (1998) reported that nonselective removal of coyotes from a north-coastal California ranch was inconsistent over time at reducing depredation. These authors speculated that a small proportion of coyotes killed sheep and that those individuals were not consistently removed. Sacks et al. (1999) found that breeding pairs (especially males) with territories overlapping sheep were responsible for most kills.

Several factors associated with breeding status likely affect vulnerability to removal. First, breeders tend to be older individuals (Gier 1968, Windberg 1995). Older coyotes are thought to be less vulnerable to capture than younger ones, but this pattern has not been demonstrated directly (Roy and Dorrance 1985, Windberg et al. 1985, Windberg and Knowlton 1990).

Second, in contrast to nonbreeders, which are often transient, breeders are obligatorily territorial (Messier and Barrette 1982, Sacks et al. 1999). Coyotes are more difficult to capture in traps within their territories than in unfamiliar areas (Hibler 1977, Woodruff and Keller 1982, Windberg and Knowlton 1990). Site-dependent vulnerability may result from (1) increased inquisitive behavior, stimulated by strange surroundings, and corresponding attraction to trap baits; or conversely, (2) greater awareness of changes in familiar areas (e.g., human scent or fresh dirt at new trap sets) and corresponding avoidance (Harris 1983). The former hypothesis predicts no site-dependent vulnerability to snaring because no investigative behavior by the coyote is required, whereas the latter hypothesis predicts individuals should be more difficult to snare or trap when in their territories.

Finally, breeders may be most vulnerable in spring and summer when attentions are focused on caring for pups. Rearing pups requires considerable time and energy (Harrison and Gilbert 1985, Hatier 1995, Sacks 1996), which may entail trade-offs that increase breeders' vulnerability to human removal efforts (Cuthill and Houston 1997). In contrast, nonbreeders are probably most vulnerable when dispersing, which occurs primarily in fall or winter (Gese et al. 1989, Harrison 1992, Waser 1996). Such potential seasonal differences in vulnerability are important to establish because sheep depredation in northern California is concentrated in winter (Scrivner et al. 1985, Sacks 1996, Conner et al. 1998).

We investigated vulnerability of coyotes on a north-coastal California sheep research facility, where corrective coyote removal was practiced year-round for several decades in a manner typical of the region. Our objectives were (1) determine biases of removal methods in terms of age and sex, (2) investigate site-dependent vulnerability, and (3) test for effects of reproductive season on vulnerability of breeding coyotes.

STUDY AREA

The Hopland Research and Extension Center (HREC) is a 21.7-km^2 research facility of the University of California located in the mountains of the Coast Range in Mendocino County, California (39°00′N, 123°05′W). The HREC is characterized by a mosaic of oak woodland, annual grassland, mixed evergreen–deciduous forest, and chaparral vegetation types. Details of vegetation and climate have been described elsewhere (Murphy and Heady 1983). Since its inception in 1951, the HREC has been used extensively for research on sheep production and is grazed year-round by 900–1,500 ewes (Timm 1990). As is typical for northern California ranches, lambing occurs between December and May, with peak numbers of lambs pastured from January to March. Coyote depredation levels and removal practices on HREC also are typical for northern California (Coolahan 1990).

METHODS

Removal and Live-Capture

Nonselective removal was conducted routinely before April 1993 and during April 1994–October 1995 of this study (Apr 1993–Feb 1998), primarily by U.S. Department of Agriculture Wildlife Services (WS) specialists. Approximately 15–25 coyotes were removed annually from HREC and adjacent properties in the 10 years preceding the study. Removal was conducted throughout the year with a combination of stationary devices (traps, snares, M-44s) and shooting from the ground. Dense evergreen vegetation and hilly terrain precluded use of aircraft

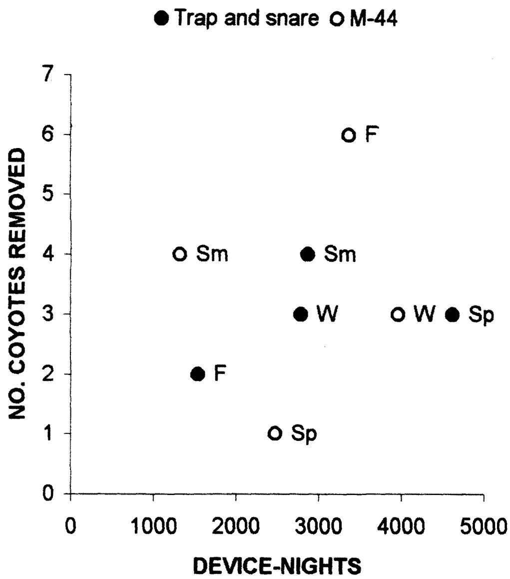

Fig. 1. Capture success versus removal effort associated with stationary devices during 4 seasons: winter (W; Jan–Mar), spring (Sp; Apr–Jun), summer (Sm; Jul–Sep), and fall (F; Oct–Dec), illustrating no relation in the observed range of effort expended, Hopland Research and Extension Center, Mendocino County, California, April 1994–October 1995.

for coyote removal at HREC and elsewhere in north-coastal California.

Capture success as a function of intensity of device use is likely a saturating curve such that beyond a certain amount of effort, increases have little effect on number of captures. Effort associated with removal devices during this study was always great enough (i.e., saturating) that seasonal differences in device intensity had little, if any, effect on numbers of coyotes captured (Fig. 1). Opportunistic shooting also occurred throughout the year, but calling-and-shooting (i.e., using sirens, calls, or recordings) was used primarily in spring and summer during the pup-rearing period.

Removal efforts on HREC were suspended from April 1993 to March 1994 to facilitate live-capture of coyotes for radiocollaring. Live-capture efforts continued alongside nonselective removal during April–December 1994, and selective removal (K. M. Blejwas, unpublished data) during November 1995–February 1998. Capture and handling procedures were presented elsewhere (Sacks et al. 1999). Personnel who conducted nonselective removals did not see radiotelemetry data. In contrast, during the selective removal period, coyotes were specifically targeted by shooting (if radiocollared) or with 1080 livestock protection collars (Connolly and Burns 1990, Timm et al. 1997) when they killed sheep.

The HREC was saturated with capture devices during live-capture and removal phases of the study period such that all age, sex, and breeding classes should have had effectively equal access to devices. During the live-capture period, we set 938 traps and 489 snares, totaling 45,059 device-nights. Thus, the total density due to live-capture efforts was 67 devices/km^2, with devices set for an average of 32 nights each. Removal effort by the WS specialist totaled 22,932 device-nights (Fig. 1). Devices for live-capture and removal were distributed similarly, primarily along roads, streambeds, firebreaks, and fences. Traps and snares used for removal caught a similar proportion of juvenile, yearling, and adult coyotes as did those used for live-capture (χ^2_2 = 0.21, P = 0.90). Additional devices were used on adjacent lands.

Age Determination

Age at capture was determined for all radiocollared coyotes from sections of premolars (n = 15), postmortem sections of lower canines (n = 33), or visual estimation of tooth wear (n = 15, including 5 pups; Gier 1968). Age also was determined postmortem for 30 uncollared coyotes via sectioned lower canines. Tooth sections were prepared and aged by Matson's Laboratory (Milltown, Montana, USA). Error associated with these aging techniques is probably very low for juveniles but likely increases with coyote age, especially for tooth wear (Linhart and Knowlton 1967). Therefore, age classes were designated as juvenile (<1 yr old), yearling (1–2 yr old), and adult (>2 yr old).

Age and Sex Bias

Determining differences in capture efficiency among demographic groups of coyotes is difficult because age structures and sex ratios of populations are usually unknown. Therefore, we used a radiocollared subsample to quantify relative vulnerability by age class and sex (Windberg and Knowlton 1990). Chi-square goodness-of-fit tests were used with subsequent capture (trap and snare) data to examine age- and sex-specific differences in overall probability of recapture. Trap and snare recaptures were combined to avoid small sample size. Under the null hypotheses, expected numbers of recaptures were calculated as the proportion of total recaptures corresponding to the proportion of all coyote-days composed by each demographic group. Coyote-days were the number of days, pooled across individuals, that coyotes were alive and radiocollared. For individuals monitored while in ≥2 age classes, days were apportioned to the appropriate age classes.

Age and sex biases calculated for traps and snares (above) provided a reference to which we could compare relative age and sex biases of other removal methods. For this comparison, we used removals (not live-captures) of radiocollared and uncollared coyotes taken during the nonselective removal period (Apr 1994–Oct 1995). M-44s were not used on HREC the previous year (Apr 1993–Mar 1994), so juveniles and yearlings were assumed to have had no prior exposure to these devices. These 2 age classes were combined for comparison with adults, which were assumed to have been exposed to M-44s previously. Due to small numbers of trap and snare removals, these samples were combined for comparisons with removals by M-44 and shooting. Additionally, comparison of age and sex biases of traps versus snares was possible using all (live and lethal) trap and snare captures from the entire study period (Apr 1993–Feb 1998).

Site-Dependent Vulnerability

To investigate site-dependent vulnerability of coyotes to traps and snares, we examined capture locations of radiocollared coyotes from the entire study period in relation to core areas. Cores were defined as the area where coyotes spent 65% of their time; these were estimated as 65% adaptive kernel (AK; Worton 1989) isopleths calculated via program CALHOME (Kie et al. 1996). The 65% cutoff was chosen because it was analogous to 1 standard deviation in 2-dimensional space (Shivik et al. 1996) and used for this purpose previously (Windberg and Knowlton 1990). We used Yates-corrected chi-square goodness-of-fit tests to determine whether ratios of captures inside versus outside of cores deviated from the 65:35 ratio expected based on coyote space use. Only resident coyotes with cores overlapping HREC were used in this analysis. This analysis assumed that capture effort either was not a factor (as suggested above; Fig. 1) or was equivalent, on average, between cores and external areas. The latter assumption seems reasonable because (1) devices were placed without regard to territorial boundaries, (2) the density of devices was high relative to areas of cores, and (3) sample sizes were high enough ($n \geq 27$) that chance differences in effort between cores and external areas for particular individuals should have had little effect on averages. Radiotelemetry methods were presented by Sacks et al. (1999).

Seasonal Vulnerability

We tested the hypothesis that vulnerability of breeding, relative to nonbreeding, coyotes was higher during pup rearing (Apr–Aug) than non-pup rearing (Sep–Mar; Sacks 1996). Breeding status was determined for radiocollared coyotes by external or postmortem examination, close association with pups or an adult of the other sex, and space use (Sacks et al. 1999). Fisher's exact tests (Zar 1984:390) were used to test for seasonal differences in relative vulnerability by (1) breeding status of radiocollared coyotes, and (2) age of uncollared coyotes (because breeding status was not known). Uncollared juveniles were compared to yearlings and adults, which were potential breeders (e.g., Windberg 1995). This test was conservative because the ratio of breeders to nonbreeders in the population probably increased somewhat from pup rearing to non-pup rearing (Knowlton 1972). Because we were interested in vulnerability of breeders to removal under routine conditions, only captures occurring before the selective removal period were examined. All live and lethal captures (i.e., in stationary devices and by shooting) were used in these analyses.

RESULTS

Between April 1993 and February 1998, 94 coyotes were captured 142 times, including 42 individuals that were removed during April 1994–October 1995 (Table 1). Ages at initial capture were distributed as follows: 50 juveniles, 20 yearlings, and 23 adults, including 48 males and 44 females (2 juv were not sexed due to scavenging, and 1 M was not aged). Nine selective removals of radiocollared coyotes (Nov 1995–Feb 1998) were not used in analyses.

Age and Sex Bias

Twenty-eight radiocollared coyotes were recaptured 37 times in traps or snares. Age affected probability of recapture (Fig. 2A; χ^2_2 = 12.57, P = 0.002), with biases toward progressively younger age classes. There was no differ-

Table 1. Numbers of coyotes removed by different conventional methods, Hopland Research and Extension Center, Mendocino County, California, April 1994–October 1995.

	Stationary devices				Shooting					
	Trap or snare		M-44		Opportunistic		With calling[a]		Denning	
	M	F	M	F	M	F	M	F	M	F
Juvenile	3	2	5	4	1	0	1	0	5[b]	1[b]
Yearling	0	3	2	2	0	1	0	0	0	0
Adult	1	4	0	0	2	0	3	0	0	0
Total	13		14[c]		4		4		7[b]	

[a] Predator call used near the den; 2 of the 3 adult males were radiocollared breeders.
[b] All 7 juveniles removed from dens were pups (<3 months old), 1 of which was not sexed.
[c] Sex of a juvenile killed by M-44 could not be determined due to scavenging of the carcass.

ence in recapture probability by sex (Fig. 2B; Yates $\chi^2_1 = 2.63$, $P = 0.105$).

Age and sex biases differed among removal methods (Table 1). M-44s were more biased toward young coyotes than were traps and snares (Fisher's exact test: $P = 0.016$), but there was no difference in sex ratio (Fisher's exact test: $P = 0.16$). Opportunistic shooting and calling-and-shooting were pooled because data were too few to compare each separately to traps and snares. Ages did not differ between shooting and traps and snares (Fisher's exact test: $P = 0.204$), but shooting took disproportionately more male coyotes (Fisher's exact test: $P = 0.016$). Of the radiocollared subset removed ($n = 12$), breeders composed 3 of 4 coyotes trapped or snared, 0 of 3 coyotes killed by M-44s, and 4 of 5 coyotes shot.

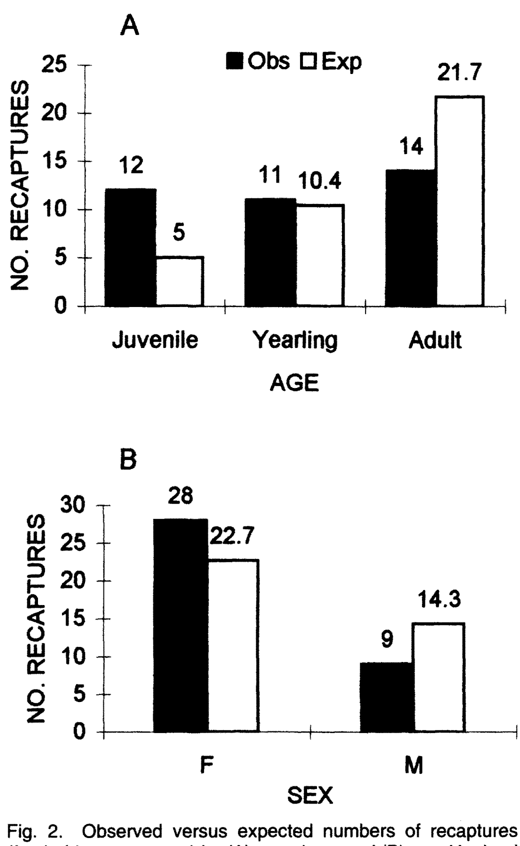

Fig. 2. Observed versus expected numbers of recaptures (foothold trap or snare) by (A) age class, and (B) sex, Hopland Research and Extension Center, Mendocino County, California, April 1993–February 1998.

Based on 109 captures of coyotes in traps and snares throughout the study period, there was no difference between these devices in relative numbers of coyote captures among 3 age classes (Fig. 3A; $\chi^2_2 = 1.39$, $P = 0.50$). Snares took proportionally more females than males relative to traps (Fig. 3B; Fisher's exact test: $P = 0.027$).

Site-Dependent Vulnerability

Coyotes were trapped and snared disproportionately more often when outside their core areas. Only 9 (33%) of 27 trap captures (Yates $\chi^2_1 = 10.55$, $P = 0.001$) and 13 (43%) of 30 snare captures (Yates $\chi^2_1 = 5.27$, $P = 0.02$) of resident coyotes occurred within their core areas compared to the 65% expected if coyotes were equally vulnerable inside and outside their cores. Ratios of captures inside versus outside of cores were not different between traps and snares (Fisher's exact test: $P = 0.16$). All 3 radiocollared resident (nonbreeding) coyotes killed by M-44s also were outside their cores at the time. In contrast, all 4 radiocollared resident (breeding) coyotes shot (during the nonselective removal period) were in their core areas at the time.

Seasonal Vulnerability

Breeding and breeding-age (yearling and adult) coyotes were captured less often during the non-pup-rearing period than the pup-rear-

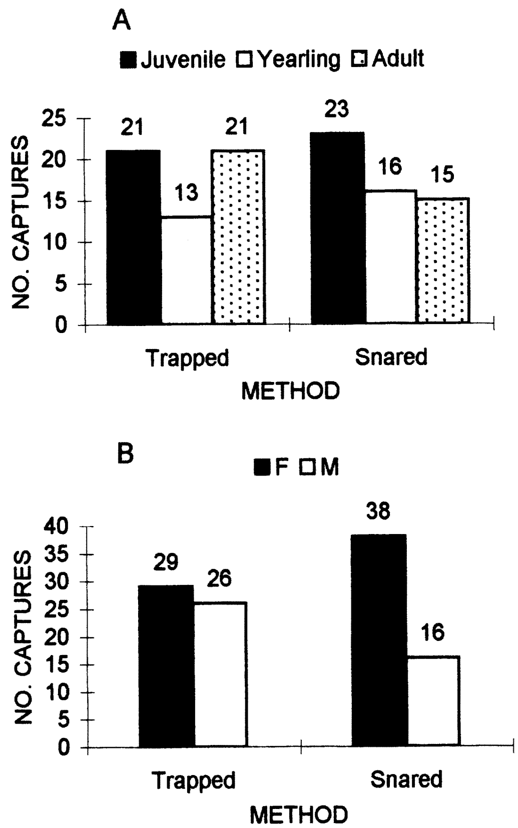

Fig. 3. Relative numbers of coyotes trapped and snared by (A) age class, and (B) sex, Hopland Research and Extension Center, Mendocino County, California, April 1993–February 1998.

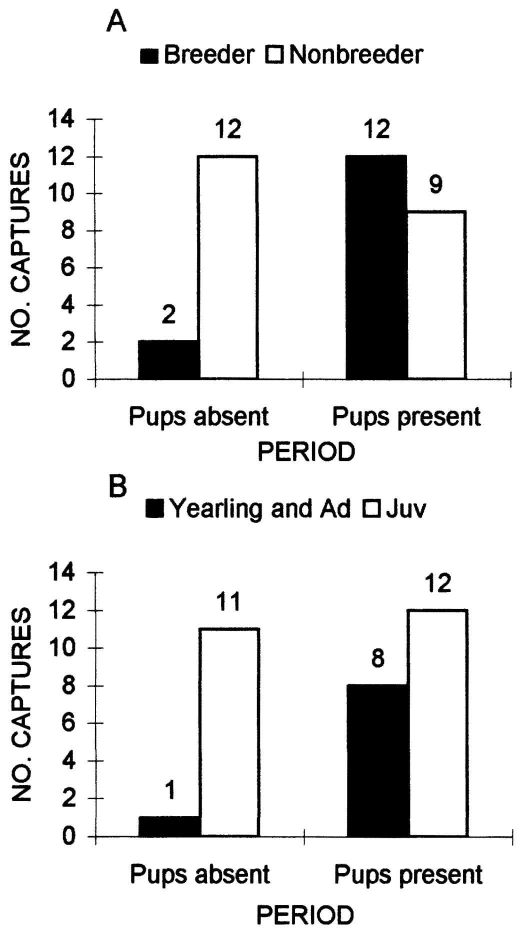

Fig. 4. Numbers of coyote captures (foothold trap, snare, M-44, shooting) in the non-pup rearing (Sep–Mar) versus pup-rearing (Apr–Aug) periods; (A) radiocollared breeders versus nonbreeders, and (B) uncollared adults and yearlings versus juveniles, Hopland Research and Extension Center, Mendocino County, California, April 1993–December 1995. Two captures of a radiocollared adult male were included with the uncollared sample because he was not monitored long enough for his breeding status to be determined.

ing period, whereas nonbreeding coyotes and juveniles were captured in similar numbers in the 2 seasons (Fig. 4). These differences occurred for radiocollared (Fig. 4A; Fisher's exact test: $P = 0.012$) and uncollared (Fig. 4B; Fisher's exact test: $P = 0.054$) coyotes.

DISCUSSION

The HREC coyote population was exposed to removal efforts for several decades, which probably made these coyotes generally difficult to capture. The most successful trapper spent an average of 140 trapnights/coyote captured, using either traps or snares. This effort was approximately 10 times that required to capture a coyote in a naive population in southern Texas (Windberg and Knowlton 1990), which had <2 times the coyote density of HREC (0.9 vs. 0.5 coyotes/km^2; Andelt 1985, Sacks 1996, respectively). Some variation in trap success also might be expected due to differences in coyote density, trapper experience, or scents used.

Social learning could partly explain how coyotes in an area exposed to regular removal efforts become trap-wise on a population-wide basis (Brand et al. 1995). Juvenile coyotes at HREC were naive toward traps by virtue of their age, yet were still difficult to trap, which suggested they had learned avoidance of devices or general "wariness" from their parents or other coyotes. Social learning was further supported by our frequent failure to capture mates of radiocollared individuals. Having breeders radiocollared would seem to make capture of uncollared mates relatively easy because pairs tend to be found together (Andelt 1985, Sacks et al. 1999). However, we set many traps where these individuals left sign, only to have them ignored, dug up, or defecated upon. If vulnerability has a hereditary basis, selection also could help explain how coyotes at HREC were difficult to capture (Andelt 1996). The overall difficulty in removing coyotes, combined with the localized nature of these efforts at HREC, makes significant population reduction unlikely with conventional methods, thus emphasizing the importance of removing particular breeding adults responsible for depredation.

Age and Sex Bias

Traps and snares were biased toward capture of younger individuals at HREC, based on differential rates of recapture, which confirms previous indirect evidence for traps (Roy and Dorrance 1985, Windberg et al. 1985, Windberg and Knowlton 1990). M-44s, which took only juveniles and yearlings at HREC, were even more biased toward younger coyotes than were traps or snares. Juvenile and yearling coyotes killed by M-44s in 1994–95 had not been exposed to these devices before, because they were not used the previous year. However, M-44s were used before March 1993, so adults alive in 1994–95 could have learned to avoid them.

Compared to traps and snares, which do not require coyotes to be aware of their presence, M-44s must be intentionally pulled by the coyote and thus may be easy for coyotes to learn to avoid. In southern Africa, Brand et al. (1995) found that black-backed jackals (*Canis mesomelas*) increasingly avoided coyote-getters (similar to M-44s) as exposure time increased, both within and among years, and most jackals taken were young. Several coyote pups at HREC were killed by M-44s near dens or rendezvous sites, where other coyotes were likely to have witnessed the events, thus potentially learning to associate M-44s with danger. Brand et al. (1995) made similar observations and speculated that individual and social learning were responsible for the observed decline in captures by coyote-getters.

Conversely, in a study where coyotes had not been exposed to lethal control previously, no difference was found in age bias between traps and M-44s (Windberg et al. 1985, Windberg and Knowlton 1990), which suggests M-44s may be more useful where coyotes have not had the opportunity to learn about them. Indeed, after the nonselective removal period in this study, an M-44 killed a 5-year-old resident radiocollared male coyote several kilometers from HREC, where M-44s had not been used in recent years. Thus, M-44s might be used more effectively on territorial breeders if used away from dens, near kill sites, a few at a time, and only when other methods have failed.

Sex biases also were indicated for some methods at HREC. Males were more likely than females to be shot, and females were more likely than males to be snared. Although analyses evaluated biases of 1 set of devices only in relation to another, 88% of coyotes shot were male and 70% of coyotes snared were female, compared to the 48:52 female-to-male ratio of 92 coyotes caught by all methods combined. Furthermore, sex ratios in coyote populations typically do not deviate greatly from 50:50 (Gese et al. 1989, Windberg 1995). Wagner (1997) also reported a male bias in calling-and-shooting. This result is consistent with the observation that breeding males defend against intruders in most instances (E. M. Gese, Utah State University, unpublished data). The bias toward females in snaring could have been due to a greater tendency to use holes rather than jump fences (e.g., because of their relatively small size). Such biases could confound attempts to determine sex ratios of coyote populations from removal records.

Site-Dependent Vulnerability

Coyotes at HREC were especially difficult to capture by stationary devices set in their core areas. A likely consequence of such site-dependent vulnerability is for breeders to be more difficult to remove. Breeders are territorial year-round, whereas nonbreeders often are either transient or intermittently resident within a breeding pair's territory (Messier and Barrette 1982, Andelt 1985, Hatier 1995, Sacks et al. 1999). Thus, nonbreeders collectively spend a greater proportion of time than breeders away from territories in unfamiliar areas where they are more vulnerable.

Both traps and snares were more likely to capture coyotes outside of their cores in this study. Site-dependent vulnerability had been documented previously for traps (Hibler 1977, Woodruff and Keller 1982, Windberg and Knowlton 1990) but not for snares. That snare success was site-dependent in this study suggests general wariness or neophobia in familiar areas was an important cause of spatial vulnerability, although heightened investigatory behavior in unfamiliar areas cannot be ruled out as an additional factor. Furthermore, device of initial capture apparently did not influence the device of subsequent captures (7 trapped and retrapped, 4 trapped and then snared, 9 snared and resnared, 8 trapped and then snared). These data suggest learned avoidance (Andelt et al. 1985) of traps and snares (but not necessarily M-44s) represents general wariness (e.g., of human disturbance) more than avoidance of specific cues (e.g., holes in fences).

In contrast to captures in stationary devices, radiocollared resident coyotes that were shot at HREC (during the nonselective removal period) were in their core areas at the time. This observation is consistent with another study that found no site-dependent vulnerability to shooting (Roy and Dorrance 1985), which indicates this method is more likely to remove territorial breeders than are stationary devices. Indeed, 1 study found that several known sheep-killing individuals were among a small group of coyotes opportunistically shot from aircraft (Connolly and O'Gara 1988). Whereas efficacy of opportunistic shooting may be relatively uninfluenced by a coyote's location, calling-and-shooting during the pup-rearing period is particularly effective on breeders in cores (i.e., near dens; Coolahan 1990).

Seasonal Vulnerability

Territorial, breeding coyotes at HREC were especially difficult to capture or remove during September through March, which included most of the lambing period when sheep depredation was most intense. Most breeders that were radiocollared during the nonselective removal period bred ≥2 years in the same territory before being removed by October 1995; this longevity was partly due to the suspension of removal efforts during April 1993–March 1994. These individuals, therefore, were especially familiar with their territories. Long-time residents may be more difficult to remove than newer residents, and length of residency may therefore affect seasonal vulnerability.

Established breeders are probably less vulnerable than nonbreeders because they are older and more experienced, and spend less time in unfamiliar areas. However, during pup rearing, added demands are placed on breeders, which can compromise their survival (Harrison and Gilbert 1985, Hatier 1995, Sacks 1996, Cuthill and Houston 1997). For example, breeders defend pups at a den and will approach a source of imitation howling or calls, which makes them vulnerable to shooting. Second, the demands of provisioning pups may force breeders to take greater risks. After whelping, a radiocollared pair at HREC became notably more active during the daytime and was frequently observed in daylight crossing open areas on their way to and from the den (Sacks 1996). Examination of bone marrow and weights of breeding female coyotes killed during or shortly after the pup-rearing period indicated they were in poor condition (Sacks 1996) and perhaps less cautious because of the need to obtain food. Third, areas of concentrated use by breeders during pup rearing were reduced to the vicinity of the den (Sacks 1996), making their location more predictable and easier to find (Coolahan 1990). This den-centered space use also effectively increased peripheral area relative to core area of territories during pup rearing, potentially increasing vulnerability of breeders to stationary devices in more parts of their territories.

MANAGEMENT IMPLICATIONS

Our results indicated several biases related to behavior of coyotes that caused conventional corrective removal methods to focus on the least important segment of the coyote population with respect to sheep depredation. Regular use of stationary devices, which generally account for most removals in north-coastal California (Coolahan 1990), was biased toward young nonbreeding coyotes, which were least likely to kill sheep (Sacks et al. 1999). Shooting, which accounted for a relatively small proportion of removals, was effective on coyotes within their territories and was thus more likely to take breeding individuals than were stationary devices. Shooting was particularly effective on breeding males when combined with calling during the pup-rearing period. However, most sheep depredation occurred during the non-pup-rearing period at HREC, during which time no method was very effective on breeders. Removal of nonoffending individuals was ineffective at stopping depredation (Sacks et al. 1999).

Thus, if removal success is measured by the number of offending coyotes removed instead of the total number of coyotes killed, more conservative use of devices might increase their effectiveness by reducing the potential for resident breeders to learn avoidance of devices. Such an approach should be most effective in situations where breeding pairs replacing those removed tend not to kill sheep immediately (e.g., if wild prey are abundant and sheep are an unfamiliar prey to most immigrants; Sacks et al. 1999). Additionally, use of 1080 livestock protection collars should effectively target individuals that kill sheep any time of the year, as was suggested by preliminary work on selective removal at HREC (Timm et al. 1997; K. M. Blejwas, unpublished data) and elsewhere (Connolly and Burns 1990).

The effectiveness of nonselective removal of coyotes likely varies throughout the western United States, depending on methods used and seasonal timing of lambing. For example, in some regions, aerial shooting of coyotes on grazing allotments is conducted in winter, before lambing and summer grazing (Gantz 1990). Wagner (1997) reported that such preventive removal can be effective at reducing depredation. Connolly and O'Gara (1988) reported that corrective use of aerial shooting was also effective in this situation. Where lambing occurs in summer, coincident with pup rearing, calling-and-shooting also may be a better corrective tool than in regions where lambing is conducted in winter, such as in north-coastal California.

Despite regional differences, many of our conclusions should be generally applicable. Evidence suggests that breeding coyotes cause most depredation of sheep (Till and Knowlton 1983, Sacks et al. 1999). Therefore, the success of control efforts probably depends on their success in removing these breeding individuals, regardless of overall removal efficiency. Age biases are likely to be present in any exploited population, and territoriality and site-dependent vulnerability to trapping have been demonstrated throughout the range of the coyote. Field experiments involving selective removal of radiocollared coyotes that kill sheep could help determine how seasonal timing of removal of breeders affects the likelihood of replacement by new breeding pairs before lambing. In accordance with changing attitudes toward predator removal, continued research also should focus on techniques that target behavior of territorial breeders.

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