DEMOGRAPHIC AND SPATIAL RESPONSES OF COYOTES TO CHANGES IN FOOD AND EXPLOITATION

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Abstract: Lethal control for reducing carnivore populations is a contentious issue throughout the world. While computer simulations have been developed modeling the effects of population reduction on coyote (*Canis latrans*) population parameters, testing these hypotheses with empirical data from the field is lacking. We documented the demographic and spatial responses of coyotes to changes in the levels of food resources and human exploitation on the Piñon Canyon Maneuver Site, southeastern Colorado. We captured, radio-collared, and tracked 92 (53 M: 39 F) coyotes from March 1983 to April 1989. Of these, 74 animals were residents from 32 packs, plus 12 transients; 6 animals were captured while making dispersal movements. We collected 14,147 telemetry locations of the radioed coyotes spanning 7 years of study. We compared coyote pack size and density, survival rates, reproduction (litter size, litter sex ratio, % yearlings reproducing), and home range size between years receiving exploitation (1987-88) versus years receiving no exploitation (1983-86) and post-removal (1989), as well as, comparisons of these parameters between removal and non-removal areas within years. Changes in estimates of pack size and coyote density, plus the number of animals removed, indicated the coyote population was reduced 44-61% and 51-75% in the removal area during 1987 and 1988, respectively. As expected, annual survival rates declined significantly for coyotes in the removal area compared to coyotes in the non-removal area. Removals brought about a drastic reduction in pack size and a corresponding decrease in density. However, both pack size and density rebounded to pre-removal levels within 8 months post-removal. Home range size did not change in response to changes in exploitation. Coyotes in the removal area appeared to maintain their normal (i.e., pre-removal) home ranges after coyotes were removed from neighboring territories. Following removals, the population shifted to a younger age structure (i.e., more yearlings). Litter size significantly increased in the removal area 2 years after the beginning of exploitation. However, changes in litter size were confounded by changes in the prey base. Litter size was significantly related to rabbit abundance, while rodent abundance was less of a factor influencing reproductive effort. Accounting for both changes in prey abundance and coyote density, litter size was significantly related to total prey abundance/coyote. With increasing prey and reduced coyote density, mean litter size doubled in the removal area compared to pre-removal levels; females in the non-removal area also increased litter size in response to increased rabbit abundance. Litter sex ratio favored males during years of no exploitation, changing to a preponderance of females during the 2 years of exploitation. Reproduction by yearlings increased from 0 % in years prior to exploitation, to 20% following 2 years of coyote removal.

Key words: *Canis latrans*, coyote, exploitation, litter, home range, prey, reproduction, survival

INTRODUCTION

Management of predator populations, particularly wild canids, has occurred for centuries. Wolves *(Canis lupus)*, coyotes (*C. latrans*), red foxes (*Vulpes vulpes*), dingos (*C. familiaris dingo*), and jackals (*C. mesomelas, C. aureus*) have been controlled by humans for the protection of game species and domestic livestock (Harris and Saunders 1993, Reynolds and Tapper 1996, Knowlton et al. 1999). Most coyote removal operations have focused on reducing coyote predation on domestic animals (Boggess et al. 1978, Andelt and Gipson 1979, Till and Knowlton 1983, Knowlton et al. 1999), or enhancing wild game populations (Beasom 1974, Stout 1982, Smith et al. 1986) by reducing coyote numbers in the area. Lethal control of coyotes remains a contentious and controversial issue among biologists and the general public (Stuby et al. 1979, Kellert 1985, Andelt 1996).

While success or failure of these control programs has generally been focused on the game species or domestic livestock effected, few studies have been conducted documenting the effect of lethal removal on the coyote population itself. Those studies that have been conducted compared parameters between or among separate areas under varying degrees of human exploitation (Knowlton 1972, Davison 1980, Knowlton et al. 1999), but which also varied in coyote density, habitat, prey species, prey density and distribution, and other biological factors important to coyotes (Knowlton et al. 1999). Computer simulations of demographic compensation in coyote populations also have been conducted (Connolly and Longhurst 1975, Connolly 1978, Sterling et al. 1983, Pitt et al. 2001) based upon the current understanding of coyote biology at the time. Many myths have been presented about the possible responses of coyotes to exploitation, but these ideas have remained conjectural and untested. A direct, experimental manipulation of a coyote population in the same study area allowing for comparison of parameters between an area under exploitation versus an area with no exploitation has not been conducted. Equally unknown is the length of time required for a coyote population to respond behaviorally or demographically to changes in the level of exploitation.

We were presented with an opportunity to directly manipulate a lightly exploited coyote population that had been studied for 4 years (Gese et al. 1988, 1989). By removing coyotes from one area of the study area, and not removing coyotes from the other part of the study area, we examined how the coyote population responded both spatially and demographically. Baseline data (1983-1986) showed that both areas were of similar habitat, prey abundance and composition, and coyote abundance. With this manipulation of the coyote population, we addressed the following questions: (i) What level of removal will show a corresponding decline in coyote survival, pack size, and density, and how long will this decline persist? (ii) When coyotes are removed from adjacent territories, do the other coyote packs expand their territories into these vacant areas? (iii) How quickly do coyotes respond to vacancies in adjacent areas and do transient animals move into these vacant areas? (iv) Does the coyote population respond with increased reproduction? (v) If the coyotes increase reproduction, how are these animals incorporated into the population? (vi) How quickly does the coyote population rebound from increased exploitation? (vii) How does prey abundance influence the ability of a coyote population to respond demographically?

STUDY AREA

The 1040-km^2 study area was located on the Piñon Canyon Maneuver Site (PCMS), Las Animas County, Colorado. The climate was classed as mid-latitude semiarid with a mean annual precipitation of 26-38 cm on different parts of the study area. Mean monthly temperatures ranged from -1 C in January to 23 C in July. Elevations ranged from 1,310 to 1,740 m. The PCMS consisted of open plains, river canyons, and limestone breaks (Gese et al. 1988). The two main vegetation types were shortgrass prairie and pinyon pine (*Pinus edulis*) juniper (*Juniperus monosperma*) woodland communities (Costello 1954, Kendeigh 1961, U.S. Department of the Army 1980, Shaw et al. 1989). The PCMS had large-scale cattle ranching prior to purchase by the U.S. Army, thus the coyote population on the PCMS was subjected to human exploitation prior to 1982. In 1982 the U.S. Army acquired the PCMS for mechanized military training. Cattle ranching and coyote exploitation continued on ranches surrounding the study area.

METHODS

From 1983 to 1986 the resident coyote population on the PCMS was not exposed to human exploitation and constituted 4 years of baseline demographics prior to manipulation (Gese et al. 1989). Beginning in 1987 and continuing into 1988, the PCMS was divided into 2 areas of similar habitat and topography (mainly open prairie): coyotes were removed through aerial gunning and trapping on a 340-km^2 area, and were not removed on a 380-km^2 area. Coyotes were removed from the removal area by aerial gunning and trapping in January and May 1987, and March and April 1988 (Knowlton 1972). No coyotes were removed from the adjacent, non-removal area. All coyotes removed were aged by tooth cementum analysis (Linhart and Knowlton 1967) of a lower canine, sexed, weighed, and female reproductive tracts were examined for placental scars or embryos.

Throughout the entire 7-year study period, coyotes were captured with padded leg-hold traps, a hand-held net gun fired from a helicopter (Barrett et al. 1982), manual capture following aerial pursuit (Gese et al. 1987), or manual capture on the ground (Gese and Andersen 1993) in both the removal and non-removal areas. Each captured coyote was sexed, aged by tooth wear (Gier 1968), weighed, ear-tagged, and fitted with a radio collar (Advanced Telemetry Systems, Isanti, MN). Collared coyotes were radio-tracked throughout the study (Gese et al. 1988, 1989) with 3 biological seasons defined (modified from Smith et al. 1981): breeding/gestation (16 Dec – 15 Apr), pup rearing (16 Apr – 15 Aug), and dispersal (16 Aug – 15 Dec). Coyotes were located 3-4 times/week from a vehicle using a portable receiver and an antenna, or via aerial telemetry if the animal was not successfully located from the ground (Mech 1983). We used ≥ 2 compass bearings with an intersecting angle $>20^o$ and $<160^o$ to plot an animal's location. Each location was plotted to the nearest 100-m grid intersection on 1:24,000 U.S. Geological Survey topographic maps using the Universal Transverse Mercator grid system. Triangulation error was determined by reference transmitters to be $\pm 4^o$ (Gese et al. 1988). We used a minimum of >35 night locations to determine seasonal home-range size (Gese et al. 1990). Adequate sample size for each coyote during each season was determined from area-observation curves (Odum and Kuenzler 1955). We measured home-range size with the 95% adaptive kernel estimator (Worton 1989, Shivik and Gese 2000) using the software program CALHOME (Kie et al. 1996). Coyote pack size was documented by visual observations

of radioed coyotes and pack associates sharing a common territory (Bowen 1982, Gese et al. 1989). Density was measured as mean pack size divided by mean home range size for each biological season (Mech 1973, 1977, Van Ballenberghe et al. 1975, Gese et al. 1989). We measured the amount of reduction in the coyote population by documenting changes in pack size and density. Coyote population density estimates were made from radio-collared coyotes (Gese et al. 1989) as previously described. Subtracting the number of coyotes killed provided an estimate of the percent reduction in coyote numbers immediately following the removal.

We calculated annual survival rates using the computer program MICROMORT (Heisey and Fuller 1985). Survival rates were a mean of 2 rates: one rate included all animals of known fate, and the second rate included animals of known and unknown fate (loss of radio contact). This second rate was a mean of 2 rates: the first rate assumed all missing animals were dead, and the second assumed they were alive (Gese et al. 1989).

We determined reproductive output from active dens, fetuses, and placental scars. Reproductive output during 1983-86 (Gese et al. 1989) was used as a baseline to compare changes in litter size and sex ratio during years before and after exploitation. Mean placental scar counts (3.4 scars/females, $n = 10$) were not different from mean litter size counts (3.2 pups/litter, $n = 16$) during baseline years (Gese et al. 1989), thus these 2 estimates were combined to determine reproductive output. Yearling reproduction was determined from coyotes removed during the aerial gunning in 1987-88 and was compared to baseline data gathered in 1983-86 (Gese et al. 1989).

Indices of relative prey abundance were determined by 2 methods. Relative abundance of lagomorphs was estimated using spotlight surveys (Chapman and Willner 1986, Schauster et al. 2002) conducted over 4 consecutive nights during the summer months. We drove a truck along established routes at 10-15 km/hr. Two observers used spotlights of 250,000 candlepower to scan both sides of the route. We recorded the number of black-tailed jackrabbits (*Lepus californicus*) and desert cottontail rabbits (*Sylvilagus auduboni*). The average number of observed rabbits/km was used as an index of abundance.

To estimate the relative abundance of small mammals, annual scent-post surveys (Linhart and Knowlton 1975, Roughton and Sweeny 1982, Schauster et al. 2002) were used over 4 consecutive nights each summer. Four scent-station lines of 10 stations each were placed >3 km apart in both the removal and non-removal areas. Each station, placed 0.5 km apart, consisted of a 1-m diameter circle of sifted dirt with a synthetic fermented egg extract tablet (Roughton and Sweeny 1982, Bullard et al. 1983) at the center. Tracks were recorded as presence/absence and cleared each morning. The visitation rate of rodents to the scent-posts were used as a passive index of abundance.

Survival rates were determined using the individual coyote as the sample unit. For home-range size, pack size, and coyote density estimates and analyses, the sample unit was the coyote pack. Litter size information was based upon the breeding female and sex ratio was based upon the litter as the sample unit. Regression analyses used the mean of the parameter for each area each year. All statistical tests were performed using the software program SYSTAT (Wilkinson et al. 1992).

RESULTS

We captured, radio-collared, and tracked 92 (53 M: 39 F) coyotes from March 1983 to April 1989. Of these, 74 animals

were residents from 32 packs, plus 12 transients; 6 animals were captured while making dispersal movements. We collected 14,147 telemetry locations of the radioed coyotes spanning 7 years of study.

A total of 25 (12 M, 13 F) and 29 (14 M, 15F) coyotes were shot or trapped in the removal area during the winter and spring of 1987 and 1988, respectively. Aerial gunning and trapping accounted for 89% and 11% of the coyotes removed, respectively. Both the removal (0.167 coyotes/km^2) and non-removal (0.182 coyotes/km^2) areas had similar coyote densities prior to exploitation. Extrapolation of resident home-range size and group size in different habitats, and the number of

transients resulted in an estimate of 57 coyotes occupying the removal area. Thus, the 25 coyotes removed in January-April 1987 resulted in a 44% reduction in the coyote population in the removal area. In 1988 we estimated a reduction of 51% (i.e., removed 29 coyotes) of the coyote population in the removal area.

The age structure of the resident coyote population changed following removals. Prior to removals, 34% of the age structure consisted of yearlings with 16% of the animals over 5 years of age (Figure 1). Following population reduction, within the removal area the yearling cohort increased to 60% of the population with only 6% of the animals exceeding 5 years of age.
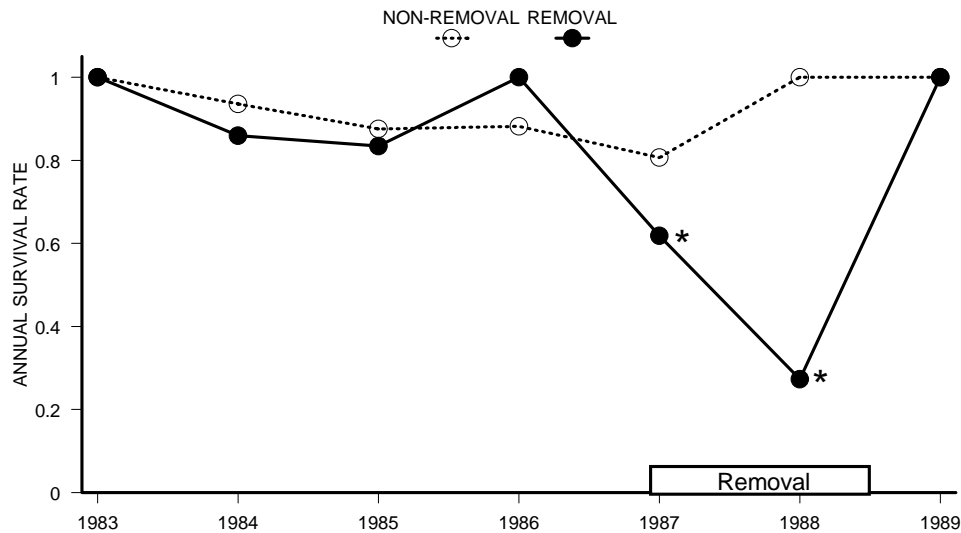

Figure 1. Age structure of resident coyotes before and after 2 years of population reductions, Pinon Canyon Maneuver Site, Colorado, 1983-1989.

Annual Survival Rates

Prior to any population reduction, annual survival of coyotes between the removal and non-removal areas were similar (Figure 2). For all years prior to removals

(1983-1986), mean annual survival was 0.922 and 0.925 in the removal and non-removal areas, respectively (all z-tests for

annual rates had $P > 0.20$). As could be expected, annual survival of coyotes in the removal area declined significantly during the 2 years of removal (1987-1988) compared to survival in the non-removal area (Figure 2; all z-tests had $P < 0.05$). Following cessation of population reduction, coyotes in both areas had annual survival rates of 1.0 in 1989.
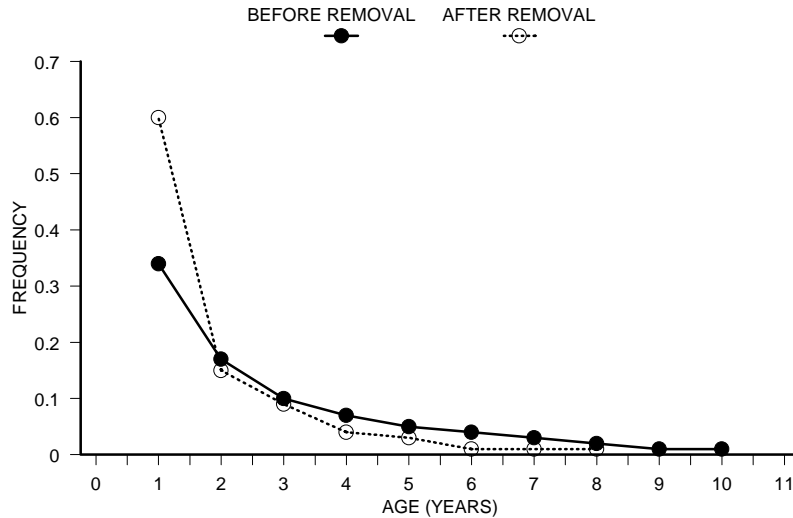
Figure 2. Annual survival rates of resident coyotes in removal and non-removal areas before, during, and after population reduction, Pinon Canyon Maneuver Site, Colorado, 1983-1989. Asterisk denotes significant difference in annual survival rates between removal and non-removal areas for that year (z-test, $P < 0.05$).

Home Range Size

A total of 14,147 telemetry locations were collected on the radioed coyotes across the study area from March 1983 to April 1989. Seasonal home-range size was not correlated with relocation sample size ($r = 0.08$, $F = 1.318$, $df = 1$, 199, $P = 0.252$). A multi-way ANOVA of the influence of area, season, and year on home-range size had an R^2 of 0.102 and showed that home-range size of the coyotes in the non-removal and removal areas did not differ significantly among years and seasons (Table 1, Figure 3A). While the area effect was close to significance ($P = 0.086$), this value was mainly driven by the increase in home-range size in the non-removal area in the winter of 1987. Independent Tukey's tests found no significant differences between the two areas on a seasonal basis (all *P*-values >0.20).

We observed movement of one radioed coyote from the non-removal area into a vacant territory in the removal area. In 1987 a 3-year old, female coyote in the non-removal area was classified as a transient due to her large home range (80.4 km²), solitary behavior, and lack of affinity for one resident area (Gese et al. 1988). In February 1988, she moved 22 km west into the removal area, established a resident home range (11.4 km²) in an area where a group of 4 coyotes had been removed in 1987, paired with another coyote, and was pregnant with 4 pups when removed in April 1988. None of the resident radioed coyotes in the non-removal area moved into the removal area, nor did any resident pack expand their territory in the removal area even when entire packs were removed from adjacent territories.

Table 1. Multi-way analysis of variance with all interaction terms examining the influence of area, season, and year on home-range size, pack size, and density of coyotes, Pinon Canyon Maneuver Site, Colorado, 1983-1989.

Source	df	Home range size		Pack size		Density	
		F	P	F	P	F	P
Area (A)	1	3.658	0.086	17.287	<0.001	9.289	0.003
Season (S)	2	0.758	0.470	101.082	<0.001	34.381	<0.001
Year (Y)	4	1.244	0.293	15.685	<0.001	9.116	<0.001
A x Y	4	1.568	0.184	7.964	<0.001	1.661	0.160
A x S	2	0.416	0.660	16.543	<0.001	5.012	0.007
S x Y	8	0.438	0.897	5.968	<0.001	2.685	0.008
A x S x Y	8	0.306	0.963	7.379	<0.001	1.948	0.055
Error	211						

Area: removal, non-removal
Season: breeding, pup rearing, dispersal
Year: 1984, 1985, 1986, 1987, 1988

Pack Size and Density

Mean pack size of resident coyotes changed in response to seasons, years, and areas (Figure 3B). A multi-way ANOVA examining the influence of area, season, and year on mean pack size showed that 72% of the variance in mean pack size was explained by the 3 variables ($R^2 = 0.720$, Table 1). During the years prior to population reduction (1983-1986), pack sizes in the removal and non-removal areas were not significantly different (all Tukey's tests had P-values >0.10). Following the removals, mean pack size in the removal area significantly decreased during the breeding and pup-rearing seasons of 1987 and 1988 (Fig. 3B; Tukey's tests had $P < 0.05$). Immediately following removals, mean pack size in the removal area declined 61% and 73% in 1987 and 1988, respectively. By comparison, mean pack size in the non-removal area showed no decline during the same time period. Within 8 months, mean pack size in the removal area had returned to pre-removal levels and was similar to pack size in the non-removal area.

With the decline in mean pack size of coyotes in the removal area during population reduction, there was a corresponding decrease in resident coyote density following removals (Figure 3C). A multi-way ANOVA examining the influence of area, season, and year on resident coyote density found that 49% of the variation in density was explained by the 3 variables ($R^2 = 0.491$, Table 1). Coyote density was similar between the 2 areas prior to removal, with a decrease in density following the removals in 1987 and 1988 (Fig. 3C). Following the removal sessions, resident coyote density declined 60% and 75% in 1987 and 1988, respectively. By the winter of 1987, coyote density was similar in both areas 8 months after removal as pack sizes rebounded (Figure 3B). By dispersal season in 1988, coyote density in the removal area had not yet reached pre-removal levels (Figure 3C) even though mean pack size was the same (Figure 3B); this difference was due mainly to changes in home-range size (Figure 3A).
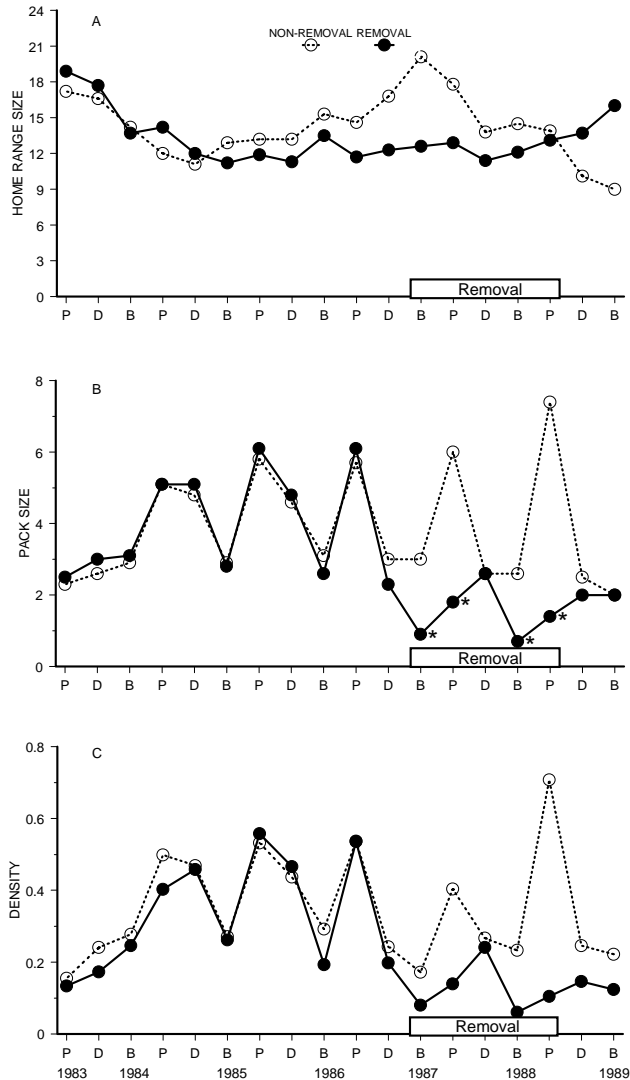
Figure 3. Changes in (A) home-range size, (B) pack size, and (C) density, of resident coyotes in removal and non-removal areas before, during, and after population reduction, Pinon Canyon Maneuver Site, Colorado, 1983-1989. Asterisk denotes significant differences (Tukey's test, $P < 0.05$).

Reproduction

Mean litter size of breeding female coyotes in the removal ($\overline{x} = 3.3$ pups/litter, $n = 17$ litters) and non-removal ($\overline{x} = 3.0$, $n = 8$ litters) areas did not differ prior to exploitation ($t = 0.63$, $P = 0.53$). After the first year of removals, mean litter size remained unchanged between the removal ($\overline{x} = 3.7$) and non-removal ($\overline{x} = 3.0$) areas.

However, mean litter size of breeding females significantly increased in the removal area in 1988 ($\overline{x} = 6.3$, $n = 7$), 2 years after the removal program began (Figure 4A; $F = 6.72$, $df = 2, 29$, $P < 0.005$). Among individual females, one 4-year-old female that had 3 pups in 1987, produced 9 pups in 1988. Another 5-year-old female that had 3 pups in 1986, whelped 8 pups in 1988. Mean litter size in the non-removal area increased in 1988 as well ($\overline{x} = 4.6$, $n = 6$), but was not significantly different than pre-removal litter size ($F = 2.48$, $df = 2, 13$, $P > 0.10$). When we examined the influence of coyote population reduction, we found that mean litter size was correlated to the density of coyotes entering the breeding season ($r = 0.717$, $F = 9.496$, $df = 1,9$, $P = 0.013$). As the coyote density coming into the breeding season declined, mean litter size increased.

Sex ratio of the litters changed in the removal area following coyote removal. Litter sex ratio in the removal area favored males (67% male, $n = 56$ pups) during years of no exploitation, changing to a ratio favoring females (59% female, $n = 44$ pups) following 2 years of exploitation ($x^2 = 6.303$, $df = 1$, $P = 0.012$). Litter sex ratio in the non-removal area remained near 50:50 during years of no exploitation (50% male, $n = 24$ pups) and 2 years after exploitation (54% male, $n = 28$ pups) ($x^2 = 0.066$, $df = 1$, $P = 0.797$). The percent of yearling female coyotes reproducing increased from 0% ($n = 11$) during years of no exploitation (Gese et al. 1989) to 20% ($n = 10$) during the 2 years following coyote removal, but was not a significant difference ($x^2 = 2.43$, $df = 1$, $P = 0.119$).
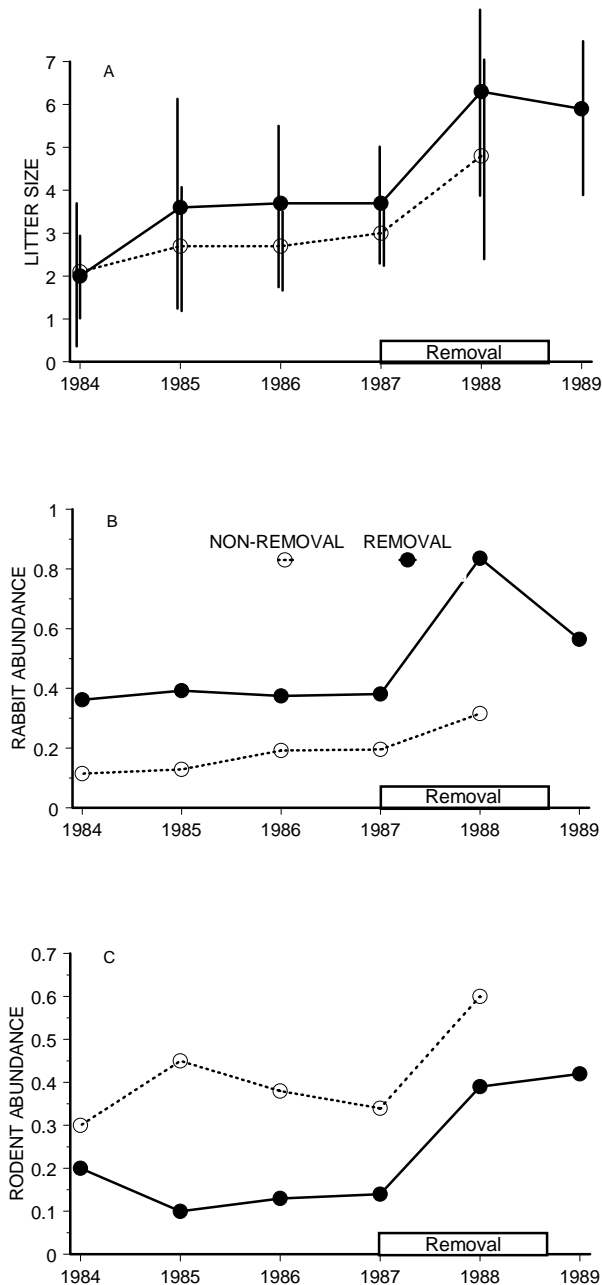
Figure 4. Changes in (A) coyote litter size (± SD), (B) rabbit abundance, and (C) rodent abundance, in the removal and non-removal areas before, during, and after coyote population reduction, Pinon Canyon Maneuver Site, Colorado, 1983-1989.

Changes in the Prey Base and Effects on Reproduction

Surveys of lagomorphs and small mammals indicated that the relative abundance of these food resources changed over the course of the study. Both lagomorphs and rodent abundance were relatively unchanged during the first 3 years of the study in both the removal and non-removal areas (Figure 4B and 4C). After the first removal session, prey abundance remained unchanged. However, 2 years after the removals began, prey abundance increased in both areas. It is unlikely the increases in prey were due to coyote population reduction, but that these cyclic prey populations were entering the initial part of a population increase and were coincidental to the removal of coyotes. However, whether there was top-down or bottom-up regulation of prey by coyotes was unknown, but the increase in prey in the non-removal area indicated the removal of coyotes was not the mechanism for the increase.

We previously found that as coyote density declined due to population reduction, mean litter size increased in response. However, the increase in prey abundance confounded the effects of population reduction and the observed increase in litter size. Examining the influence of prey abundance on coyote litter size showed that mean litter size was significantly related to rabbit abundance the previous summer ($r = 0.840$, $F = 21.528$, $df = 1,9$, $P = 0.001$). As rabbit abundance increased, mean litter size the following spring in both areas increased accordingly (Figure 5A). Mean litter size and rodent abundance the previous summer were not significantly correlated (Figure 5B; $r = 0.338$, $F = 1.160$, $df = 1,9$, $P = 0.309$). To examine the combined effects of increased food resources and reduced coyote density on mean litter size, we combined the rabbit and rodent indices for a total prey index, then divided that index by the estimate of coyote density entering the breeding season to acquire an estimate of total prey/coyote. Regression analysis showed a significant

correlation between total prey/coyote and mean litter size across all years and areas (r = 0.869, F = 27.858, df = 1,9, P = 0.001). As more prey per coyote increased, mean litter size increased in response (Figure 5C).
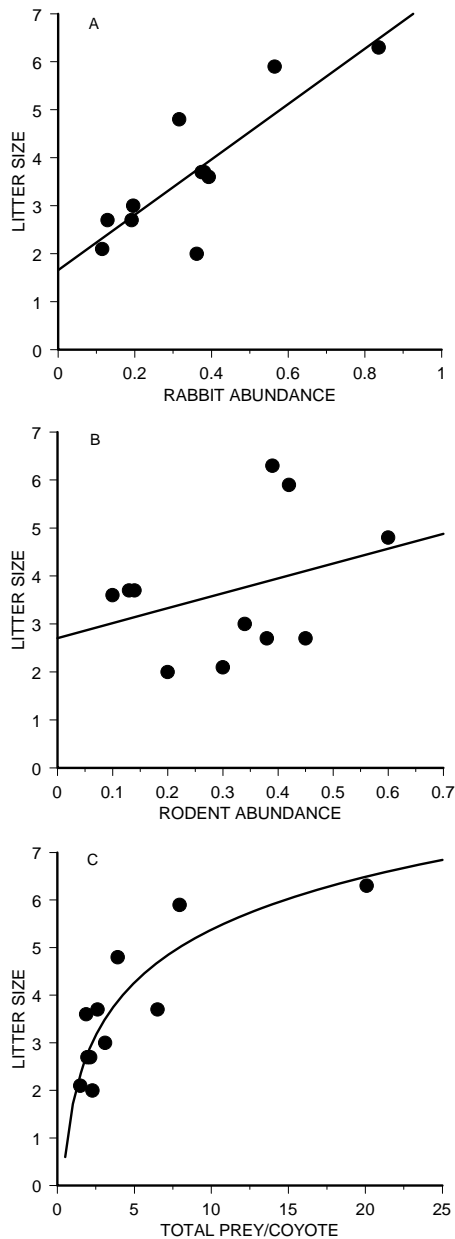

Figure 5. Relationships between coyote litter size and indices of (A) rabbit abundance, (B) rodent abundance, and (C) total prey abundance/coyote, Pinon Canyon Maneuver Site, Colorado, 1983-1989.

Stepwise regression showed that total prey

abundance and coyote density prior to the breeding season were the most influential factors on mean litter size (r = 0.924, F = 23.444, df = 2,8, P <0.001).

DISCUSSION

The spatial response of the resident coyotes in the removal area following population reduction was negligible. With entire territories vacant in adjacent areas, the resident coyotes remained within their own exclusive territories. The coyotes that immigrated into the removal area were probably transients and dispersing animals from the non-removal area and areas surrounding the PCMS as these areas were generally exposed to low levels of exploitation (Gese et al. 1989). The observation of a radio-collared transient moving west into the removal area from the non-removal area supports this hypothesis. In addition, offspring from the packs in the removal area likely colonized vacant territories during the dispersal season as evidenced by the younger age structure in the removal area 2 years after removals began.

As predicted, following population reduction, coyote pack size and density both declined substantially. Removals were effective in reducing pack size and consequently resident population density by as much as 60-70%. With this reduction in density, vacancies apparently were found and filled quickly by transient and dispersing coyotes so that within 8 months the density within the removal area had recovered. This level of population reduction appeared to be sustainable for 2 years. Removals exceeding this level or lasting longer would likely cause a more prolonged decline in overall coyote density. Pitt et al. (2001) modeled that population recovery through reproductive compensation may take 2-3 years if removal exceeded 60%.

Changes in litter size and sex ratio, and yearling reproduction has been reported in studies of different areas under various degrees of exploitation (Knowlton 1972, Davison 1980, Knowlton et al. 1999). Knowlton (1972) reported litter sizes averaged 4.3 pups in south Texas in areas under light exploitation. In areas of heavy exploitation, litter size averaged 6.9 pups. Davison (1980) concluded that recruitment was directly related to hunting mortality rates. Connolly and Longhurst (1975), through simulation modeling, suggested an average litter size of 4.5 in an uncontrolled population, increasing to 9 pups/litter as the coyote population was reduced to half the pre-control density. Direct manipulation of a previously unexploited resident coyote population, however, has not been reported. We found that litter size in the removal area nearly doubled when we reduced the population to over half the pre-removal density, similar to the model proposed by Connolly and Longhurst (1975). Similarily, a reduction of a red fox (*Vulpes vulpes*) population in South Dakota resulted in a 63% increase in litter size during years of fox removal compared to years of no removal (Trautman et al. 1974).

However, we caution that the increase in prey abundance also contributed to the change in litter size observed and that the combination of population reduction and food brought about the increase in mean litter size. Coyote litter size is usually related to food abundance. Todd and Keith (1983) reported that coyote pregnancy rate and litter size declined when snowshoe hare (*Lepus americanus*) populations declined in Alberta. Gier (1968) noted that 65% of the yearlings conceived during years of rodent abundance, whereas no yearlings bred during years of rodent scarcity. Clark (1972) reported that more yearlings bred and litter sizes were larger during years of jackrabbit (*L. californicus*) abundance. We

suggest that the lower density of coyotes in the removal area and the increased prey availability to the surviving female coyotes, brought about an increase in their reproductive capabilities (Knowlton 1972, Henderson 1972, Connolly and Longhurst 1975). The mechanism by which this occurs is unknown, but may be a consequence of the breeding females acquiring more food due to more prey and reduced competition, entering estrus in better physiological condition, shedding more ova entering estrus, and producing more offspring.

While it has been suggested that human exploitation brings about more coyotes due to increased litter size, we point out that the observed increase in litter size during this study did not increase overall coyote density, but simply replaced the removed cohort. Increased reproduction must be considered in the context of a reduced population, and the upper threshold of coyote density is still dictated by food abundance as mediated by social tolerance (Knowlton et al. 1999). In addition, some coyote populations with abundant food resources and no human exploitation are already at the maximum reproductive output (e.g., Gese et al. 1996) and the breeding females would not be physically capable of increasing litter size.

Litter sex ratio in the removal area changed from a preponderance of males during years of no exploitation to a ratio favoring females during the 2 years of exploitation. Changes in litter sex ratios have been inferred from observed adult sex ratios. Areas under light exploitation favored males (Gier 1968, Hawthorne 1971, Mathwig 1973), while areas with heavy exploitation favored females (Wetmore et al. 1970, Knowlton 1972).

Yearling pregnancy rate increased from 0% to 20% in 2 years after the initial removal began. Gier (1968) and Knowlton (1972) believed that yearling pregnancy

rates increased with increased levels of exploitation. Connolly and Longhurst (1975) suggested that 10% of yearlings breed in areas of no exploitation, increasing to 70% in areas where the population is reduced to half the pre-control density. Yearling reproduction on our study area did not increase to the magnitude proposed by Connolly and Longhurst (1975), but we measured the reproductive rate only 2 years after exploitation started. A higher yearling pregnancy rate could occur with continued exploitation.

Biologists generally agree that coyote control can induce increased birth and natural survival rates in a coyote population (Knowlton et al. 1999). However, the magnitude at which these rates change at various control intensities has not been well documented (Connolly and Longhurst 1975). We concluded that with an estimated 60-70% reduction in the coyote population on our study area, resident coyotes did not increase their home ranges in response to vacant space adjacent to their home range. Immigration of coyotes from the surrounding areas into the removal area probably resulted. The coyote population in the removal area responded to exploitation in 2 years through increased litter size, a litter sex ratio favoring females, and a slight increase in yearling reproduction. We emphasize that results from this study may not be universally applicable to other coyote populations. Prior to population reduction, the coyote population in this study was already at very low density, had small pack sizes, and whelped small litters due to low food abundance. Populations at high density and reproductive output due to high food availability would not be capable of similar demographic responses as they would already be at or near upper limits. Also, our control lasted for 2 years only. Prolonged control actions could have more lasting impacts on coyote population size,

persistence, and recovery.

ACKNOWLEDGMENTS

LITERATURE CITED

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