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EFFECT OF SHORT-TERM COYOTE REMOVAL ON POPULATIONS OF COYOTE HELMINTHS

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ABSTRACT: Coyote (*Canis latrans*) removal programs often are initiated despite the potential population regulatory mechanism of parasitism with increased coyote density. We investigated the effect of intensive, short-term coyote removal on population levels of helminths in juvenile and adult coyotes from western Texas. Coyotes were killed by aerial gunning every 3 mo for 2 yr on two 5,000 ha areas, which reduced the overall coyote density of these areas by about 50%. Two other 5,000 ha areas were used as comparison sites where a limited number of coyotes were killed each season. Densities on comparison sites remained stable throughout the study at a mean ± 1 SE of 0.14 ± 0.01 coyotes/km^2. Twelve helminth species consisting of seven nematodes (*Ancylostoma caninum, Physaloptera rara, Toxascaris leonina, Dirofilaria immitis, Spirocerca lupi, Oslerus osleri,* and *Capillaria aerophila*), three cestodes (*Taenia pisiformis, Taenia multiceps,* and *Mesocestoides* sp.), one acanthocephalan (*Oncicola canis*), and one trematode (*Alaria marcianae*) were found in 252 coyotes. Of these, *A. caninum, P. rara, T. multiceps, T. pisiformis, T. leonina,* and *S. lupi* were common species. Rank-transformed values for the mean abundances of *A. caninum* and *T. multiceps* and *A. caninum, T. multiceps,* and *S. lupi* were reduced in juvenile and adult coyotes, respectively, from the removal sites compared to respective helminth abundances in similar age class coyotes from comparison sites. Because *A. caninum* has been suggested as a population regulator of coyotes, a coyote removal program that results in a reduced density of coyotes and at the same time causes a reduced abundance of *A. caninum,* may in fact negate the regulatory effect that *A. caninum* has on coyote populations.

Key words: *Canis latrans,* coyote, density-dependence, helminths, population reduction.

INTRODUCTION

Coyotes (*Canis latrans*) are considered a nuisance species throughout most of their range because they are cited as predators of livestock (National Agricultural Statistics Service, 1995; Conner et al., 1998), mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) fawns (Whittaker and Lindzey, 1999), pronghorn (*Antilocapra americana*; Smith et. al., 1986), northern bobwhite (*Colinus virginianus*) eggs (Lehmann, 1984), and wild turkeys (*Meleagris gallopavo*; Ransom et al., 1987). Coyote control programs frequently are initiated because of the coyote's indiscriminate predation on a variety of species (Stout, 1982; Smith et al., 1986; Wagner and Conover, 1999). Methods of lethal coyote control have included toxic baits (Linhart and Robinson, 1972), calling and shooting (Beasom, 1974), aerial hunting (Andelt, 1987), denning (Till and Knowlton, 1983), foothold traps (Linhart et al., 1986), M-44 devices (Connolly, 1988), snares (Guthery and Beasom, 1978), and livestock protection collars (Savarie and Sterner, 1979). However, humans typically fail to consider the compensatory relationship between coyote abundance and their reproductive capabilities and survival of juveniles (Windberg, 1995). Knowlton (1972) found that litter size varied inversely with coyote density in Texas.

Density-dependent processes such as predation, parasitism, and competition can regulate a population. For coyotes, neonatal mortality caused by parasites has been suggested as a regulatory factor (Pence et al., 1988). Radomski (1989) determined that a threshold level of >300 hookworm (*Ancylostoma caninum*) larvae/kg was needed to cause mortality in coyote neonates, which corresponded to the number of hookworms reported from naturally-infected free-ranging juvenile coyotes from southern Texas.

In theory, the abundance of a pest species can be reduced if the most vulnerable life stage of the species is identified and attacked (Caughley and Sinclair, 1994). However, if parasites regulate coyote populations, then programs that reduce the abundance of coyotes could be counterproductive. When coyote control efforts are conducted, the abundance of direct life cycle parasites of coyotes (e.g., hookworm) should be reduced, which in turn, could increase the survival of coyote neonates. However, the relationship between coyote density and the prevalence and abundance of coyote helminths has not been investigated. Therefore, our objective was to determine the diversity and abundance of coyote helminths in areas with and without intensive coyote control. This study was part of a larger project that investigated the effects of coyote removal on the faunal community of a short-grass prairie (Henke and Bryant, 1999).

MATERIALS AND METHODS

The study was conducted on University of Texas lands in Andrews and Martin counties (Texas, USA; 32°5′ to 32°35′N, 102°10′ to 102°50′W) between April 1990 and January 1992. Andrews and Martin counties are characterized as a semiarid, short-grass prairie with a cool temperate, dry-steppe climate and mild winters. Average annual precipitation is 35 cm, and typical temperatures range from −5 to 38 C (Connor et al., 1974). The chief industries of the region are oil and cattle production. For a more complete description of the study area, see Henke and Bryant (1999).

Four sites, approximately 5,000 ha each, were chosen for study. Two sites in northeastern Andrews and western Martin counties served as the treatment sites where coyotes were removed, and the other two sites, in southern and western Andrews County, respectively, served as comparison sites where only a limited number of coyotes were removed. To avoid ambiguity, the sites on which coyotes were controlled were referred to as treatment sites because coyote control was the treatment, whereas the sites that received limited coyote removal were referred to as comparison sites. In addition, treatment sites had a 5-km border zone from which coyotes also were removed to reduce effects of those animals with home ranges that may have overlapped treatment sites and to decrease immigration into treatment sites. Treatment and comparison sites were at least 19.5 km apart, which was considered sufficient to reduce the probability of coyotes visiting multiple sites based on knowledge of the average territorial radius of resident and transient animals in Texas (Andelt, 1995). Coyotes were collected seasonally by aerial gunning, which involved shooting them with a 20-gauge shotgun from a helicopter during the hours immediately after sunrise and before sunset for 3 consecutive days each season. Data obtained in April, July, October, and January represented the four seasons of spring, summer, autumn, and winter, respectively. Data obtained during January were considered winter data of the previous year. Complete coyote removal was attempted on the treatment sites (i.e., treatment sites and 5-km buffer zone; intensive coyote removal); however, only coyotes killed within the treatment sites (i.e., not within buffer zone) were used in the analyses. For comparative purposes, five coyotes were collected from each comparison site each season (i.e., limited coyote removal). Coyotes were collected in accordance with Texas Parks and Wildlife Scientific Permit No. SPR-0993-636 (Austin, Texas, USA).

All coyotes were retrieved immediately and eviscerated in the field. Ethyl alcohol was cooled to approximately −70 C by means of dry ice and was used to freeze the viscera. Coyote viscera were placed in individually labeled plastic bags and kept frozen at −10 C until necropsy. An upper canine tooth was extracted for age determination. Coyotes were classified as juveniles or adults by interpretation of cementum annuli examined microscopically from tooth sections (Linhart and Knowlton, 1967).

Helminths were collected, counted, and examined according to the methods outlined in Wallace and Pence (1986). Representatives of all species of helminths found in this study were deposited in the U.S. National Parasite Collection (Beltsville, Maryland, USA; Accession Numbers 77533–77543).

The terms prevalence and abundance follow definitions of Bush et al. (1997). Common helminth species were defined arbitrarily as those with ≥20% prevalence across the collective host sample; all other species were considered uncommon.

Jaccard's similarity coefficient (S_j) was used to measure the similarity of shared species between host populations by treatments and within seasons and years (Krebs, 1989). The percentage similarity index (PS_i) was used to measure similarity of helminth communities between treatments within seasons and years, based on the relative proportion of helminth individuals contributed by each helminth species (Pielou, 1975). The numerical dominance index (DI) was used to rank helminth species by the number of individuals that each species contributed to the total number of helminth individuals by treatment within seasons and years (Leong and Holmes, 1981).

Initially, we used a completely randomized block design with repeated measures. Sites that received the same treatment were used as blocks of the same treatment. Data were pooled across blocks when no differences were detected; therefore, coyotes were considered individual habitats within treatments and used as replicates for subsequent analyses. Thereafter, we used a completely randomized design with repeated measures. The frequency distribution pattern of mean abundance of helminths for the common species was tested for normality (PROC UNIVARIATE NORMAL; SAS Institute Inc., 1990). Homogeneity of variances among treatments was evaluated with the Bartlett's test (Steel and Torrie, 1980). Because a non-normal distribution pattern (overdispersion) occurred, values for mean abundance of helminths were rank-transformed (PROC RANK; SAS Institute Inc., 1990) prior to further statistical analyses. Rank-transformed values for mean abundance of helminths were examined for main effects of treatment (intensive coyote removal, limited coyote removal), age (juvenile, adult), season (spring, summer, autumn, winter), year (1990, 1991), and interactive effects with analysis of variance (ANOVA; SAS Institute Inc., 1990) for each common helminth species and with multivariate analysis of variance (MANOVA; SAS Institute Inc., 1990) for the collective common species. If significant interactions were detected, single variates of the interaction were analyzed separately within each grouping of the other main effects. Multiple comparisons were made using Tukey's studentized range (HSD) test when significant effects were found (Cochran and Cox, 1957). Prevalence data were not analyzed due to insufficient sample sizes within cells; which in turn, would have resulted in low statistical power to render a valid interpretation of the analysis. All tests were considered significant at $P \leq 0.05$. Descriptive statistics are presented as the mean ± 1 SE.

RESULTS

Coyote removal

We removed 80 and 354 coyotes from the comparison and treatment sites, respectively. The number of coyotes removed from the treatment sites in each of the eight consecutive seasons was 67, 30, 51, 53, 55, 31, 41, and 26, respectively. Of the coyotes removed from the treatment sites, 172 animals were taken within the borders of the designated sites and assessed for helminths while 182 coyotes were killed in the associated buffer zones. The estimated coyote density on treatment sites was reduced from 0.12 ± 0.01 coyotes/km^2 in April 1990 to 0.06 ± 0.01 coyotes/km^2 in January 1992, while coyote density on comparison sites remained stable throughout the study at 0.14 ± 0.01 coyotes/km^2 (Henke and Bryant, 1999). The number of juvenile and adult coyotes assessed was 34 and 46, respectively, from comparison sites and 65 and 107, respectively, from treatment sites (Tables 1, 2).

Helminth fauna

Twelve helminth species consisting of seven nematodes (*A. caninum, Physaloptera rara, Toxascaris leonina, Dirofilaria immitis, Spirocerca lupi, Oslerus osleri,* and *Capillaria aerophila*), three cestodes (*Taenia pisiformis, Taenia multiceps,* and *Mesocestoides* sp.), one acanthocephalan (*Oncicola canis*), and one trematode (*Alaria marcianae*) were found in 99 juvenile coyotes, and 11 helminth species (same species as juvenile coyotes except *A. marcianae*) were found in 153 adult coyotes. Prevalences of helminths ranged from <1 to 100%; all coyotes were infected with *A. caninum.* Juvenile coyotes were infected with one to seven helminth species with an average of 3.6 ± 0.4 species/coyote, while adult coyotes were infected with one to seven helminth species with an average of 3.2 ± 0.3 species/coyote. Total helminths collected from juvenile and adult coyotes was 12,129 (122.5 ± 46.7) and 11,167 (73.0 ± 32.7) helminths, respectively. Four nematodes (*A. caninum, P. rara, T. leonina,* and *S. lupi*) and two cestodes (*T. pisiformis,* and *T. multiceps*) commonly occurred in juvenile and adult coyotes (Tables 1, 2). The remaining six species were uncommon.

Coefficient of Jaccard indices and percent similarity values were quite variable in both age classes of coyotes, but more so in juvenile coyotes (Table 3). Temporal and spatial variability in shared species and helminth community composition was due predominately to the occurrence of cestodes and uncommon species.

Helminth species that numerically dominated within each host age class, treatment, season, and year were *A. caninum, P. rara,* and *T. multiceps* (Table 4). These three species represented >75% and >85% of the helminths collected in juvenile coyotes from comparison and treatment sites, respectively. However, *T. multiceps* represented a minor proportion of the DI value for juvenile coyotes from treatment sites. A similar pattern was observed in adult coyotes except during winter 1991 on treatment sites when the three dominate helminth species represented <50% of the helminths collected (Table 4).

Treatment (i.e., intensive coyote removal), season, and year were important factors in determining collective helminth abundances in juvenile and adult coyotes (Table 5). Abundances were similar between sites during 1990, but treatment sites had substantially lower abundances than comparison sites during 1991 (Fig. 1). Although this trend was observed for both age classes of coyotes, it was more pronounced in adults. Juvenile coyotes had a higher mean abundance of helminths during autumn than during spring, while the mean abundance of helminths in adult coyotes was greatest during spring than autumn. Remaining seasonal combinations were similar for juvenile and adult coyotes.

Rank-transformed abundances differed over the main and interactive effects of treatment, season, and year for juvenile coyotes (Table 5). In juvenile coyotes, rank-transformed abundances of four of the six common species varied either by treatment (*T. multiceps*), season (*T. pisiformis*), year (*P. rara*), or treatment × season (*A. caninum*) effects (Table 5). Juvenile coyotes from the comparison sites were infected with more *T. multiceps* than juvenile coyotes from the treatment sites. Rank-transformed abundances of *A. caninum* were similar between comparison and treatment sites during each season except winter, when the rank-transformed abundance of *A. caninum* was greater on comparison sites. Within comparison sites, rank-transformed abundances of *A. caninum* during autumn and winter were greater than during spring and summer; whereas on treatment sites the rank-transformed abundances of *A. caninum* were greater during autumn and summer than during winter and spring. Rank-transformed abundances of *T. pisiformis* were greatest during autumn, followed by winter, then spring and summer. Juvenile coyotes were infected with more *P. rara* during 1990 than 1991. Rank-transformed abundances of *T. leonina* and *S. lupi* in juvenile coyotes did not vary by main or interactive effects.

In adult coyotes, rank-transformed abundances of the six common species varied by the main and interactive effects (Table 5). Rank-transformed abundances of *A. caninum, T. multiceps,* and *S. lupi* varied by treatment and treatment × year (Table 5). In addition, *A. caninum* and *T. multiceps* varied by season (Table 5). During 1990 the rank-transformed abundances of the three helminth species were similar between comparison and treatment sites, but the abundances reduced on treatment sites during 1991. Within comparison sites, rank-transformed abundances of *A. caninum* during 1991 were greater than during 1990, while both years had similar rank-transformed abundances within treatment sites. Rank-transformed abundances of *T. multiceps* and *S. lupi* were similar between 1990 and 1991 within comparison and treatment sites. Seasonally, rank-transformed abundances of *A. caninum* were greatest during summer, followed by spring, autumn, and winter; whereas the rank-transformed abundances of *T. multiceps* were greatest during the winter and summer, followed by spring and autumn.

TABLE 1. Descriptive statistics for common helminths from juvenile coyotes collected on sites with and without intensive coyote removal in western Texas, 1990–91.

	Comparison sites							
	1990				1991			
Helminth	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Ancylostoma caninum								
NI/NE (%)[a]	3/3 (100)	3/3 (100)	7/7 (100)	7/7 (100)	5/5 (100)	3/3 (100)	2/2 (100)	4/4 (100)
Abundance[b]	39.0 ± 12.0	35.7 ± 8.2	173.1 ± 44.2	96.0 ± 41.4	69.2 ± 37.0	88.0 ± 42.9	105.5 ± 77.5	168.5 ± 70.9
Total[c]	117	107	1212	672	346	264	211	674
Physaloptera rara								
NI/NE (%)[a]	1/3 (33.3)	3/3 (100)	6/7 (85.7)	6/7 (85.7)	4/5 (80.0)	2/3 (66.7)	2/2 (100)	3/4 (75.0)
Abundance[b]	7.7 ± 7.7	72.0 ± 67.0	44.6 ± 25.2	7.3 ± 2.5	3.8 ± 1.7	15.7 ± 15.2	2.5 ± 0.5	7.7 ± 3.5
Total[c]	23	216	312	51	19	47	5	31
Toxascaris leonina								
NI/NE (%)[a]	0/3 (0.0)	2/3 (66.7)	5/7 (71.4)	4/7 (57.1)	2/5 (40.0)	2/3 (66.7)	0/2 (0.0)	2/4 (50.0)
Abundance[b]	0	6.0 ± 4.6	7.4 ± 2.5	7.9 ± 4.7	3.2 ± 3.0	14.7 ± 7.9	0	3.7 ± 2.2
Total[c]	0	18	52	55	16	44	0	15
Taenia pisiformis								
NI/NE (%)[a]	0/3 (0.0)	0/3 (0.0)	2/7 (28.6)	4/7 (57.1)	1/5 (20.0)	0/3 (0.0)	1/2 (50.0)	2/4 (50.0)
Abundance[b]	0	0	0.7 ± 0.5	13.1 ± 11.5	1.0 ± 1.0	0	33.5 ± 33.5	1.0 ± 0.7
Total[c]	0	0	5	92	5	0	67	4
Taenia multiceps								
NI/NE (%)[a]	1/3 (33.3)	1/3 (33.3)	3/7 (42.9)	4/7 (57.1)	2/5 (40.0)	1/3 (33.3)	2/2 (100)	1/4 (25.0)
Abundance[b]	0.7 ± 0.7	4.0 ± 4.0	26.4 ± 20.5	114.3 ± 46.4	5.6 ± 3.4	11.3 ± 11.3	9.0 ± 2.0	1.0 ± 1.0
Total[c]	2	12	185	800	28	34	18	4
Spirocerca lupi								
NI/NE (%)[a]	1/3 (33.3)	1/3 (33.3)	1/7 (14.3)	1/7 (14.3)	1/5 (20.0)	0/3 (0.0)	2/2 (100)	1/4 (25.0)
Abundance[b]	1.0 ± 1.0	0.3 ± 0.3	0.1 ± 0.1	0.6 ± 0.6	0.4 ± 0.4	0	1.5 ± 0.5	0.2 ± 0.2
Total[c]	3	1	1	4	2	0	3	1

[a] Number of hosts infected/number of hosts examined (% prevalence).
[b] Abundance was defined according to Bush et al. (1997).
[c] Cumulative number of helminths in host sample.

TABLE 1. Extended.

Helminth	Treatment sites							
	1990				1991			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Anclystoma caninum								
NI/NE (%)[a]	6/6 (100)	5/5 (100)	8/8 (100)	11/11 (100)	8/8 (100)	9/9 (100)	8/8 (100)	10/10 (100)
Abundance[b]	60.2 ± 13.4	112.4 ± 36.7	103.7 ± 33.0	42.5 ± 13.9	34.6 ± 6.4	59.6 ± 17.0	57.7 ± 21.1	32.0 ± 14.5
Total[c]	361	562	830	468	277	536	462	320
Physaloptera rara								
NI/NE (%)[a]	6/6 (100)	4/5 (80.0)	8/8 (100)	9/11 (81.8)	6/8 (75.0)	5/9 (55.6)	5/8 (62.5)	4/10 (40.0)
Abundance[b]	11.3 ± 1.9	27.2 ± 23.5	59.6 ± 28.5	18.0 ± 7.6	4.1 ± 2.2	22.3 ± 11.7	16.7 ± 10.7	2.4 ± 1.5
Total[c]	68	136	477	198	33	201	134	24
Toxascaris leonina								
NI/NE (%)[a]	3/6 (50.0)	3/5 (60.0)	4/8 (50.0)	6/11 (54.5)	6/8 (75.0)	4/9 (44.4)	4/8 (50.0)	6/10 (60.0)
Abundance[b]	8.8 ± 5.9	9.6 ± 6.3	8.1 ± 5.9	10.0 ± 6.5	1.9 ± 0.8	2.7 ± 1.4	4.1 ± 2.6	1.7 ± 0.7
Total[c]	53	48	65	110	15	24	33	17
Taenia pisiformis								
NI/NE (%)[a]	1/6 (16.7)	0/5 (0.0)	3/8 (37.5)	3/11 (27.3)	0/8 (0.0)	3/9 (33.3)	4/8 (50.0)	1/10 (10.0)
Abundance[b]	0.3 ± 0.3	0	4.4 ± 2.6	0.6 ± 0.4	0	3.6 ± 2.6	1.1 ± 0.5	0.3 ± 0.3
Total[c]	2	0	35	7	0	32	9	3
Taenia multiceps								
NI/NE (%)[a]	2/6 (33.3)	0/5 (0.0)	0/8 (0.0)	3/11 (27.3)	1/8 (12.5)	3/9 (33.3)	1/8 (12.5)	1/10 (10.0)
Abundance[b]	39.7 ± 39.1	0	0	5.0 ± 2.7	0.2 ± 0.2	0.8 ± 0.5	0.6 ± 0.6	0.2 ± 0.2
Total[c]	238	0	0	55	2	7	5	2
Spirocerca lupi								
NI/NI (%)[a]	2/6 (33.3)	2/5 (40.0)	2/8 (25.0)	1/11 (9.1)	4/8 (50.0)	2/9 (22.2)	3/8 (37.5)	2/10 (20.0)
Abundance[b]	0.3 ± 0.3	1.2 ± 0.8	0.4 ± 0.3	0.2 ± 0.2	1.2 ± 0.8	0.4 ± 0.3	1.6 ± 1.2	0.3 ± 0.2
Total[c]	2	6	3	2	10	4	13	3

TABLE 2. Descriptive statistics for common helminths from adult coyotes collected on sites with and without intensive coyote removal in western Texas, 1990–91.

	Comparison sites							
	1990				1991			
Helminth	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Ancylostoma caninum								
NI/NE (%)[a]	6/6 (100)	7/7 (100)	3/3 (100)	3/3 (100)	5/5 (100)	7/7 (100)	9/9 (100)	6/6 (100)
Abundance[b]	31.3 ± 11.4	22.1 ± 2.8	13.3 ± 3.0	80.7 ± 61.7	147.8 ± 71.0	73.4 ± 21.0	40.4 ± 8.0	44.0 ± 22.2
Total[c]	188	155	40	242	739	514	364	264
Physaloptera rara								
NI/NE (%)[a]	6/6 (100)	6/7 (85.7)	3/3 (100)	3/3 (100)	5/5 (100)	2/7 (28.6)	3/9 (33.3)	4/6 (66.7)
Abundance[b]	6.8 ± 2.0	3.7 ± 1.2	19.3 ± 15.8	15.3 ± 9.8	19.6 ± 16.9	0.4 ± 0.3	0.9 ± 0.6	11.3 ± 5.4
Total[c]	41	26	58	46	98	3	8	68
Toxascaris leonina								
NI/NE (%)[a]	4/6 (66.7)	2/7 (28.6)	1/3 (33.3)	3/3 (100)	2/5 (40)	6/7 (85.7)	4/9 (44.4)	3/6 (50.0)
Abundance[b]	4.2 ± 2.1	1.1 ± 1.0	6.0 ± 6.0	7.3 ± 4.5	2.4 ± 1.6	11.1 ± 5.5	7.3 ± 7.0	0.7 ± 0.3
Total[c]	25	8	18	22	12	78	66	4
Taenia pisiformis								
NI/NE (%)[a]	3/6 (50.0)	2/7 (28.6)	0/3 (0)	2/3 (66.7)	1/5 (20.0)	1/7 (14.3)	2/9 (22.2)	1/6 (16.7)
Abundance[b]	5.3 ± 3.5	3.7 ± 2.4	0	17.7 ± 15.7	0.8 ± 0.8	1.9 ± 1.9	2.6 ± 2.1	4.7 ± 4.7
Total[c]	32	26	0	53	4	13	23	28
Taenia multiceps								
NI/NE (%)[a]	0/6 (0.0)	3/7 (42.9)	0/3 (0.0)	2/3 (66.7)	2/5 (40.0)	4/7 (57.1)	2/9 (22.2)	2/6 (33.3)
Abundance[b]	0	1.7 ± 0.8	0	143.7 ± 84.9	42.0 ± 30.4	72.1 ± 36.3	17.2 ± 17.0	3.8 ± 2.7
Total[c]	0	12	0	431	210	505	155	23
Spirocerca lupi								
NI/NE (%)[a]	0/6 (0.0)	2/7 (28.6)	0/3 (0.0)	1/3 (33.3)	1/5 (20.0)	4/7 (57.1)	2/9 (22.2)	4/6 (66.7)
Abundance[b]	0	0.4 ± 0.3	0	1.0 ± 1.0	0.2 ± 0.2	0.9 ± 0.4	0.4 ± 0.3	2.3 ± 1.6
Total[c]	0	3	0	3	1	6	4	14

[a] Number of hosts infected/number of hosts examined (% prevalence).

[b] Abundance was defined according to Bush et al. (1997).

[c] Cumulative number of helminths in host sample.

TABLE 2. Extended.

	Experimental sites							
	1990				1991			
Helminth	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Ancylostoma caninum								
NI/NE (%)^{a}	30/30 (100)	10/10 (100)	10/10 (100)	9/9 (100)	13/13 (100)	13/13 (100)	12/12 (100)	10/10 (100)
Abundance^{b}	36.4 ± 7.9	58.9 ±20.3	35.6 ± 15.7	13.9 ± 3.7	65.9 ± 47.5	31.1 ± 11.3	6.7 ± 0.9	13.9 ± 6.5
Total^{c}	1091	589	356	125	857	401	81	139
Physaloptera rara								
NI/NE (%)^{a}	29/30 (96.7)	7/10 (70)	8/10 (80)	9/9 (100)	12/13 (92.3)	4/13 (30.8)	7/12 (58.3)	6/10 (60)
Abundance^{b}	20.8 ± 4.8	24.6 ± 12.0	11.9 ± 7.8	16.6 ± 5.9	6.2 ± 1.7	4.5 ± 2.7	1.7 ± 1.0	0.7 ± 0.2
Total^{c}	624	246	110	149	81	59	20	7
Toxascaris leonina								
NI/NE (%)^{a}	14/30 (46.7)	4/10 (40)	5/10 (50)	7/9 (77.8)	7/13 (53.8)	7/13 (53.8)	2/12 (16.7)	7/10 (70)
Abundance^{b}	10.1 ± 4.2	3.0 ± 1.8	12.6 ± 9.2	6.0 ± 4.4	3.2 ± 1.3	6.8 ± 2.4	1.2 ± 1.2	15.2 ± 10.4
Total^{c}	304	30	126	54	42	89	15	152
Taenia pisiformis								
NI/NE (%)^{a}	10/30 (33.3)	2/10 (20.0)	0/10 (0.0)	2/9 (22.2)	5/13 (38.5)	1/13 (7.7)	0/12 (0.0)	2/10 (20.0)
Abundance^{b}	3.1 ± 1.1	1.4 ± 1.1	0	0.2 ± 0.1	4.1 ± 2.6	2.5 ± 2.5	0	0.2 ± 0.1
Total^{c}	92	14	0	2	54	33	0	2
Taenia multiceps								
NI/NE (%)^{a}	12/30 (40.0)	4/10 (40.0)	0/10 (0.0)	3/9 (33.3)	3/13 (23.1)	1/13 (7.7)	0/12 (0.0)	2/10 (20.0)
Abundance^{b}	7.3 ± 4.0	4.6 ± 3.1	0	2.1 ± 1.2	0.6 ± 0.3	10.5 ± 10.5	0	0.3 ± 0.2
Total^{c}	218	46	0	19	8	137	0	3
Spirocerca lupi								
NI/NE (%)^{a}	10/30 (33.3)	1/10 (10)	2/10 (20)	2/9 (22.2)	2/13 (15.4)	1/13 (7.7)	0/12 (0.0)	1/10 (10)
Abundance^{b}	0.9 ± 0.3	0.1 ±0.1	0.4 ± 0.3	1.1 ± 0.8	0.3 ± 0.2	0.1 ± 0.1	0	0.1 ± 0.1
Total^{c}	26	1	4	10	4	1	0	1

TABLE 3. Coefficient of Jaccard (S_j) and percent similarity (PS_i) indices for helminth species comparing sites with (treatment sites) and without (comparison sites) host removal from coyotes collected in western Texas. Values range from 0 (complete dissimilarity) to 1.0 and 100 (complete similarity) for S_j and PS_i, respectively.

	Juvenile coyotes		Adult coyotes	
Season-year	S_j	PS_i	S_j	PS_i
Spring 1990	0.56	59.1	0.50	72.9
Summer 1990	0.56	45.9	0.75	82.4
Fall 1990	0.75	79.0	0.60	68.4
Winter 1990	1.00	54.0	0.75	45.2
Spring 1991	0.71	91.0	0.86	79.5
Summer 1991	0.38	81.8	0.80	73.4
Fall 1991	0.62	72.5	0.38	69.8
Winter 1991	0.67	93.5	0.86	50.6

Seasonal effects were observed for rank-transformed abundances of *P. rara* and *T. pisiformis* (Table 5). Rank-transformed abundances of *P. rara* and *T. pisiformis* were greatest in spring, followed by winter, summer, and autumn. In addition, adult coyotes were infected with more *P. rara* during 1990 than during 1991. Rank-transformed abundances of *T. leonina* varied by season × year (Table 5). During 1990 the rank-transformed abundances of *T. leonina* was less during the summer than the winter, spring, and autumn, while during 1991 the rank-transformed abundances were greatest during winter and summer, followed by spring and autumn. Also, within spring and autumn, the rank-transformed abundances of *T. leonina* were greater during 1990 than during 1991, the opposite trend was true during summer, while no differences between years were noted during winter.

DISCUSSION

Helminths may limit host population abundance through the density-dependent effects on host survival and reproduction (Spratt, 1990). Such density-dependent processes should be most apparent with direct life cycle helminths. In the present study the only direct life cycle helminths that were considered common were *A. caninum* and *T. leonina.* However, of these parasites only *A. caninum* were affected by a reduction in coyote density on treatment sites. We acknowledge that 2 yr of coyote removal, which resulted in an overall reduction in coyote density of about 50%, may have been insufficient to observe pronounced effects in the abundance of coyote helminths and limited our likelihood to assess potential interactions of environmental and stochastic influences. However, the intensity and duration of our removal effort typified ranching practices of the area. Despite this potential experimental limitation, we were able to demonstrate that *A. caninum,* a parasite that potentially regulates coyote populations, was affected even with only a 50% reduction in coyote density (Fig. 2). In fact, the pattern of abundances for the collective helminth species in juvenile and adult coyotes was due largely to the trends observed for the abundances of *A. caninum.*

Ancylostoma caninum is a blood-sucking nematode. Blood loss has been estimated at about 0.08 ml per worm per day (Miller, 1971). Obviously, the severity of clinical hookworm disease is a density-dependent function of the number of hookworms present and concordant blood loss versus the compensatory replacement of blood. The latter is a function of an uncompromised nutritional status and age of the infected animal (Miller, 1971; Radomski, 1989). If the threshold for compensatory replacement of blood loss is not obtained, clinical manifestation and even death can result. Because of its potentially lethal effect in young pups, *A. caninum* has been suggested as a population regulator of coyotes (Pence et al., 1988), although empirical data are lacking to confirm this theory. However if the assertion of Pence et al. (1988) is true, then a coyote removal program that results in reduced density of coyotes and at the same time causes a reduced abundance of *A. caninum,* may in fact negate the regulatory effect that *A. caninum* has on coyote populations. In addition, juvenile:adult ratios on treatment

TABLE 4. Dominance index values for the six common helminth species by site of collection for juvenile and adult coyotes collected on sites with and without coyote removal from western Texas. Dominance values were calculated using all helminth species found within respective host (age, collection site, season, and year) categories.

	Comparisons sites								Treatment sites							
	1990				1991				1990				1991			
Helminth	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Juvenile coyotes																
Ancylostoma caninum	85.4	23.8	68.5	39.6	83.2	66.7	69.4	92.3	48.8	73.5	58.1	55.3	81.5	66.0	67.9	86.2
Physaloptera rara	12.2	48.1	17.6	3.0	4.6	11.9	1.6	4.2	9.2	17.8	33.4	23.4	9.7	24.8	19.7	6.5
Toxascaris leonina	0.3	4.0	2.9	3.2	3.8	11.1	0.0	2.0	7.2	6.3	4.5	13.0	4.4	3.0	4.8	4.6
Taenia pisiformis	0.0	0.0	0.3	5.4	1.2	0.0	22.0	0.5	0.3	0.0	2.4	0.8	0.0	3.9	1.3	0.8
Taenia multiceps	0.5	2.7	10.4	47.1	6.7	8.6	5.9	0.5	32.2	0.0	0.0	6.5	0.6	0.9	0.7	0.5
Spirocerca lupi	1.3	0.2	0.1	0.2	0.5	0.0	1.0	0.1	0.3	0.8	0.2	0.2	2.9	0.5	1.9	0.8
Other[a]	0.3	21.2	0.2	1.5	0.0	1.1	0.1	0.4	2.0	1.6	1.4	0.8	0.9	0.9	3.7	0.6
Adult coyotes																
Ancylostoma caninum	63.9	67.4	34.5	30.3	69.4	45.6	58.0	65.8	45.7	61.6	59.6	34.7	81.9	54.9	67.5	45.4
Physaloptera rara	13.9	11.3	50.0	5.8	9.2	0.3	1.3	17.0	26.2	25.7	18.4	41.4	7.7	8.0	16.7	2.3
Toxascaris leonina	8.5	3.5	15.5	2.8	1.1	6.9	10.5	1.0	12.7	3.1	21.1	15.0	4.0	12.1	12.5	49.7
Taenia pisiformis	10.9	11.3	0.0	6.6	0.4	1.2	3.7	7.0	3.9	1.5	0.0	0.6	5.2	4.5	0.0	0.6
Taenia multiceps	0.0	5.2	0.0	53.9	19.7	44.8	24.7	5.7	9.1	4.8	0.0	5.3	0.8	18.6	0.0	1.0
Spirocerca lupi	0.0	1.3	0.0	0.4	0.1	0.5	0.6	3.5	1.1	0.1	0.7	2.8	0.4	0.1	0.0	0.3
Other[a]	2.8	0.0	0.0	0.2	0.1	0.7	1.2	0.0	1.3	3.2	0.2	0.2	0.0	1.8	3.3	0.7

[a] Other category includes *Dirofilaria immitis, Oslerus osleri, Alaria marcianae, Oncicola canis, Capillaria aerophila,* and *Mesocestoides* sp.

TABLE 5. *F* statistics for the main and interactive effects of treatment (coyote removal), season (spring, summer, autumn, and winter), and year (1990 and 1991) from a repeated measures ANOVA and MANOVA for the ranked abundance of six common helminth species from juvenile and adult coyotes collected on sites with and without coyote removal from western Texas.

Helminth species	Treatment	Season	Year	Trt × Season	Trt × Year	Season × Year	Trt × Season × Year
Juvenile coyotes							
ANOVA							
Ancylostoma caninum	2.52	1.53	0.89	2.64*	6.60	0.54	0.55
Physaloptera rara	0.18	0.54	6.69**	0.90	1.26	0.38	1.18
Toxascaris leonina[a]	0.07	0.91	0.61	1.18	0.01	0.83	1.24
Taenia pisiformis	0.27	3.12*	0.42	1.46	0.16	0.80	0.71
Taenia multiceps	10.44**	0.33	0.05	1.33	0.14	2.33	0.94
Spirocerca lupi[a]	0.01	1.38	0.61	0.70	0.07	2.08	1.12
MANOVA	6.19*	3.51*	2.54	2.47	5.77*	0.40	0.34
Adult coyotes							
ANOVA							
Ancylostoma caninum	18.33***	3.27*	0.11	0.98	8.67**	0.46	1.04
Physaloptera rara	0.14	7.48***	34.17***	1.22	0.09	1.01	1.24
Toxascaris leonina	0.03	1.17	0.24	0.06	0.05	3.13*	1.50
Taenia pisiformis	2.11	2.65*	1.53	0.71	1.02	0.91	0.93
Taenia multiceps	4.08*	3.28*	0.13	1.46	3.75*	1.37	1.74
Spirocerca lupi	3.66*	1.37	0.12	2.16	5.02*	0.37	0.12
MANOVA	25.92***	3.29*	0.91	1.09	14.26***	1.79	1.69

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

[a] ANOVA model not significant ($P > 0.05$).

sites switched from more adults during 1990 to favor juveniles during 1991 (Henke and Bryant, 1994). Pence et al. (1988) believed that the potential mortality resulting from infection of *A. caninum* could selectively predispose initial litters of younger female coyotes to greater losses than older females. Considering the data of our study, coyote removal programs may reduce the intensity of infection within juvenile females. This may result in greater survival of pups because of reduced exposure to *A. caninum* through transplacental and transmammary transmission routes.

A treatment effect was not noted for *T. leonina,* a nematode infection canids typically acquire by ingesting infective eggs or larvae in rodent paratenic hosts (Sprent, 1959). Although abundances of *T. leonina* are reported to vary significantly between host sexes (Pence and Meinzer, 1979), host sex should not be considered a confounding variable because it did not deviate from a 1:1 ratio in our dataset (Henke and Bryant, 1994). The intrinsic factor of sex was not included in our analysis due to already low sample sizes within variable categories. Including sex would have doubled our data categories from 16 to 32. Perhaps overdispersion in *T. leonina* coupled with low sample sizes of infected coyotes were the reasons for our nonsignificant results concerning this direct life cycle parasite. Abundances of *T. leonina* did exhibit a season × year interaction with the trend of *T. leonina* abundance paralleling the trend of mammal consumption by coyotes (Henke, 1992).

A 12-mo time lag was required to observe reductions in abundances of *S. lupi* and *T. multiceps* in adult coyotes on treatment sites. Our quantification of *S. lupi* is an underestimation. Only larvae and adults isolated from the aorta and esophagus, re-

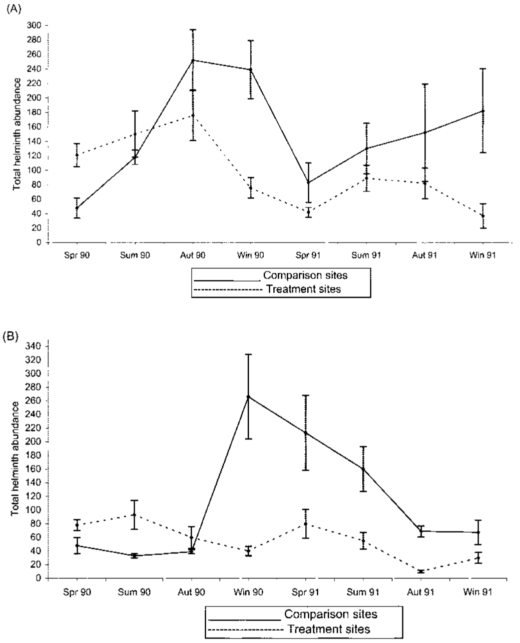

FIGURE 1. Total helminth abundance in juvenile (A) and adult (B) coyotes between comparison and treatment sites after a seasonal (Spr = spring; Sum = summer; Aut = autumn; Win = winter) coyote removal program was initiated in western Texas, 1990–91. Bars represent 1 SE as calculated from two sites/treatment.

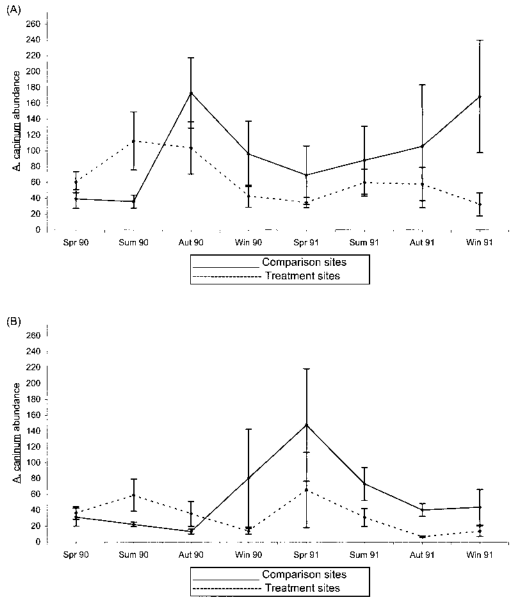

FIGURE 2. Abundance of *A. caninum* in juvenile (A) and adult (B) coyotes between comparison and treatment sites after a seasonal (Spr = spring; Sum = summer; Aut = autumn; Win = winter) coyote removal program was initiated in western Texas, 1990–1991. Bars represent 1 SE as calculated from two sites/treatment.

spectively, were counted. However, aortic lesions were observed in 77 (78%) of the juvenile coyotes and in 135 (88%) of the adult coyotes (Henke, unpubl. data), which suggests a higher prevalence of *S. lupi* than that reported herein. Spirocercosis is chronic and prevalence and severity increase with the age of the host (Pence and Custer, 1981). This explains why treatment effects were observed only in adults and not in juvenile coyotes. Although *S. lupi* has not been suggested as a regulatory factor for coyotes, the severity of aortic lesions may contribute to the mortality of coyotes (Pence and Stone, 1978). As stated previously, a coyote removal program that reduces coyote density may reduce the abundance of a deleterious parasite. This ultimately may improve the health and survival of the coyote population.

Taenia multiceps has both a pastoral cycle involving canids and domestic ruminants and a sylvatic cycle with canids and lagomorphs. Either or both cycles could have been occurring in our study. Cattle production was one of the chief industries of the area with the average producer grazing cattle at a moderate rate of about one animal unit (i.e., cow and calf) per 5.5 ha (Henke, 1992). Stocking rates remained stable throughout the sites during the study and coyote density was reduced on treatment sites after approximately 1 yr of coyote removal. Therefore, it appears reasonable that the abundance of *T. multiceps* also could be reduced. If the sylvatic cycle dominated, abundance of black-tailed jackrabbits (*Lepus californicus*) increased three-fold on treatment sites after 9 mo of coyote removal (Henke and Bryant, 1999). However, lagomorphs were consumed less frequently on treatment sites during 1991 than other prey items (Henke, 1992). This could explain the reduced abundance of *T. multiceps* on treatment sites during 1991.

Several helminth species exhibited seasonal effects. This was not surprising because the coyote diet is quite diverse throughout the year. Typically, they are opportunistic feeders (MacCracken and Hansen, 1987), and much of coyote prey can serve as intermediate hosts for helminths (Pence and Windberg, 1984). In addition, the extrinsic variable of season is actually comprised of many factors. These include, but are not limited to, variability of food habits, coyote social structure and behavior, nutritional stresses, and reproductive stresses (Pence and Windberg, 1984).

Coyote removal programs appear to be counterproductive and may actually result in more coyotes after the removal than before program initiation because of increased pup survival due to reduced abundances of deleterious helminths. Because we did not attempt to quantify pup survival, our theory is therefore speculative. Nonetheless, our data stimulate new concerns about current strategies of coyote population control and management. Additional research is needed to validate these new findings.

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