Effect of Predator Control on Coyote Age Structure, Weight, and Reproduction

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Abstract

Predator control on coyotes (*Canis latrans*) has been extensive throughout the western United States. A common biological expectation is that reproduction increases as density of coyotes is reduced. However, this expectation does not consider social structure, age structure, or prey availability before and after predator control is undertaken. We examined the effects of predator control on coyote age structure, weight, and reproduction in three study units in north-central Montana. Study units ranged from 140 to 2679 km^2 and were subjected to different levels of control intensity. Coyote age structure did not change significantly over time within individual units. Among treatment areas, only the area most intensively controlled differed significantly in age structure, having younger coyotes. Based on corpora luteal counts, coyote reproduction increased only within the largest unit, which was subjected to intense control. Coyotes were younger, larger, and more reproductively active when subjected to intensive control over a large area. Significant differences in age or reproduction were not apparent for units of smaller size or less intensive control efforts.

Key Words: age structure, *Canis latrans,* Coyote, predator control, reproduction.

Introduction

Since the extirpation of larger carnivores, such as grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) within the majority of livestock producing areas of the western United States, coyotes (*Canis latrans*) have been a primary target of predator control activities. Recent declines in deer (*Odocoileus* spp.) and pronghorn antelope (*Antilocapra americana*) populations and reintroduction of black-footed ferrets (*Mustela nigripes*) in Montana led to predator control activities in an attempt to provide increased survivorship of those species.

The effectiveness of predator control on survival of prey populations has been the subject of much study and debate (Schladweiler 1980, Stout 1982, Guthery and Beasom 1997, Hamlin 1997, Sacks et al. 1999, Wagner and Conover 1999, Ballard et al. 2001). However, little information is available on the reproductive response of coyotes to prolonged coyote control. Knowlton (1972) developed a model to predict the response of coyote populations subjected to control that assumed, under favorable conditions, reproductive rates would increase as density decreased. An expected biological response of increased reproduction was predicated on decreased intraspecific competition for resources. This assumption did not consider the influence of changes in social structure of coyotes, potential differences in reproduction due to altered age structure, or status of the current population in terms of resource allocation. Reproductive rates generally vary depending on age, food availability, and social status (Bekoff 1982, Voight and Berg 1987). The percentage of sexually mature females, ovulation rate, degree of successful implanting, and *in utero* viability are important variables in determining coyote reproductive rates (Knowlton 1972). Coyotes are able to reproduce as juveniles (< 1 year old), but conception rates and litter sizes are variable (Todd et al. 1981, Voight and Berg 1987).

Reproductive rates of coyotes may be inversely related to population density. Knowlton (1972) observed an increase in mean litter size with decreasing coyote densities in Texas. Although many factors may affect individual reproduction, the relationship between coyote density and reproductive rate may be significantly influenced by competition for food resources. Clark (1972) documented fluctuations in Wyoming coyote populations in relation to variations in jackrabbit (*Lepus* spp.) populations.

We examined the effect of predator control on coyote reproductive rates, age structure, and weight. The study was conducted in conjunction with predator control activities designed to achieve specific management goals associated with wild ungulate survival and black-footed ferret reintroductions.

Study Area

The study area consisted of three units within central and north-central Montana (Fig. 1): (1) The Charles M. Russell/UL Bend National Wildlife Refuge and surrounding Bureau of Land Management and private lands of north central Montana (CMR/BLM unit); (2) the Fort Belknap Indian Reservation and private lands to the east (FB unit), also in north-central Montana; and (3) the eastern one-half of hunting district 530 (HD 530 unit) as described in the Montana deer hunting regulations located northeast of Roundup in central Montana.

The CMR/BLM unit was nearly 1620 km^2 in size during the initial 1993 and 1994 sampling sessions, but was reduced to approximately 140 km^2 surrounding black-footed ferret release sites on the UL Bend National Wildlife Refuge for subsequent sampling efforts. Timbered drainages or "coulees" of the Missouri River breaks, surrounded by elevated sagebrush (*Artemisia* spp.) prairie comprise the major habitat features of the CMR/BLM unit. Ponderosa pine (*Pinus ponderosa*) and Rocky Mountain juniper (*Juniperus scopulorum*) comprise the coniferous trees within and along coulees and cottonwood (*Populus* spp.) and willow (*Salix* spp.) occurred in riparian areas. Elevations ranged from approximately 630 m at Fort Peck Reservoir to 948 m on prairie uplands. Average annual precipitation was 29.8 cm

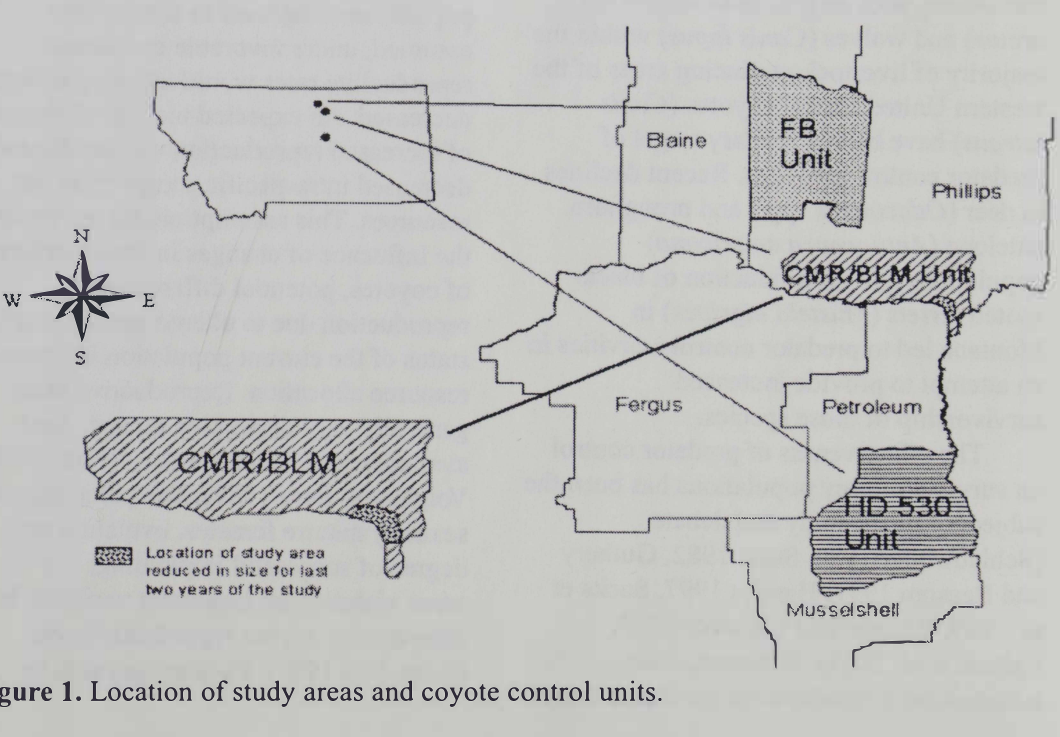

Figure 1. Location of study areas and coyote control units.

for the CMR/BLM area (Western Regional Climate Centers [WRCC] 2000). Livestock grazing and small grain farming were the primary agricultural uses of private and Bureau of Land Management property. The CMR/BLM's southern boundary was the Missouri River and Fort Peck Reservoir.

Sagebrush prairie with isolated timbered buttes and brush-laden creek bottoms comprised the major habitats of the nearly 2460 km^2 FB unit. Ponderosa pine and Rocky Mountain juniper dominate the overstory of the buttes and cottonwood and willow persist along creek drainages. Elevations range from 720 to 800 m, and the area received an average of 29.8 cm of precipitation annually (WRCC 2000). Agricultural use within FB occurred primarily in the form of prairie rangeland and small grain farming.

HD 530 was the largest unit, approximately 2679 km^2, and consisted of riparian, agricultural, timbered breaks, and sagebrush prairie habitats. Alfalfa production occurred primarily in conjunction with riparian areas, whereas small grain farming was interspersed with native prairie uplands. Timbered breaks, dominated by ponderosa pine, were associated with creek drainages feeding the Musselshell River. Annual precipitation was approximately 33 cm (WRCC 2000) with elevations ranging from 720 to 800 m.

Methods

Coyotes were killed through aerial gunning from helicopter and fixed-wing aircraft by Animal Plant Health Inspection, Wildlife Services (WS) personnel, as well as by trapping and free-hand shooting from the ground. Coyotes killed by use of a helicopter were delivered to a ground crew where they were weighed and necropsied. A spring scale was used to determine weights to the nearest kilogram. We collected skulls or jaws and removed a canine from which age was assigned by cementum analysis at Matson's Laboratory, Milltown, MT. Ages were recorded in increments of 0.5 years. A juvenile was recorded as 0.5 years old, a yearling as 1.5 years old, and a coyote with a cementum analysis of 2 was considered 2.5 years old.

We prosected reproductive tracts from female coyotes in the field or at the Montana Fish, Wildlife and Parks, Wildlife Research Laboratory (MFWPWL). We examined reproductive tracts from females ≥10 months old but excluded those from juveniles that were harvested during the summer/fall as they would not have had the opportunity to breed. Reproductive tracts were fixed in 10-percent buffered formalin and transported to the MFWPWL where ovary pairs were excised and weighed. We hand sectioned ovary pairs collected in the winter of 1993 and counted the corpora luteal scars (CL). All ovary pairs collected after 1993 were packed in water and sent to Matson's Laboratory, Milltown, MT, for histological sectioning and staining. There, they stained ovarian tissue with hematoxlyin/eosin, sectioned them every 200 microns, and mounted sections on a slide. We conducted CL counts at the MFWPWL by examining the slides under a 40X-power microscope. Age of reproduction was the coyote's age during the last breeding season. For example, a yearling coyote collected in summer/fall would have been a juvenile during the breeding season earlier in the year, and if CL were present, we recorded that individual as being bred as a juvenile.

Coyote control activities on CMR/BLM and FB were conducted to enhance black-footed ferret reintroductions and conduct disease surveys. Coyotes were killed in HD 530 to examine the effects of predator control on survival and recruitment of deer and antelope. The study areas were subjected to different levels of predator harvest prior to implementation of the study. The CMR/BLM was subjected to limited coyote harvest consisting primarily of hunter-killed animals, incidental to deer and elk hunting seasons. We did not consider harvest rates to measurably affect the population prior to the study. Coyote harvest on the FB study area occurred primarily from tribal members opportunistically harvesting coyotes.

Coyote mortality prior to implementation of this study was likely more intensive than on the CMR/BLM but not consistent or directed. HD 530 was subjected to the most intensive coyote control prior to implementation of the study. Coyotes within HD 530 were harvested by aerial gunning by WS from a fixed-wing aircraft and hunting or trapping by local ranchers to reduce livestock losses. Coyote control action by WS in response to livestock depredation resulted in an average annual removal of approximately 89 coyotes (0.03/ km^2) from the study area in the three years prior to initiation of the study.

Aerial gunning from a helicopter on the CMR/BLM unit occurred in late winter/ early spring (winter/spring) and late summer/early fall (summer/fall). Winter/ spring sampling periods focused on a general disease survey, and harvest consisted of few coyotes collected from varying locations throughout the area. The intent of collections during the summer/fall periods also was a disease survey with increased effort aimed at reducing predator numbers. Collections started in winter 1993 and continued through fall 1996. Winter/ spring collections in 1993 and 1994 occurred over a large geographic area (1620 km^2) surrounding the black-footed ferret reintroduction area. Due to management concerns, collections starting during summer/fall 1995 were intensified but confined to a 140-km^2 area immediately within and surrounding the ferret release site on the CMR/BLM (Fig. 1). An effort was made to harvest all coyotes within the 140-km^2 study area. We did not conduct a summer/fall collection in 1993, reproductive data were not available for 1994, and winter/spring sampling was not conducted during 1996.

Coyote control was conducted on FB from 1993 through 1998. The study site remained constant in size throughout the study, and effort was made to collect all available coyotes. Helicopter collections on FB occurred during winter/spring of 1993, 1994, and 1995 and during both sampling periods in 1996, 1997, and 1998. Reproductive tracts were not available for 1994 or 1995, and weights were not available for 1995. Additional coyotes were killed through aerial gunning from a fixed-wing airplane in 1997 and 1998, but these carcasses were not available for examination.

Coyote control in HD 530 was intensified, starting in 1997, to stimulate or increase deer and antelope survival. Hunting from fixed-wing aircraft was increased and a helicopter was used to kill coyotes during a one-week period in March. Only coyotes killed by use of a helicopter during March 1997-1999 were available for examination.

We used Analysis of Variance (ANOVA) to test for significant differences among mean ages, weights, and CL counts. We conducted Chi-square tests to determine if sex ratios differed significantly from parity. We used the 95 percent Least Squares Multiple Range (LSD) test to determine differences among units and sampling years for age, weight, and CL counts when significant differences were detected using ANOVA. Coyotes were grouped into two age classes: juveniles (<1 year old) and adults ($\geq$1 year of age) for analysis of weight and CL counts. We used a P-value ≤ 0.05 to determine whether differences were significant for all tests.

Results

CMR/BLM Unit

Two hundred, ninety-six coyotes were killed on the CMR/BLM unit by aerial gunning, trapping, and shooting from the ground from 1993 through 1996. A helicopter was used to collect 294 coyotes that averaged 15.5 coyotes/day. Total coyote harvest during 1993 and 1994 on the larger 1640-km^2area averaged 0.04 coyotes/km^2/ year. Subsequent collections on the 140-km^2area increased in intensity and averaged 0.64 coyotes/km^2/year. We determined sex for 284 carcasses, which had a combined sex ratio of 142 males and 142 females. Slight variation occurred among years but sex ratio was not different from parity for any year ($P > 0.05$) (Table 1).

Table 1. Sex ratios of coyotes collected on the CMR/BLM, FB, and HD 530 units from 1993 through 1999. NC indicates a year when collections did not occur.

Year		1993	1994	1995	1996	1997	1998	1999	Total
CMR/BLM	Female	28	32	50	32	NC	NC	NC	142
	Male	25	30	51	36	NC	NC	NC	142
FB	Female	15	15	9	16	21	40	NC	116
	Male	14	18	11	16	25	41	NC	125
HD 530	Female	NC	NC	NC	NC	18	12	7	37
	Male	NC	NC	NC	NC	29	14	10	53

Age structure for all years combined was 37 percent juveniles (105), 22 percent yearlings (63), and 41 percent adults (116). Average age, pooled for 1993, 1995, and 1996, was 2.52 for females (n = 142) and 2.25 for males (n = 142) but was not different (P = 0.33, F = 0.96, df = 283). Mean age, with males and females pooled for each year, ranged from a low of 2.1 years in 1994 (n = 62) to a high of 2.7 years in 1996 (n = 68). However, mean age did not differ among years (P = 0.37, F = 1.06, df = 283) (Fig. 2).

Mean weight of adult males collected during summer/fall was significantly greater ($\bar{x}$ = 13.5 kg, n = 40) than those of winter/spring ($\bar{x}$ = 12.6 kg, n = 24) (P = 0.03, t = 4.56, df = 218). Mean weight of adult males increased with successive years but did not differ significantly (P = 0.13, F = 1.98, df = 63) (Fig. 3). Mean weight of adult females did not differ (P = 0.48, t = 0.52, df = 82) between winter/spring ($\bar{x}$= 11.2 kg, n = 32) and summer/fall ($\bar{x}$= 11.4 kg, n = 51) or among years (P = 0.51, F = 0.77, df = 82) (Fig. 4). Mean weight of adult females was lower than the mean for adult males (P < 0.05, F = 64.72, df = 146) when all years and seasons were pooled.

Mean weight for pooled male and female juveniles differed among years for winter/spring (P = 0.03, F = 3.80, df = 34) and summer/fall (P= 0.03, F = 4.11, df = 36). Mean juvenile weight for winter/spring ranged from 10.6 kg in 1996 (n = 6) to 12.1 kg in 1994 (n = 15) and was consistently greater than summer/fall weight which ranged from 6.6 kg (n = 10) in 1994 to 8.4 kg (n = 8) in 1995.

Mean number of CL scars on ovaries from breeding age females did not differ among years for the CMR/BLM unit (P = 0.33, F = 1.11, df = 81). Mean CL counts ranged from 2.21 in 1993 (n = 24) to 1.15 CL per female in 1995 (n = 22) (Fig. 5). No CL were observed in the nine juveniles examined in 1993. One of 11 ovary pairs from juveniles in 1995 and one of seven ovary pairs in 1996 contained CL. Juveniles with CL present comprised 4.5 percent of the 1995 (n = 22) and 3.8 percent of the 1996 (n =26) reproductive age females harvested. Juveniles were prevalent in the harvest, comprising 37.5 percent, 50.0 percent, and 26.9 percent of the reproductive age females examined on the CMR/BLM unit in 1993, 1995 and 1996, respectively (Table 2), but did not contribute substantially to reproduction.

FB Unit

We determined the sex of 241 of 252 coyotes killed by aerial hunting in the FB unit. Helicopter harvest rates over the six years of the study averaged 16.8 coyotes/day (n = 241) resulting in a yearly average take of 0.02 coyotes/km^2. The pooled sex ratio for all years (125 males: 116 females)

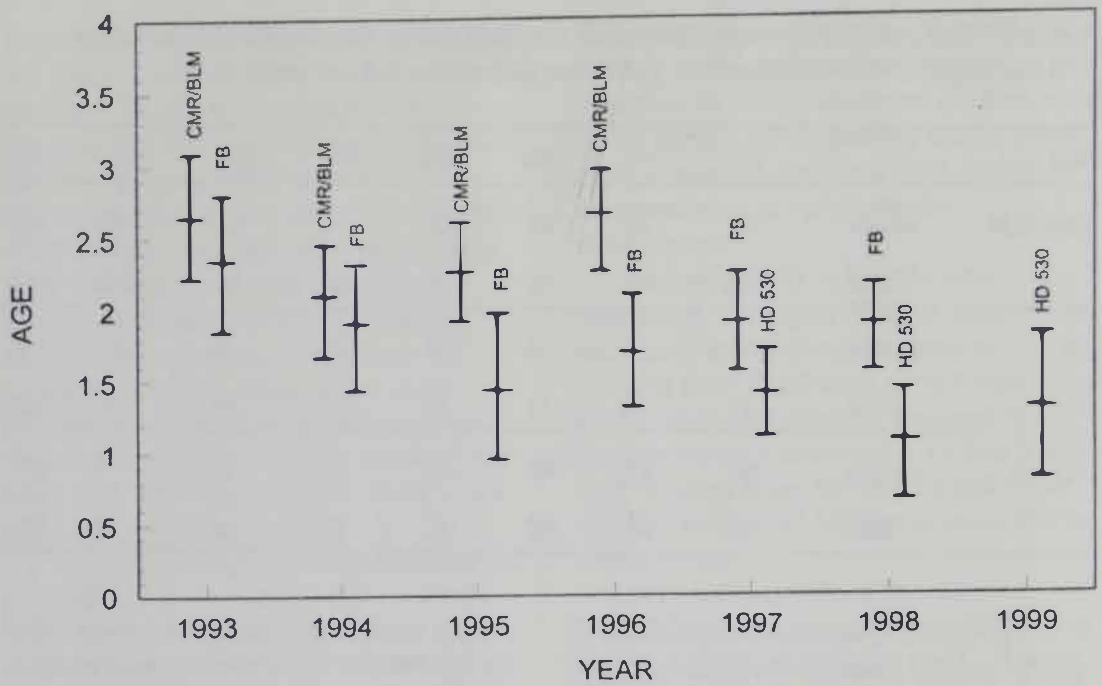

Figure 2. Mean ages and 95 percent confidence intervals of coyotes collected on the CMR/ BLM, FB, and HD 530 study units. Male and female coyotes were pooled within each year.

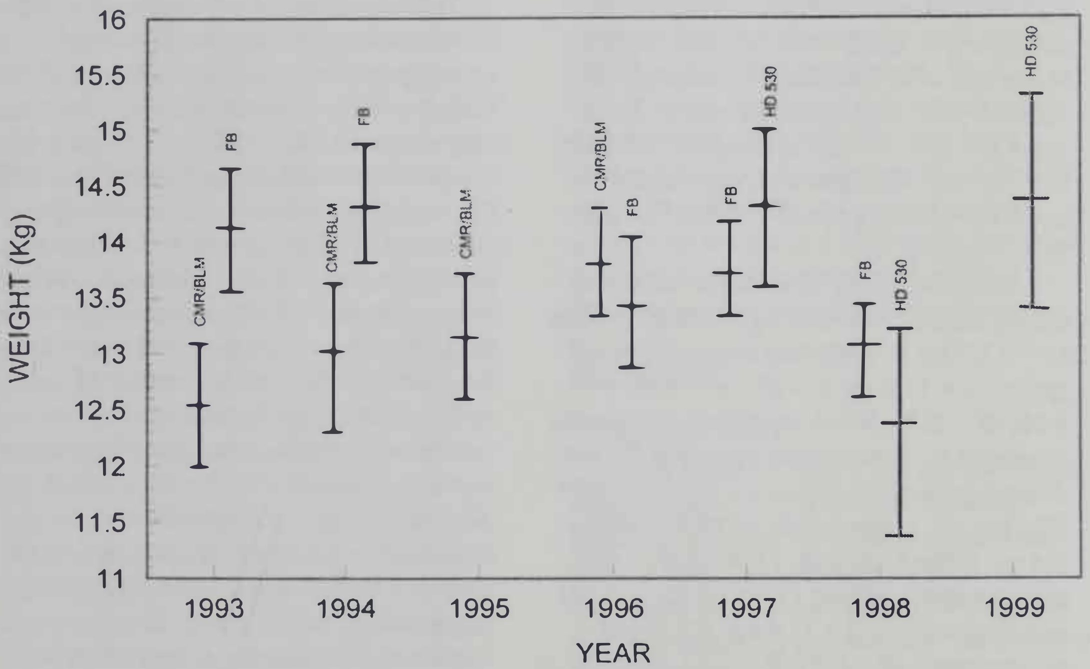

Figure 3. Mean weights and 95 percent confidence intervals for adult male coyotes collected on the CMR/BLM, FB, and HD 530 study units.

did not differ from parity ($P > 0.05$, $X^2 = 0.336$, df = 1). Sex ratio also did not differ among years ($P > 0.05$) (Table 1).

Juveniles, yearlings, and adults comprised 39, 25, and 36 percent, respectively, of the 232 coyotes aged. Mean age for females ($\bar{x} = 1.93$, $n = 113$) was not different than for males ($\bar{x} = 1.86$, $n = 119$) ($P = 0.74$, $t = 0.11$, df = 231) when all years were pooled. Mean age for all coyotes collected during 1993 was 2.33 ($n = 29$) years. Mean age then decreased by year

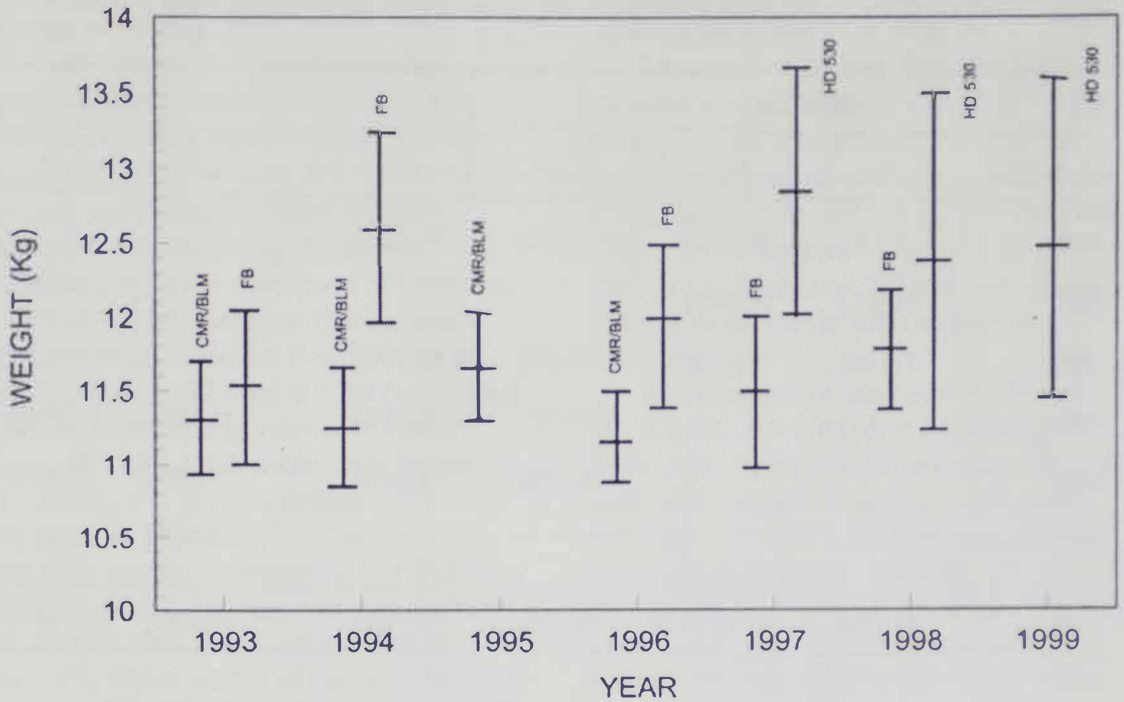

Figure 4. Mean weights and 95 percent confidence intervals by year for adult female coyotes collected on the CMR/BLM, FB, and HD 530 study units.

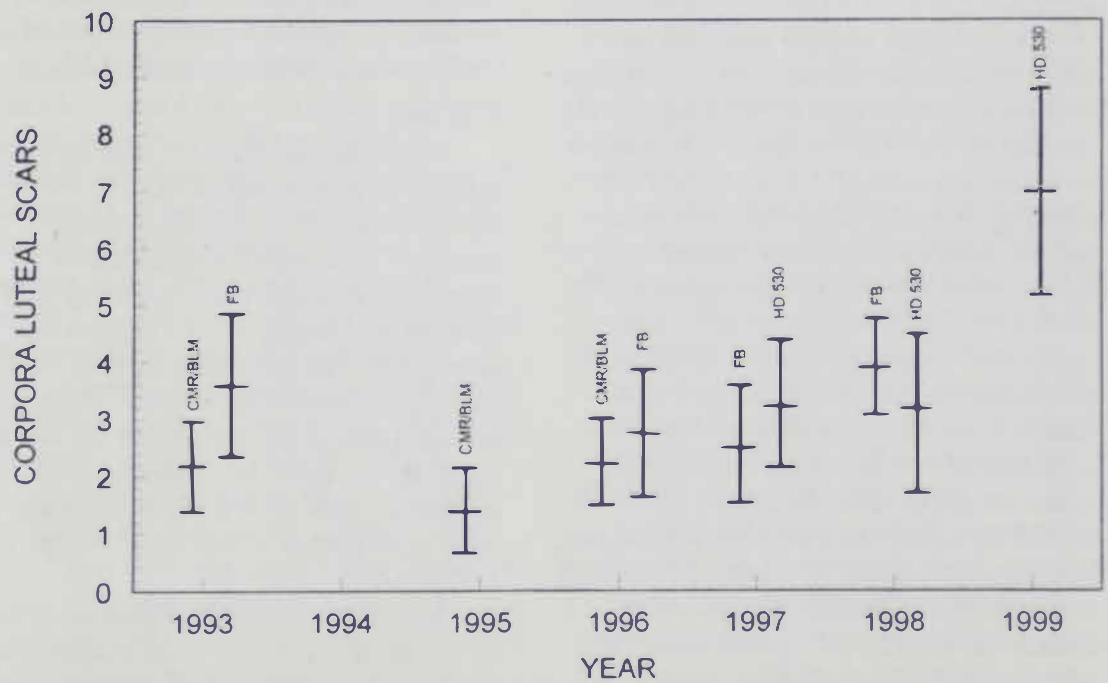

Figure 5. Mean number of CL and 95 percent confidence intervals observed in females collected on the CMR/BLM, FB, and HD 530 study units.

Table 2. Reproductive tracts examined by age class for the CMR/BLM, FB and HD 530 units. The percentage of ovaries containing CL scars is presented within the ( ).

Unit	CMR/BLM		FB		HD 530	
Age Class	JUV.	AD.	JUV.	AD.	JUV.	AD.
1993	9 (0%)	15 (60%)	2 (0%)	11 (82%)	-	-
1995	11 (9%)	11 (54%)	-	-	-	-
1996	7 (14%)	19 (79%)	5 (0%)	11 (73%)	-	-
1997	-	-	10 (0%)	9 (89%)	11 (36%)	7 (100%)
1998	-	-	11 (18%)	18 (94%)	8 (38%)	4 (100%)
1999	-	-	-	-	3 (67%)	4 (100%)
TOTAL	27 (7%)	45 (67%)	28 (7%)	49 (86%)	22 (41%)	15 (100%)

until reaching a low of 1.45 years in 1995 (n =20) and rebounded in 1997 (n = 46) and 1998 (n = 73) to 1.91 years of age. Differences among years were not significant (P = 0.59, F = 0.75, df = 231) (Fig. 2).

Mean weight of adult males did not differ between winter/spring ($\bar{x}$ = 13.8 kg, n = 46) and summer/fall ($\bar{x}$ = 13.2 kg, n = 16) seasons (P = 0.07, t = 3.30, df = 61) but did differ among years (P = 0.04, F = 2.77, df = 61) (Fig. 3). Mean weight of adult females did not differ between sampling season (P = 0.06, t = 3.72, df = 65) or among years (P = 0.33, F = 1.17, df = 65) (Fig. 4). Adult males ($\bar{x}$ = 13.6 kg, n = 62) weighed more than adult females ($\bar{x}$ = 11. 8 kg, n = 66) when all years and sampling seasons were combined (P < 0.05, t = 68.76, df = 127). Mean weight of juveniles ranged from 11.2 to 12.3 kg during winter/spring, but did not differ among years (P = 0.1401, F = 1.81, df = 62). Juveniles collected in 1997 were heavier ($\bar{x}$ = 8.3 kg, n =3) than those collected in 1998 ($\bar{x}$ = 6.6 kg, n = 16) during summer/fall (P < 0.05).

A total of 77 breeding age females were examined from the FB unit (Table 2). Mean CL counts varied from 2.5 in 1997 (n = 19) to 3.9 in 1998 (n = 29) (Fig. 5), but differences among years were not significant (P = 0.40, F=0.99, df = 76). Juveniles comprised 15, 31, 53, and 38 percent of the females sampled in 1993, 1996, 1997 and 1998, respectively. We observed no evidence of reproduction by juveniles except during 1998 when 2 of 11 (18%) juvenile ovaries contained CL.

HD 530

We examined 90 of 315 coyotes killed through aerial gunning in HD 530 from 1997 through 1999. The 90 coyotes examined were killed with the use of a helicopter, averaged six coyotes/day, and resulted in a density of 0.04 coyotes/km^2 killed/year. The remaining coyotes were shot from a fixed-wing aircraft. Males predominated in the sample (59 %), but sex ratios did not differ from parity within individual years (P > 0.05) or when all years were pooled (P > 0.05, X^2 = 2.84, df = 1) (Table 1).

Juveniles comprised 62 percent of the 90 carcasses examined, while yearlings and adults made up 20 percent and 18 percent, respectively. Mean age of males (1.16, n = 53) was not different (P = 0.23, t = 1.44, df = 89) than mean age of females (1.53, n = 37). Mean age of coyotes ranged from a low of 1.08 in 1998 to a high of 1.44 in 1997 but did not differ ($P = 0.59$, F = 0.52, df = 89) among years (Fig. 2).

HD 530 was not sampled during summer/fall precluding comparisons between seasons. Mean weights of adult males differed ($P = 0.04$, F = 3.91, df = 18) among years (Fig. 3). Based on LSD analysis, weights during 1998 were significantly lower than those of 1997 and 1999 ($P < 0.05$). Mean weight for adult females (Fig. 4) ranged from 12.4 kg in 1998 ($n = 4$) to 12.8 kg in 1997 ($n = 7$) and did not differ among years ($P = 0.853$, F = 0.16, df = 14). Adult males were heavier ($\bar{x}$ = 13.8 kg, $n = 15$) than females ($\bar{x}$ = 12.6 kg, $n = 19$) ($P = 0.03$, F = 5.44, df = 33). Juvenile coyotes collected on HD 530 from 1997 through 1999 ranged in weight from 11.2 kg in 1998 ($n = 17$) to 12.6 kg in 1997 ($n = 29$). Mean weight of juveniles differed among years ($P = 0.02$, F = 4.18, df = 53). Juveniles harvested in 1997 were significantly heavier than in 1998 ($P < 0.05$), but juveniles harvested in 1999 did not differ from either 1997 or 1998.

We examined 37 female reproductive tracts from HD 530 (Table 2). Juveniles comprised 59 percent of the total sample and 61, 67 and 43 percent of the ovaries examined in 1997, 1998 and 1999, respectively. Juvenile ovaries containing CL comprised 36 percent of the 1997 ($n = 11$), 43 percent of the 1998 ($n = 7$), and 33 percent of the 1999 ($n = 6$) samples in which CL were observed. The percentage of the juvenile cohort with CL present in ovaries increased annually from 36 percent in 1997 ($n = 11$) to 38 percent in 1998 ($n = 8$), and 67 percent in 1999 ($n = 3$). CL counts differed among years ($P = 0.03$, F = 3.75, df = 36) (Fig. 5). CL counts in 1999 ($\bar{x}$= 7.0, $n = 7$) were greater than 1997 ($\bar{x}$ = 3.3, $n = 18$) and 1998 ($\bar{x}$ = 3.2, $n = 12$) ($P < 0.05$), but 1997 and 1998 did not differ ($P > 0.05$). However, sample sizes were small.

Unit Comparison

Males predominated on FB and HD 530 when all years were pooled; however, sex ratios did not differ from parity ($P > 0.05$). Sex ratios of harvested coyotes were equal on the CMR/BLM unit.

Mean age of coyotes from the three units differed ($P < 0.05$, F=11.17, df =607) when all years were pooled. HD 530 had the lowest cumulative mean age of 1.31 ($n = 90$), followed by FB at 1.90 ($n = 241$) and CMR/BLM with a mean age of 2.30 ($n = 284$) years. Based on LSD analysis all units differed significantly from each other ($P < 0.05$) (Fig. 6).

Mean weight of adult males differed ($P_m = 0.002$, F = 6.64, df = 89) among the three units during the winter/spring when all years were pooled. Weight of adult males was lower ($P < 0.05$) for coyotes collected on the CMR/BLM ($\bar{x}$ = 12.6 kg, $n = 32$) than on FB ($\bar{x}$ = 13.8 kg, $n = 54$) or HD 530 ($\bar{x}$ = 13.8 kg, $n = 19$) but did not differ between FB and HD 530 ($P > 0.05$). Mean weight of adult females also differed among the three units during winter/spring (P_f= 0.002, F = 6.97, df = 100). Mean weight of adult females on the CMR/BLM ($\bar{x}$ = 11.2 kg, $n = 32$) was lighter during winter/spring then those from the FB ($\bar{x}$ = 11.9 kg, $n = 54$) or HD 530 ($\bar{x}$ = 12.6 kg, $n = 15$) units ($P < 0.05$). Mean weight of adult females during winter/spring on FB and HD 530 did not differ ($P > 0.05$) from mean weight of adult males.

Mean weight of neither adult females nor adult males differed between CMR/BLM and FB during summer/fall ($P_f = 0.52$, $t = 0.42$, df = 62; $P_m = 0.46$, $t = 0.55$, df = 55). Mean weight of adult females was 11.4 kg ($n = 51$) on CMR/BLM and 11.2 ($n = 12$) on FB. Adult male weights averaged 13.5 kg ($n = 40$) and 13.2 ($n = 16$) on the CMR/BLM and FB respectively.

Mean CL counts differed among units when all years of collection were pooled ($P = 0.003$, F = 6.18, df = 185). Female coyotes on the CMR/BLM unit had a mean CL count of 2.0/female, the lowest among the three units. Mean CL counts were 3.3/female on FB and 3.9/female in HD 530 (Fig. 7). FB and HD 530 did not differ from each other ($P > 0.05$) but they did differ from CMR/BLM ($P < 0.05$).

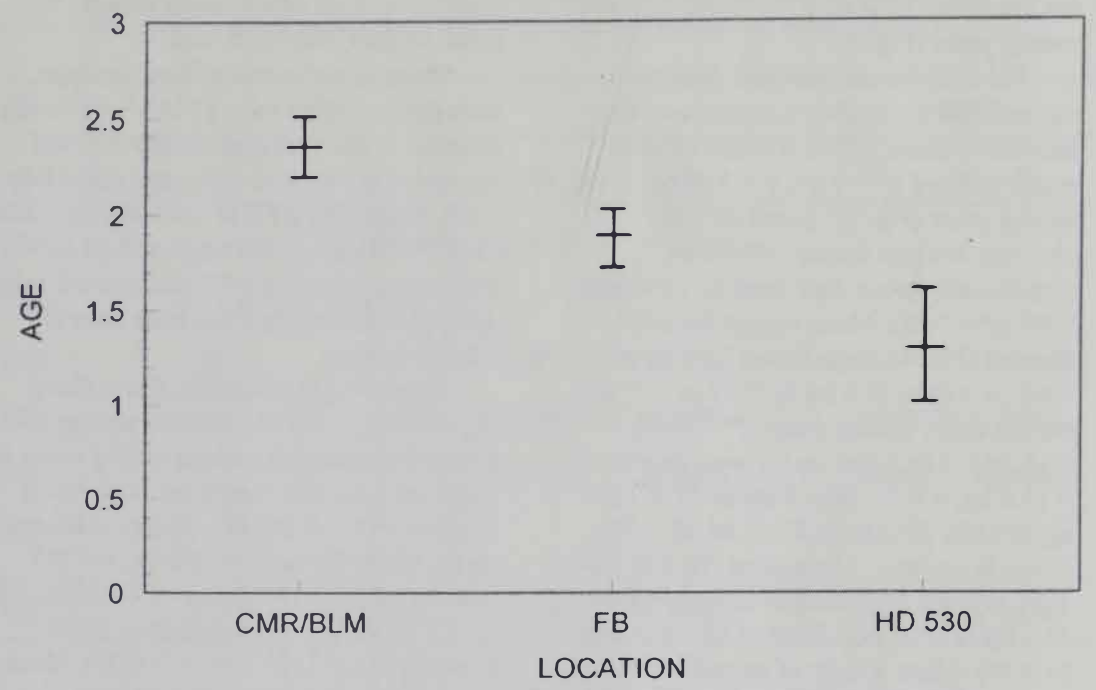

Figure 6. Mean ages of coyotes collected within CMR/BLM, FB, and HD 530 units, all years pooled.

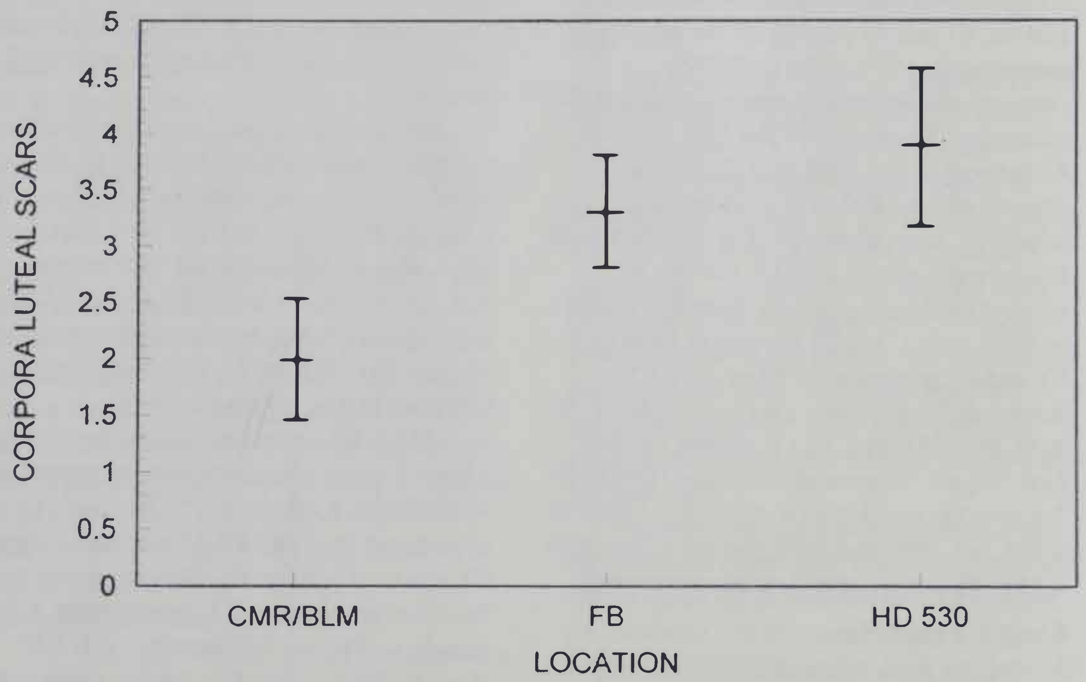

Figure 7. Mean number of CL produced by unit. All years of collection for individual units were pooled.

Discussion

Pyrah (1984) observed population densities of coyotes ranging from 0.15 to 0.26/km^2 in the Missouri River "breaks" of north-central Montana and lower densities of 0.07 to 0.20/km^2 in adjoining prairie habitats. The CMR/BLM and HD 530 units contained both "breaks" and prairie habitats (HD 530 breaks were associated with the Mussellshell River). The FB unit consisted primarily of prairie habitat interspersed with riparian areas and timbered buttes. Average daily helicopter harvest rates suggest densities were greatest on FB and the CMR/BLM, both of which had a harvest rate of more than twice that observed on HD 530.

Predator control conducted within these habitats yielded three different scenarios. The CMR/BLM was a large area (1620 km^2) with light coyote harvests (0.04/km^2) for two years then reduced to a small area (140 km^2) with more intensive control, averaging 90.5 coyotes (0.65/km^2) for the last two years. Initial coyote densities likely were high due to good habitat, abundant prey, and lack of prior control activities. FB was a large area (2460 km^2) initially sampled once a year with an average of 28.5 coyotes (0.01/km^2) collected/year. Predator control was intensified, conducted twice a year, and an average of 69 coyotes (0.03/km^2) were killed/year for the last two years. An effort was made to kill all coyotes during sampling sessions during the last two years of the study. Additional mortality occurred opportunistically by tribal members shooting coyotes from the ground. Populations appeared moderately high due to fair habitat, abundant prey, and limited control activities. HD 530 was a large area (2679 km^2) sampled intensively for three years, the harvest averaged 105 coyotes (0.04/km^2) per year. Although habitat was good and prey abundant, predator control activities prior to initiation of the study were more intensive than the other two areas, possibly resulting in a lower population density.

Comparisons among the three scenarios suggested that the CMR/BLM and its primarily "breaks" habitat was characterized by older coyotes that weighed less and were not as reproductively active as similar-age females observed in other units. The prairie-dominated FB unit produced coyotes of greater weight, younger age, and higher reproductive activity than the CMR/BLM. Reproductive rates exceeded those in the CMR/BLM but were lower, although not significantly, than those in HD 530. Coyotes in HD 530 that included a mixture of "breaks," prairie, and agriculture generally were younger but weighed more than coyotes in the other two units. Production of CL and number of breeding juveniles were highest in HD 530.

We observed little change in mean coyote age or sex ratio within each unit. Control activities did not significantly increase or decrease the age structure of harvested coyotes suggesting that population age structure within individual units did not change during the study. Mean weight of adult male coyotes varied over time for each study unit but apparently unrelated to control activities. Mean weight of adult female coyotes within individual units did not significantly change over the course of the study. Corpora lutea counts did not differ over time on either the CMR/BLM or FB units, and few juveniles bred successfully throughout the study. On the HD 530 unit, however, CL production increased significantly during the final year of the study, and the percentage of breeding juveniles increased over the three years of study.

Limited variation observed in age, weight, and reproduction within the CMR/BLM and FB, suggested relatively consistent environmental conditions and prey abundance for surviving coyotes. Control actions, limited due to size of the area (CMR/BLM) or intensity of kill (FB), were not sufficient to reduce competition for resources to a level that we would expect to influence reproduction within these units. Immigration likely helped replace coyote numbers within the study units and thus, maintained coyote densities.

In HD 530 harvested coyotes maintained relatively stable ages and weights throughout the study. CL counts and the number of breeding juveniles generally increased over the three years of study, but small sample sizes reduced our confidence in the results. Changes in prey abundance also could have contributed to an observed increase in CL production. Whether prey was more abundant because of favorable environmental conditions or decreased competition resulting from reduced coyote numbers was not determined. Assuming that environmental conditions remained stable, an increase in juvenile breeding activity and mean CL production may have directly resulted from intense coyote control and limited immigration.

Pyrah (1984) observed dispersal of both juvenile and adult coyotes. Juveniles dispersed greater distances and in greater numbers than adults (Pyrah 1984). Reduction in densities of the coyote population in the CMR/BLM and FB units may have stimulated emigration of what Pyrah (1984) described as adult den supernumeraries (from surrounding areas) resulting in fairly rapid replacement of the adult portion of the populations following control. Immigration likely occurred in HD 530, but given its large size and ongoing control activities in adjacent areas as the result of livestock depredation, movement into the study unit may have been limited.

Although many conditions can affect reproduction, others have demonstrated that abundance of food directly influences coyote productivity. Clark (1972) and Todd et al. (1981) observed a correlation of coyote density, percentage of breeding females, and litter size with prey density. Likewise, reducing coyote density through predator control led to increased densities or survivorship in prey species such as antelope (Smith et al. 1986, Willis et al. 1993, and Newell 2000) and some rodent species (Henke and Bryant 1999). Findings of these studies suggest that coyote reduction resulted in increased prey densities, which in turn should result in increased coyote reproduction. Initiation of coyote control programs could bring about a cycle in which increased coyote control would increase coyote reproduction until a physiological maximum is reached. Theoretically, an increase in coyote reproduction should be evident, provided control efforts successfully reduce coyote numbers to the point where competition for prey is impacted.

Removal efforts on the CMR/BLM and FB units probably were not effective in lowering coyote densities below that which could be compensated by immigration and normal levels of reproduction. Therefore, reproduction did not increase. The higher rate of reproduction in HD 530 suggested control efforts affected coyote densities that resulted in increased abundance of prey species for surviving and immigrating coyotes. Higher CL counts and a greater percentage of juvenile coyotes reproducing in that unit may be at least partially attributed to intensive coyote control.

Although predator control has occasionally been successful in decreasing losses of domestic livestock (U.S. Department of the Interior 1978, Wagner and Conover 1999), success of programs intended to increase survival of wild ungulates has been less certain. Studies done in Montana and elsewhere indicated a potential benefit for antelope and deer populations (Austin et al. 1974, Beasom 1974, Smith et al. 1986, Newell 2000). Electric fences (Matchett 1997) and lethal control (Vosburgh and Stoneberg 1998) were used in an effort to protect black-footed ferrets within the ferret recovery area in Montana. Despite continued coyote control, Montana coyote populations have persisted. Increased reproductive potential due to decreased coyote population density may have been one reason for the coyote's ability to maintain a population over a large area. However, based on the results of this study, reproduction only increased under intensive control. Limited control efforts may merely compensate for natural mortality.

To effectively increase survivorship of prey species, control efforts need to be intensive enough to reduce the coyote population below levels compensable by immigration and increases in reproduction. Coyote control conducted over small areas or of limited intensity should only be undertaken for programs that require a short window of predator control. Programs not aimed at coyote control but which require the killing of coyotes, such as disease monitoring, may be conducted on a limited scale without the concern of increasing overall coyote reproduction or greatly influencing age structure of the population.

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