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Effects of removal on a lightly exploited coyote population in eastern Nevada

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Abstract: Coyote (*Canis latrans*) removal is a common, yet controversial, management practice to increase game populations throughout the West. I studied the effect of removal on coyote populations in eastern Nevada from 2004 to 2008 and reviewed 27 available publications to determine the level of human exploitation on my study populations. Removals were performed by USDA Wildlife Services (WS) to benefit game populations and involved the use of trapping, neck snaring, and ground and aerial shooting. To determine if the removal had an effect on the coyote populations, I measured 3 parameters: the presence or absence of skewed sex ratios; proportions of juveniles in the population; and average adult age. Sex was determined at the time of ground removal efforts. Canine teeth were acquired from 96% of coyotes removed from the ground; cementum annuli analysis was performed for aging. Due to WS removal efforts prior to 2004, coyote populations likely were in a lightly exploited state when the study began. Where removal efforts were the highest (65% of total), there was a resulting decline in the mean age of coyotes, an increase in percentage of juveniles in the population, and a skewed sex ratio, indicating that this population may be heavily exploited. No change in these parameters occurred in areas where 35% of the total removals occurred. This information should help wildlife managers understand the exploitation levels of their own coyote populations.

Key words: *Canis latrans,* exploited population, human–wildlife conflicts, mule deer, Nevada, removal, Wildlife Services

Predator management was a practice brought to North America by Europeans. As settlers moved west across North America, predators were reduced in numbers or extirpated from the landscape through shooting, trapping, and use of toxicants (Kellert 1985, Harris and Saunders 1993). Before predator removal efforts began in North America, the gray wolf (*Canis lupus*) and red wolf (*Canis rufus*) inhabited most of the continent (Wilson et al. 2003), confining the coyote (*Canis latrans;* Figure 1) to open plains and arid regions (Schmidt 1986). As wolves were extirpated, coyotes became among the most widely distributed predators in North America (Bekoff and Wells 1986).

Though coyotes are considered facultative omnivores, they consume whatever is readily available, including hunted prey, carrion, vegetation, and mast (Green et al. 1994, Ballard et al. 2001, Hurley et al. 2011). Their diet can range from entirely herbivorous to carnivorous (Gier 1968, 1975). Coyotes forage in areas where they most frequently detect prey and have the highest capture rates (Gese et al. 1996, Bartel and Knowlton 2005). Although half of coyotes' diet may consist of plant and insect matter during the warmer months of the year, they depend primarily upon mammals during the cooler portions of the year (Andelt 1987, Hamlin 1997, Hernández et al. 2002). Because coyotes prey on game species, predator control programs frequently target them as a means of increasing game species populations.

Population declines and lags in population recovery for ungulates, such as caribou (*Cervus elaphus*), moose (*Alces alces)*, and pronghorn (*Antilocapra americana*), have been attributed to wolves and mountain lions (*Puma concolor*) predation. Controlling these predators' numbers has putatively reversed these trends (Gasaway et al. 1983, Smith et al. 1986, Boertje et al. 1996), but this relationship has not been demonstrated in coyote–mule deer (*Odocoileus hemionus*) systems (VanBallenberghe and Ballard 1994, Ballard et al. 2001, Brown and Conover 2011, Hurley et al. 2011). Lack of evidence identifying coyotes as a source of mule deer population declines may be attributed to inadequate coyote removal levels or insufficient study designs; a long time frame and large sample size are needed to study these complex predator–prey relationships (Connolly 1978*a*, Ballard et al. 2001, Hurley et al. 2011).

Although there is a lack of evidence that coyotes can lower mule deer populations, coyotes do consume mule deer, fawns in particular (Hamlin et al. 1984, Voigt and Berg 1987, Green et al. 1994). Coyote predation has been documented to reduce mule deer fawn survival in north-central Montana (Hamlin et al. 1984). While there is no evidence that coyotes reduce mule deer populations that currently are at carrying capacity, some studies suggest that they may slow the recovery of populations that are already below carrying capacity (Connolly 1978*a*, Ballard et al. 2001, Hurley et al. 2011). This has resulted in a controversy within the wildlife management community on whether coyote removal can prevent declines in mule deer populations, facilitate population recoveries, and be useful as a management tool (Connolly 1978*a*, Skogland 1991, Bartmann et al. 1992, Ballard et al. 2001).

Despite uncertainty regarding the benefits of coyote removal, it remains a popular program in many states (Bartel and Brunson 2003). The Nevada Department of Wildlife (NDOW) spent $102,241 and removed 357 coyotes as part of predator removal efforts on the Statewide Deer and Multi-Species Enhancement Project during the 2011 to 2012 fiscal year. In addition, NDOW spent another $264,977 in 2012 on various predator removal and observation programs around the state to increase game species populations (Nevada Department of Wildlife 2011).

Coyote removal frequently occurs with the goal of reducing the coyote population; often the desired result of reduction is not achieved; instead the population dynamics are changed (e.g., average age; Ballard et al. 2001). Regular anthropomorphic mortalities, such as aerial shooting, trapping, poisoning, vehicle collisions, and shooting from the ground can be significant sources of coyote mortality (Gese et al. 1989, Hurley et al. 2011). In a study within Grand Teton National Park, Wyoming, coyotes living entirely in the park had a 22% human-caused mortality rate; coyotes living outside the park had a 78% human-caused mortality rate (Tzilkowski and Knowlton 1979). Removal efforts not only can change the population dynamics, but also can modify coyote behavior and movement (Knowlton and Gese 1995). Coyote populations respond to a decrease in population by increasing their productivity and the proportion of females breeding (Jean and Bergeron 1984, Andelt 1987, Knowlton and Gese 1995, Knowlton et al. 1999). For example, Knowlton (1972) found that as coyote removal efforts intensified, the average litter size increased from 4.3 to 6.9.

Figure 1. Coyote (*Canis latrans*) in a wooded environment (*Photo courtesy U.S. Fish and Wildlife Service*).

Human activities can result in different levels of exploitation within coyote populations. Many authors have defined their coyote study population as exploited, citing factors, such as low survival, high proportion of pups in the population, high number of uterine swellings, high number of breeding females, and low average age (Gese et al. 1989, Windberg 1995, Crabtree and Sheldon 1999, Dumond and Villard 2000). Authors at times contradict one another; Gese et al. (1989) refer to their coyote population as lightly exploited while others refer to it as unexploited (Kamler and Gipson 2004, Nelson and Lloyd 2005). Windberg et al. (1985) defined their population as lightly exploited, while Gese et al. (1989) defined it as heavily exploited. Additionally, some authors give a level of exploitation in their coyote population without providing an explanation for how they made this determination (Howard and DelFrate 1991, Sacks et al. 1999, Dumond and Villard 2000).

Despite contradictions in the literature regarding the definition of different levels of exploitation, there is overall agreement on the impact of increasing exploitation levels.

Crabtree and Sheldon (1999) have one of the most detailed descriptions of human-exploited coyote populations. They cite the amount of human-related mortality, pup survival, average adult age, and proportions of pups in the populations as factors that vary in direct response to exploitation (Table 1). In addition, (Gese 2005), Knowlton (1972), and Windberg (1995) included further metrics for quantifying exploitation. Gese (2005) reported sex ratios of coyote litters changing from 34 to 59% female after 2 years of removal. Knowlton (1972) found that heavily exploited populations had more breeding females and larger litters and that 65% of catches in intensive control areas were female. Windberg (1995) considered a population to be lightly exploited when 34% of the study population consisted of juveniles.

I investigated the results of a 5-year coyote removal project conducted during 2004 to 2008 in eastern Nevada by USDA Wildlife Services (WS). My objectives were to measure the response of coyote populations to removal efforts to quantify the level of exploitation of 2 neighboring coyote populations. This report will help NDOW, as well as other state and federal agencies, make future coyote removal decisions and plans for predator management.

Study area

This project was conducted in southeastern Nevada in Game Management Units (GMU) 231 (4,609 km^2) and 222 (2,467 km^2). The 2 units were bordered by Utah to the east and by U.S. highway 93 to the west. The northeast corner of the study sites were bordered by Great Basin National Park; GMU 231 is in Lincoln and White Pine counties, and GMU 222 is in Lincoln, White Pine, and Nye counties. Elevations ranged from 1,440 to 3,344 m. Yearly mean precipitation ranged from 5 to 30 cm, and mean monthly low temperatures ranged from -17 to 10° C; mean monthly high temperatures ranged from 5 to 35° C (Prism Climate Group 2014). Climate and vegetation were characteristic of the temperate desert division as described by Bailey (2009).

Vegetation at both GMUs was dominated at lower elevations by big sagebrush (*Artemisia tridentata*), basin big sagebrush (*A.t. tridentata*), Wyoming big sagebrush (*A.t. wyomingensis*), low sagebrush (*A.t. arbuscula*), black sagebrush (*A. nova*), white sagebrush (*A. ludoviciana*), Utah juniper (*Juniperus osteosperma*), Rocky Mountain juniper (*J. scopulorum*), Antelope bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothanmus* spp.). At higher elevations vegetation consisted of these species, as well as mountain big sagebrush (*A.t. vaseyana*), quaking aspen (*Populus tremuloides*), singleleaf piñon (*Pinus monophylla*), limber pine (*P. flexilis*), western bristlecone pine (*P. longaeva*), Jeffrey pine (*P. jeffreyi*), ponderosa pine (*P. ponderosa*), white fir (*Abies concolor*), Engelmann spruce (*Picea engelmannii),* Douglas fir (*Pseudotsug amenziesii*), dwarf juniper (*Juniperu* spp.), elderberry (*Sambucu* sp.), serviceberry (*Amelanchier* sp.), Nevada ephedra (*Ephedra nevadensis*), littleleaf mountain mahogany (*Cercocarpus intricatus*), and curlleaf mountain mahogany (*Cercocarpus ledifolius*). Riparian areas consisted of wild rose (*Rosa woodsii*), water birch (*Betula occidentalis*), chokecherry (*Prunus virginiana*), cottonwood (*Populus* spp.), and horsetail (*Equisetum* spp.).

Methods

Coyote removal

Wildlife Services personnel conducted all coyote removals during this study through a combination of ground- and aerial-removal techniques. Ground-removal efforts included foothold traps, snares, denning, and shooting. To increase shooting success, WS personnel used electronic calls, sirens, mouth calling,

Table 1. Factors determining level of exploitation in a coyote population (Crabtree and Sheldon 1999).

Level of exploitation[a]	Annual removal by humans (%)	Pup survival (%)	Average adult age
None to lightly	0–24	20–60	3–4 years
Moderately	25–49	50–90	2 years
Heavily	≥50	70–100	50% yearlings

[a]Crabtree and Sheldon(1999).

and decoy dogs. Aerial removal efforts were conducted from a fixed-wing aircraft. A combination of sirens, electronic calls, and mouth calling were conducted prior to flying to acquire the approximate location of coyotes; maximizing flight hour success. Aerial removal for this project did not begin until July 2006 for GMU 231 and October 2007 for GMU 222. Prior to those dates only ground removals occurred. Removal efforts were performed year round, weather permitting, in the portions of GMUs considered mule deer fawning and range habitat as determined by WS. (J. Bennett, Wildlife Services, personal communication).

Determining coyote sex and age

During ground-removal efforts, WS recorded coordinates of removal sites, sex of the individual removed, and method of removal. A lower canine tooth was extracted from ground-removal coyote carcasses by WS for age estimation. All collected teeth were sent to Matson's Laboratory (Milltown, Montana) for coyote age estimation using cementum annuli analysis. Age data were sent directly from Matson's Lab to NDOW. Because of the nature of aerial removal, only GPS locations of kills were collected by WS.

I received data from NDOW with a oral and written descriptions of the project and data collection methods (T. Wasley, Nevada Deparment of Wildlife, personal communication). I arranged the data by GMU (222 and 231), date of kill, sex, age at time of death, and removal type. GMU 222 and 231 were similar in topography, deer, and alternate prey abundance, and habitat types (M. Scott, Nevada Department of Wildlife, personal communication). Therefore, I assumed that GMU 222 and 231 had similar coyote population demographics and age structures.

Determining degree of exploitation

Crabtree and Sheldon's (1999) criteria for determining the degree of exploitation (Table 1), include knowledge of annual human removal, pup survival, and average adult age. Because annual human removal and pups survival data were not available for the study populations, I reported other parameters that additional authors used to determine the level of exploitation, including percentage of juveniles removed (Windberg 1995), sex ratios of removed animals, adult survival, juvenile mortality, and adult mortality (Knowlton 1972, Gese et al. 1989). I then reviewed 27 published studies (Table 2) and reported their study population parameters used to define the level of exploitation. To determine the level of exploitation in my 2 study populations, I considered 3 parameters: the presence or absence of skewed sex ratios; changes in the proportion of juveniles in the population over time; and changes in average age over time. I selected these 3 parameters because they were the only ones available that were commonly cited in other publications.

Season definition

Dates were associated with all coyotes collected and reported during the study. I divided all coyotes by season and year for analysis: breeding and gestation from December 16 to April 15; pup rearing from April 16 to August 15; and dispersal from August 16 to December 15 (Gese 2005). Thus, a year started on December 16 of the previous calendar year and ended December 15 of the current calendar year. The exceptions are 2004, which started January 1, 2004, and 2008, which ended December 31, 2008.

Stastical analysis

Coyote population assessment

To determine the similarity between the 2 GMUs' study parameters, I conducted a Chi-square goodness-of-fit test on average adult age of coyotes and proportion of juveniles in each GMU for the first year that removal efforts took place (2004). I conducted a chi-square test of independence separately on coyotes removed in each GMU to determine if either population was signficantly different from a 50:50 sex ratio. I also used a Welch 2-sample t-test to determine if the number of coyotes removed in each GMU in 2004 differed.

To determine if the rate of coyote removal in each GMU was constant over time, I tested whether the number of removals followed a Poisson distribution using an intercept-only generalized linear model on the number of coyotes removed each season. Goodness-of-fit to a Poisson distribution for number of coyotes removed was assessed by comparing

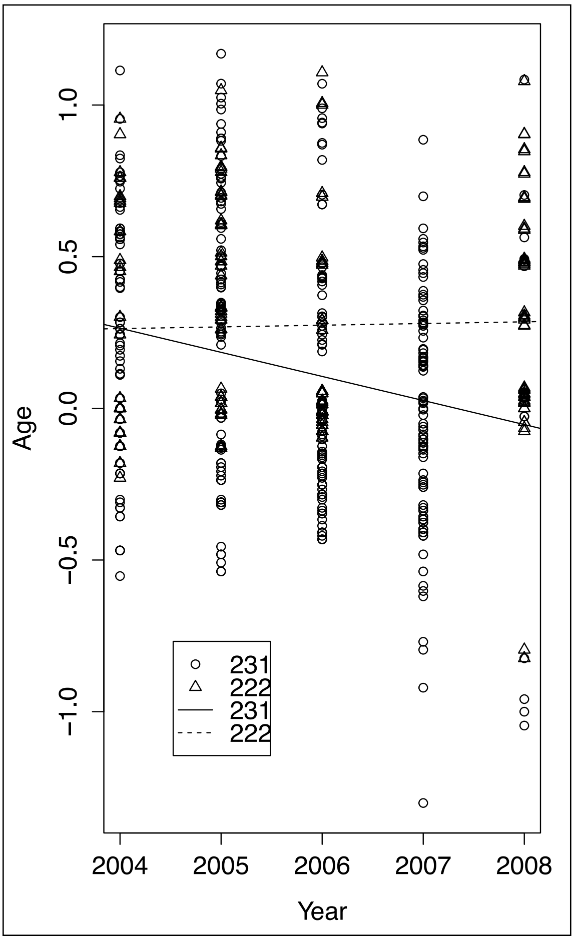

Figure 2. Change over time in average age of coyotes at time of death in GMU 222 and 231 from 2004 to 2008, Nevada.

model deviance to a chi-square distribution, with degrees of freedom equal to sample size (number of seasons) minus 1, to account for estimation of lambda, the Poisson mean.

On this project, age information was not included for all coyotes removed. Due to the nature of aerial removal, age information was not collected. Additionally, age estimates were not collected for 25 ground-removal coyotes. Only coyotes with age estimates could be used to determine if there was a difference in age at time of death for each year. Change in age at time of death over time was analyzed with analysis of covariance (ANCOVA).

To determine if sex ratios differed from a 50:50 in each GMU seasonally, I used a chi-square test of independence. Some seasons reported extremely skewed sex ratios. I assumed this to be data collector or input error; therefore, I excluded any season that had a sex ratio >65% of either sex. This is the highest percentage of coyote sex skeweness found in the available literature (Nelson and Lloyd 2005).

To determine if there were changes in the percentages of juveniles throughout the years for each GMU, I conducted a generalized linear hypothesis test on the percentage of juveniles in the populations removed each year. I used the Stepdown Bonferroni *P*-value adjustment to account for family-wise Type I error due to only being interested in consecutive year to year comparisons.

I used a Shapiro-Wilk normality test on all data to test if statistical assumptions were met. I log transformed any data that did not meet normality or constant variance assumptions. I used an alpha of $P \leq 0.05$ as a measure of significance for all statistical tests. All analyses were conducted in program R (R Version 2.14.2).

Results

Coyote removals

Coyote removal had been conducted in both GMUs since the 1940s. From 1991 to 2010, WS used a combination of aerial removal, calling, denning, M-44s, snaring, and trapping to remove a mean of 248 ± 33 coyotes per year from Lincoln County and 647 ± 37 coyotes per year from the southern portion of White Pine County, totaling 4,960 and 12,929 coyotes, respectively (J. Bennett and J. Sengl, Wildlife Services, personal communication; Table 3; Figure 2).

Between May 1, 2005, and June 30, 2008, GMU 231 received 17,011 foothold trap nights, 27,556 snare nights, and 208.5 flight hours; GMU 222 received 9,015 foothold trap nights, 16,219 snare nights, and 98 flight hours. No data for foothold trap nights, snare nights, or flight hours exists from January 1, 2004 to April 30, 2005, during which period 179 coyotes were removed (J. Bennett, Wildlife Services, personal communication).

A total of 942 coyotes were removed from GMU 222 and 231 between 2004 and 2008 (Table 4). Annual mean coyote removal rate was 135 ± 21 for GMU 231 and 53.4 ± 17 for GMU 222. Between 2004 and 2008, 589 coyotes that

Table 2. Publications defining various levels of exploited coyote populations and the variables used to determine those levels (n. a. = data not available).

Authors	Exploitation level	Juvenile definition (years)	Average age (years)	Percent of juveniles	Sex ratio*	Percent juvenile survival	Percent adult survival	Percent of mortality from humans
Mathwig 1973	Light[1]	<1	1.67[2]	n. a.	50:50[2]	n. a.	41	n. a.
Bowen 1978	Light[1]	<0.5	n. a.	n. a.	50:50[2]	45[3]	45[3]	n. a.
Windberg et al. 1985	Light[1, 4]	0.5–1.5	n. a.	36–38	50:50	42	70	57
Crabtree 1989	Light	<0.9	3.53[2]	n. a.	50:50	22	90	>90
Gese et al. 1996	Light	<1	3.18[2]	33%[1]	50:50[2]	n. a.	n. a.	n. a.
Chamberlain and Leopold 2001	Light[1, 4]	<1	n. a.	n. a.	50:50[2]	n. a.	58–100	50
Pruss 2002	Light	≤1.5	n. a.	n. a.	n. a.	66	74	77
Gese 2005 (pre removal)	Light	<1	n. a.	n. a.	50:50	n. a.	92–93	light
Andelt 1985	Light[1]	<0.75	n. a.	n. a.	50:50[1]	64[3]	32[3]	≥38
Windberg 1995	Light	<1.5	3.2[2]	34	50:50	9–73	64–74	n. a.
Dumond and Villard 2000	Light	0.5–1	5.3–5.6	n. a.	50:50	n. a.	n. a.	n. a.
Kamler and Gipson 2004	Light	n. a.	n. a.	n. a.	n. a.	n. a.	76–93	4–21
Gese et al. 1989	Light	<1	n. a.	23	50:50	51	87	81
Chronert 2007	Light	≤1	n. a.	n. a.	50:50[2]	60–64	60–64	36
Nellis and Keith 1976	Moderate[1]	<1	n. a.	56[2]	50:50	71[3]	36–42[3]	≥29 juv., 41 adult
Andrews and Boggess 1978	Moderate[1]	<1	n. a.	25–32	53.2% ♂	61	36[3]	n. a.
Meinzer and Guthery 1980	Moderate	<.5	3.25	31	50:50	36[5]	36[5]	n. a.
Nelson and Lloyd 2005	Mod. to heavy	0.67-0.92	n. a.	55	60–65% ♂	n. a.	n. a.	n. a.
Wetmore et al. 1969	Heavy[1]	0.33–1	n. a.	79%	64% ♀[6]	33	16–38	n. a.
Knudsen 1976	Heavy[1]	<1	2.53[2]	42–56	50:50	41–72[3]	42–82[3]	98
Mitchell 1979	Heavy	<1	2.21[2]	n. a.	50:50[1]	59[3]	48[9]	n. a.
Berg and Chesness 1978	Heavy[1]	0.5	3.4[2]	47	50:50	n. a.	n. a.	n. a.

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Authors	Exploitation level	Juvenile definition (years)	Average age (years)	Percent of juveniles	Sex ratio*	Percent juvenile survival	Percent adult survival	Percent of mortality from humans
Davison 1980 (Utah population)	Heavy[1]	<1	1.75[2]	80	50:50	23	47	70 juv., 74 adult
Davison 1980 (Idaho population)	Heavy[1]	<1	2.58[2]	62	50:50	45	50	78 juv., 83 adult
Tzilkowski 1980	Heavy[1]	<1	2.7[2]	n. a.	50:50	22–100	67–86	93
Pyrah 1984	Heavy[1]	n. a.	n. a.	n. a.	n. a.	52[5]	52[5]	91
Atwood et al. 2004	Heavy	<1	n. a.	n. a.	50:50[2]	n. a.	n. a.	n. a.
VanDeelen and Gosselink 2006	Heavy	<1	n. a.	47[2]	50:50[2]	13	59	n. a.
Gese 2005 (post removal)	Heavy[4]	<1	n. a.	n. a.	50:50[2]	n. a.	22–60	44–51
Hibler 1977	Heavy[4]	<1	n. a.	n. a.	50:50[2]	92–95[3]	67–100[3]	68–70 juv., 22–68 adult
This project GMU 222	Heavy[4]	<1	3.08[2,7]	46	58% ♀	n. a.	n. a.	n. a.
This project GMU 231	Heavy[4]	<1	2.74[2,7]	75	62% ♀	n. a.	n. a.	n. a.

*Not significantly different from a 50:50 sex ratio ($P < 0.05$).
[1]Exploitation level determined in other publication.
[2]Calculated or defined by author.
[3]Mortality rates.
[4]Discrepency between author and citation source on level of exploitation.
[5]Entire population included in analysis.
[6]Only occurred in 1967–1968.

were removed had age data associated with their removal; another 23 animals had sex but not age data and were used for age and sex analysis, respectively. Annual mean coyote removal for age and sex analysis GMU 231 was 82 ± 13. Annual mean coyote removal for age and sex analysis GMU 222 was 37 ± 8. Coyotes were removed year round in GMU 231 but not in GMU 222. Coyote removals were not consistant across years in either GMU. Removals for GMU 222 varied from 0 to 65 per season and averaged 18 ± 6. Removals for GMU 231 varied from 16 to 104 per season and averaged 26 ± 7 (Table 4).

Coyote population assessment

Coyote populations in both GMU 222 and 231 were similar in 2004. Average adult age in 2004 for GMU 222 was 3.26 and 2.70 for GMU 231; these differences were not significant ($\chi^2_1 = 0.05$, $P = 0.82$). The percentage of juveniles in the populations also were similar in both GMUs ($\chi^2_1 = 0.02$, $P = 0.88$; Table 5). The sex ratios for GMU 222 ($\chi^2_1 = 0.4$, $P = 0.53$) and 231 ($\chi^2_1 = 0.18$, $P = 0.67$) did not differ from a 50:50 sex ratio (Table 6). The ANCOVA analysis also shows coyote ages in both GMUs were similar (Figure 2). Age at time of death was similar in both GMUs during 2004 but began to diverge thereafter. The total number of coyotes removed in 2004 in each GMU 222 (267 removals), and GMU 231 (675 removals) did differ ($t_{7.7} = 2.68$, $P = 0.03$).

Removals were not randomly conducted in either GMU 222

Table 3. Coyotes removed by Wildlife Services from 1991 to 2010 in Lincoln and southern White Pine counties for livestock protection. GMUs 222 and 231 are locate in these 2 Nevada counties.

Lincoln County								White Pine County							
Year	Aircraft	Shooting	Denning	M-44	Snaring	Trapping	Total	Year	Aircraft	Shooting	Denning	M-44	Snaring	Trapping	Total
1991	0	13	0	0	0	54	67	1991	93	72	0	0	3	102	270
1992	20	24	6	0	0	78	128	1992	220	138	87	0	5	381	831
1993	31	21	0	0	0	55	107	1993	419	127	4	0	3	225	778
1994	43	8	0	0	0	52	103	1994	182	104	1	0	2	231	520
1995	61	6	1	0	0	39	107	1995	193	115	1	0	15	281	605
1996	54	3	0	0	1	70	128	1996	323	103	27	0	2	302	757
1997	40	19	14	0	2	42	117	1997	267	68	22	3	8	228	596
1998	35	22	0	0	1	85	143	1998	197	77	11	2	1	217	505
1999	36	17	7	0	1	171	232	1999	254	105	15	12	6	349	741
2000	59	46	9	4	8	132	258	2000	324	92	24	2	9	280	731
2001	69	25	6	8	2	104	214	2001	279	76	15	0	8	266	644
2002	95	17	6	10	0	112	240	2002	273	63	5	3	13	247	604
2003	91	25	10	5	3	77	211	2003	176	59	5	0	38	292	570
2004*	141	26	15	8	21	142	353	2004*	244	36	27	0	68	228	603
2005*	20	20	0	150	13	238	441	2005*	93	58	3	0	47	187	388
2006*	171	41	0	12	53	268	545	2006*	258	84	0	0	91	207	640
2007*	126	26	0	4	57	303	516	2007*	503	124	0	0	103	272	1002
2008*	130	18	0	0	27	312	487	2008*	380	83	0	0	78	314	855
2009	102	11	0	0	13	171	297	2009	251	61	0	0	70	180	562
2010	176	21	0	0	10	59	266	2010	439	50	0	0	59	179	727

* Signifies years of removal by Wildlife Services to benefit wildlife.

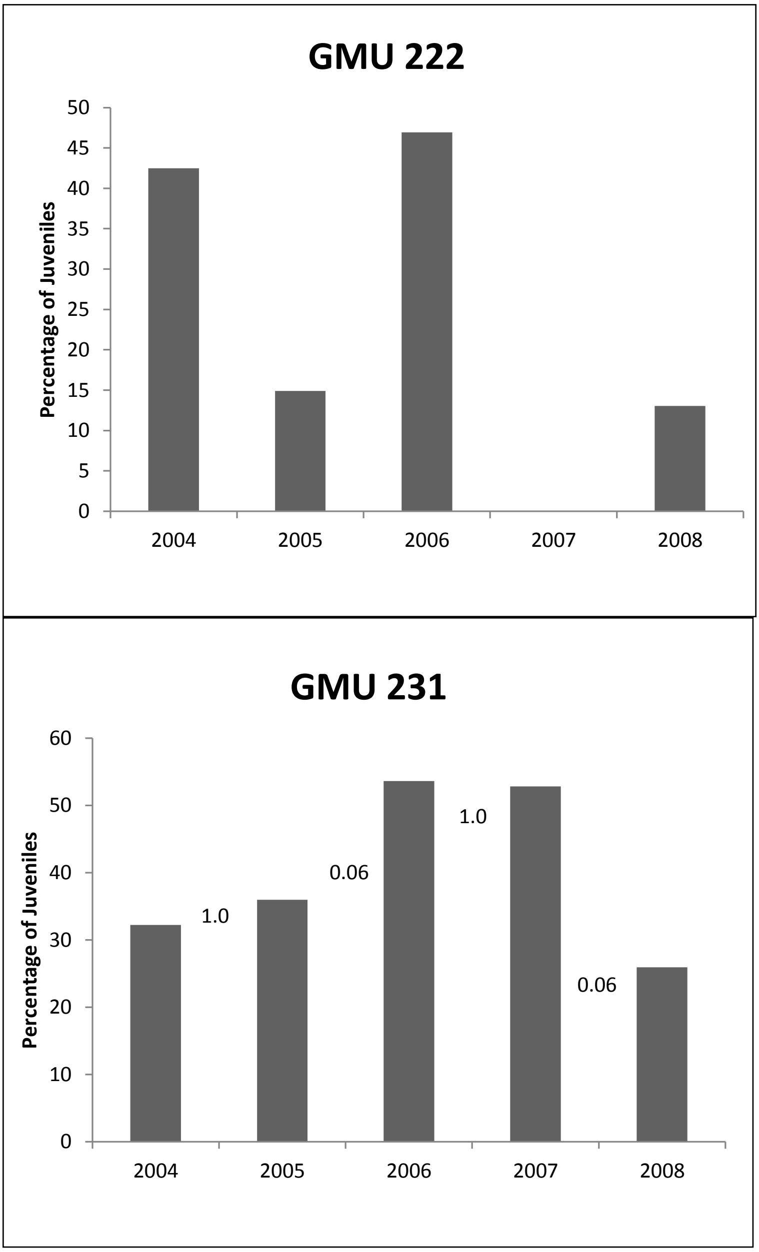

Figure 3. *P*-values for the comparisons juveniles in the population in GMU 222 and 231 for 2 successive years are reported between the respective bars, 2004 to 2008, Nevada.

(χ^2_{13} = 378.61, P < 0.001) or GMU 231 (χ^2_{13}= 184.73, $P \leq$ 0.001). GMU 222 removals were focused during the first 2 seasons of each year, while removals in GMU 231 occurred year round although not at a constant rate (Table 4).

The mean age of adult coyotes in GMU 222 for all years was 3.08 (SE = 0.22); mean age of adult coyotes overall in GMU 231 was 2.74 (SE = 0.16). The oldest coyote was removed from GMU 231 in 2005 and was approximately 14 years old. Age at time of death data were log transformed to meet assumptions of normality. Age at time of death decreased over time in GMU 231 from 2.7 in 2004 to 1.8 in 2008, no change was observed in GMU 222 (Figure 2; Table 5).

Significantly different sex ratios ranged from 57% male to 62% female (Figure 2), though most sex ratios calculated did not differ from a 50:50 sex ratio. No difference in sex ratios occurred in GMU 222 in 2004 or 2008; sex ratios were skewed in 2004 and remained skewed throughout the removals in GMU 231 (Table 6).

No significant trend in percentage of juveniles occurred between consecutive years in GMU 222 or GMU 231 (Figure 3). An increasing trend was observed in GMU 231 from 2004 to 2006, but was not significant (Figure 3). Signifcant differences in GMU 222 occurred between years but no overall pattern was observed (Figure 3).

Discussion

By most accepted standards (Crabtree and Sheldon 1999), the coyote populations in GMU 222 and 231 were only lightly exploited prior to the implementation of large-scale removal efforts. In GMU 222, the mean adult age was 3.26 years; the percentage of juveniles removed from the population was 43%, and sex ratio was balanced. Similarly ,in GMU 231, mean adult age was 2.7 years; the percentage of juveniles removed from the population was 32%, though there was

Table 4. Total number of coyotes moved by sex and game management units 222 and 231, Nevada.

		GMU 222				GMU 231			
		Ground removals		Aerial removals		Ground removals		Aerial removals	
Dates		Males	Females	All coyotes	Total	Males	Females	All coyotes	Total
	Breeding	10	16	0	26	21	16	0	37
2004	Pup rearing	8	5	0	13	8	8	0	16
	Dispersal	0	1	0	1	17	17	0	34
	Breeding	6	5	0	11	17	20	0	37
2005	Pup rearing	12	24	0	36	0	21	0	21
	Dispersal	0	0	0	0	0	29	0	29
	Breeding	3	17	0	20	0	45	0	45
2006	Pup rearing	14	16	0	30	0	18	18	36
	Dispersal	0	0	0	0	15	21	57	93
	Breeding	0	0	0	0	15	24	41	80
2007	Pup rearing	0	0	0	0	14	9	8	31
	Dispersal	0	0	6	6	30	21	53	104
	Breeding	12	7	40	59	2	1	42	45
2008	Pup rearing	19	27	19	65	18	5	7	30
	Dispersal	0	0	0	0	1	0	36	37

Table 5. Average age and percentage of juvenile coyotes in the population from 2004 to 2008 in GMU 222 and 231, Nevada (n. a. = data not available).

	2004	2005	2006	2007	2008
Area	Average adult age				
GMU 222	3.3	3.3	3.0	0	2.9
GMU 231	2.7	3.8	3.0	1.7	1.8
	Percentage of juveniles in population				
GMU 222	43	15	47	n. a.	13
GMU 231	32	36	54	53	26

a skewed sex ratio during the first season. The level of exploitation in GMU 222 was relatively constant throughout the project, with no appreciable change in either age at time of death, juveniles in the population, or sex ratios. In contrast, the coyote population in GMU 231 was altered by large-scale removal efforts, changing from lightly to heavily exploited. As a result of increased removal efforts, mean age of coyotes removed decreased, sex ratios became skewed, and the percentage removed in 2006 and 2007 that were juveniles increased to >50%.

There was a decrease in percentage of juveniles removed from the population in 2008; this is most likely due to no removals occurring during dispersal season, the time of the year when juveniles are the most susceptible to removal efforts.

Prior to the implementation of large-scale removal efforts, coyote exploitation levels were similar in both GMU 222 and 231. This is likely due to the topography, weather, precipitation, flora, fauna, and removal efforts being similar in both GMUs. It is also likely that coyote populations in both GMUs had received similar amounts of removal effort from WS, local hunters, and trappers. It is important to remember that this was not a study, but a removal project to benefit mule deer. Due to this, little data were collected on coyotes. It is assumed that removals provided an accurate sample of the coyote population dynamics at the time those animals were removed.

Coyote removals that occurred in GMUs

Table 6. Sex ratio of coyotes killed by season in GMU 222 and 231, Nevada.

		GMU 222					GMU 231				
Dates		Total	χ^2	df	*P* value	Sex ratio	Total	χ^2	df	*P* value	Sex Ratio
	Breeding	26	1.38	1	0.24	50:50	37	0.68	1	0.41	57% ♂
2004	Pup rearing	13	0.69	1	0.41	50:50	16	0	1	1	50:50
	Dispersal	1	n/a	n/a	n/a	n/a	34	0	1	1	50:50
	Breeding	11	0.09	1	0.76	50:50	37	0.24	1	0.62	50:50
2005	Pup rearing	36	4.0	1	0.05	67% ♀*	21	21	1	<0.001	100% ♀*
	Dispersal	0	n/a	n/a	n/a	n/a	29	29	1	<0.001	100% ♀*
	Breeding	20	9.8	1	0.002	85% ♀*	45	45	1	<0.001	100%♀*
2006	Pup rearing	30	0.133	1	0.72	50:50	18	18	1	<0.001	100% ♀*
	Dispersal	0	n/a	n/a	n/a	n/a	36	1	1	0.32	58% ♀
	Breeding	0	n/a	n/a	n/a	n/a	39	2.08	1	0.15	62% ♀
2007	Pup rearing	0	n/a	n/a	n/a	n/a	23	1.09	1	0.30	50:50
	Dispersal	0	n/a	n/a	n/a	n/a	51	1.59	1	0.21	50:50
	Breeding	19	1.32	1	0.25	50:50	3	n/a	n/a	n/a	n/a
2008	Pup rearing	46	1.39	1	0.24	50:50	23	7.35	1	0.007	78% ♂*
	Dispersal	0	n/a	n/a	n/a	n/a	1	n/a	n/a	n/a	n/a

*Likely inaccurate sex ratio due to operator error.

222 and 231 were similar to other removals that attempted to reduce the overall coyote populations; they were not localized reductions. Late winter and spring are often cited as the most efficient times to conduct coyote removal because: coyote populations are at their lowest; snow pack makes coyotes most vulnerable to aerial gunning; breeding pairs are more vulnerable; and it is closer to ungulate fawning season when coyote removal can create temporary voids in critical fawning habitat (Knowlton et al. 1999, Ballard et al. 2001, Brown and Conover 2011, Hurley et al. 2011). Removal efforts occurred year round in GMU 231, but not in GMU 222. Few to no removals occurred in the dispersal season in GMU 222 during all years; it is unclear if this was intentional or due to GMU 222 receiving only ~35% of the removal efforts over the course of the removals.

Though the coyote population in GMU 231 changed from a lightly to a heavily exploited population from 2004 to 2008, it is possible that the density of coyotes in the area remained unchanged or possibly increased. Although counterintuitive, this situation can occur because coyote populations are able to maintain themselves under considerable removal efforts through increases in productivity, survival, and immigration. Only a 10% survival rate in offspring must survive and reproduce to maintain most coyote populations (Knowlton et al. 1999). Removing <75% of a coyote population may actually increase the population through increases in reproduction; if 75% of coyotes in a population are killed each year, the population can be exterminated in approximately 50 years (Connolly and Longhurst 1975). Coyote removal has been a common practice throughout much of the western United States, with the goal of increasing game populations and reducing livestock losses (Mitchell et al. 2004, Harrington and Conover 2007, Brown and Conover 2011, Hurley et al. 2011). There have been 2 general approaches for predator control: (1) large-scale through removals, such as bounties, professional hunters and trappers, and liberal hunting seasons; and (2) localized removal of problematic individuals or groups of individuals, often only at certain times of the year when prey are vulnerable (Connolly 1978*b*, Hamlin 1997, Ballard et al. 2001). These localized removal efforts have successfully reduced depredations, but no reduction in the predator population was measured (Hamlin 1997).

It is important for NDOW or any state agency to outline goals prior to implementing removal efforts. It seems to be a tradition that killing coyotes will benefit game species such as mule deer, with little to no oversight. If reducing coyote populations is the goal, I recommend that data be obtained on the coyote population prior to removals. Surveys, such as scat transects (Andelt and Andelt 1984, Henke and Knowlton 1995) or passive tracking indexes (Engeman and Allen 2000, Engeman et al. 2000), are relatively cheap and quick ways to monitor coyote populations before, during, and after removal efforts. I also rocommend determining if the game population in focus is below carrying capacity is also recommended prior to removals; coyotes often focus on prey besides mule deer (Hamlin et al. 1984, Ballard et al. 2001).

My data indicate that the enhanced removal efforts in GMU 231 were sufficient to increase the level of exploitation to high. My results support the hypothesis that average age of coyotes will decrease as the population becomes more exploited.

Management implications

Predator removal in Nevada and throughout the West continues to be a controversial issue, especially as game species, such as mule deer, remain below biological and cultural carrying capacities. I observed an increase in level of exploitation in GMU 231, which received most coyote removal. I observed no change in level of exploitation in GMU 222, which received less removal.

Managers should identify all limiting factors for game species of concern and identify carrying capacity before implementing coyote removal efforts. Removal programs that are on too small a scale or fail to remove an adequate number of coyotes may not produce desired results. It is important to understand both coyote and game species dynamics prior to removal to understand how many coyotes must be removed to gain the desired effect in game species populations. Resources should always be allocated to monitor both populations enough to understand if predator removal is having the desired effect.

Literature cited

Andelt, W. F. 1985. Behavioral ecology of coyotes in south Texas. Wildlife Monographs 90:3–45.

Andelt, W. F. 1987. Coyote predation. Pages 128–140 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ashton-Potter, Concord, Ontario, Canada.

Andelt, W. F., and S. H. Andelt. 1984. Diet bias in scat deposition-rate surveys of coyote density. Wildlife Society Bulletin 12:74–77.

Andrews, R. D., and E. K. Boggess. 1978. Ecology of coyotes in Iowa. Pages 249–265 *in* M. Bekoff, editor. Coyotes: biology, behavior, and management. Academic Press, New York, New York, USA.

Atwood, T. C., H. P. Weeks, and T. M. Gehring. 2004. Spatial ecology of coyotes along a suburban-to-rural gradient. Journal of Wildlife Management 68:1000–1009.

Bailey, R. G. 2009. Ecoregions of the United States. Pages 93–114 *in* Ecosystem geography. Second edition. Springer-Verlag, New York, New York, USA.

Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter, and J. C. deVos Jr. 2001. Deer–predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. Wildlife Society Bulletin 29:99–115.

Bartel, R. A., and M. W. Brunson. 2003. Effects of Utah's coyote bounty program on harvester behavior. Wildlife Society Bulletin 31:736–743.

Bartel, R. A., and F. F. Knowlton. 2005. Functional feeding responses of coyotes, *Canis latrans*, to fluctuating prey abundance in the Curlew Valley, Utah, 1977–1993. Canadian Journal of Zoology 83:569–578.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121:3–39.

Bekoff, M., and M. C. Wells. 1986. Social ecology and behavior of coyotes. Pages 251–338 *in* D. S. Lehrman, editor. Advances in the study of behavior. Volume 16. Academic Press, New York, New York, USA.

Berg, W. E., and R. A. Chesness. 1978. Ecology of coyotes in northern Minnesota. Pages 229–247 *in* M. Novak, editor. Coyotes: biology, behavior, and management. Academic Press, New York, New York, USA.

Boertje, R. D., P. Valkenburg, and M. E. McNay. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. Journal of Wildlife Management 60:474–489.

Bowen, W. D. 1978. Social organization of the coyote in relation to prey size. Dissertation, University of British Columbia, Vancouver, British Columbia, Canada.

Brown, D. E., and M. R. Conover. 2011. Effects of large-scale removal of coyotes on pronghorn and mule deer productivity and abundance. Journal of Wildlife Management 75:876–882.

Chamberlain, M. J., and B. D. Leopold. 2001. Survival and cause-specific mortality of adult coyotes (*Canis latrans*) in central Mississippi. American Midland Naturalist 145:414–418.

Chronert, J. M. 2007. Ecology of the coyote (*Canis latrans*) at Wind Cave National Park. Thesis, South Dakota State University, Brookings, South Dakota, USA.

Connolly, G. E. 1978*a*. Predators and predator control. Pages 369–394 *in* J. L. Schmidt and D. L. Gilbert, editors. Big game of North America. Stackpole, Harrisburg, Pennsylvania, USA.

Connolly, G. E. 1978*b*. Predator control and coyote populations: a review of simulation models. Pages 327–345 *in* M. Bekoff, editor. Coyotes: biology, behavior, and management. Academic Press, New York, New York, USA.

Connolly, G. E., and W. M. Longhurst. 1975. The effects of control on coyote populations: a simulation model. University of California Division of Agriculture Science Bulletin 1872:1–37.

Crabtree, R. L. 1989. Sociodemography of an unexploited coyote population. Dissertation, University of Idaho, Moscow, Idaho, USA.

Crabtree, R. L., and J. W. Sheldon. 1999. Coyotes and canid coexistence in Yellowstone. Pages 127–163 *in* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut, USA.

Davison, R. P. 1980. The effect of exploitation on some parameters of coyote populations. Dissertation, Utah State University, Logan, Utah, USA.

Dumond, M., and M. A. Villard. 2000. Demography and body condition of coyotes (*Canis latrans*) in eastern New Brunswick. Canadian Journal of Zoology 78:399–406.

Engeman, R. M., and L. Allen. 2000. Overview of a passive tracking index for monitoring wild canids and associated species. Integrated Pest Management Reviews 5:197–203.

Engeman, R. M., M. J. Pipas, K. S. Gruver, and L. Allen. 2000. Monitoring coyote population changes with a passive activity index. Wildlife Research 27:553–557.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84:1–50.

Gese, E. 2005. Demographic and spatial responses of coyotes to changes in food and exploitation. Wildlife Damage Management Conference 11:271–285.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1989. Population dynamics of coyotes in southeastern Colorado. Journal of Wildlife Management 53:174–181.

Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1996. Social and nutritional factors influencing the dispersal of resident coyotes. Animal Behaviour 52:1025–1043.

Gier, H. T. 1968. Coyotes in Kansas. Kansas State College Agriculture Experiment Station Bulletin 393:1–118.

Gier, H. T. 1975. Ecology and behavior of the coyote (*Canis latrans*). Pages 247–262 *in* M. W. Fox, editor. The wild canids. Van Nostrand Reinhold, New York, New York, USA.

Green, J. S., F. R. Henderson, and M. D. Collinge. 1994. Coyotes. Pages 51–56 *in* S. E. Hygnstrom, R. M. Timm, and G. E. Larson, editors. Prevention and control of wildlife damage. University of Nebraska Cooperative Extension, Lincoln, Nebraska, USA.

Hamlin, K. L. 1997. Survival and home range fidelity of coyotes in Montana: implications for control. Intermountain Journal of Sciences 3:62–72.

Hamlin, K. L., S. J. Riley, D. Pyrah, A. R. Dood, and R. J. Mackie. 1984. Relationships among mule deer fawn mortality, coyotes, and alternate prey species during summer. Journal of Wildlife Management 48:489–499.

Harrington, J. L., and M. R. Conover. 2007. Does removing coyotes for livestock protection benefit free-ranging ungulates? Journal of Wildlife Management 71:1555–1560.

Harris, S., and G. Saunders. 1993. The control of canid populations. Symposia of the Zoological Society of London 65:441–464.

Henke, S. E., and F. F. Knowlton. 1995. Techniques for estimating coyote abundance. Pages 71–78 *in* D. Rollins, C. Richardson, T. Blankenship, K. Canon, and S. Henke, editors. Coyotes in the Southwest: a compendium of our knowledge. San Angelo, Texas, USA.

Hernández, L., R. R. Parmenter, J. W. Dewitt, D. C. Lightfoot, and J. W. Laundré. 2002. Coyote diets in the Chihuahuan Desert, more evidence for optimal foraging. Journal of Arid Environments 51:613–624.

Hibler, S. J. 1977. Coyote movement pattern with emphasis on home range characteristics. Thesis, Utah State University, Logan, Utah, USA.

Howard, V. W., and G. G. DelFrate. 1991. Home ranges and movements of coyotes in the northern Chihuahuan Desert. Proceedings of the Great Plains Wildlife Damage Management Conference 10:39–49.

Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, J. R. Skalski, and C. L. Maycock. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildlife Monographs 178:1–33.

Jean, Y., and J. M. Bergeron. 1984. Productivity of coyotes (*Canis latrans*) from southern Quebec. Canadian Journal of Zoology 62:2240–2243.

Kamler, J. F., and P. S. Gipson. 2004. Survival and cause-specific mortality among furbearers in a protected area. American Midland Naturalist 151:27–34.

Kellert, S. R. 1985. Public perceptions of predators, particularly the wolf and coyote. Biological Conservation 31:167–189.

Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. Journal of Wildlife Management 36:369–382.

Knowlton, F. F., and E. M. Gese. 1995. Coyote population processes revisited. Pages 1–6 *in* D. Rollins, C. Richardson, T. Blankenship, K. Canon, and S. Henke, editors. Coyotes in the Southwest: a compendium of our knowledge. San Angelo, Texas, USA.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: an interface between biology and management. Journal of Range Management 52:398–412.

Knudsen, J. J. 1976. Demographic analysis of Utah-Idaho coyote population. Thesis, Utah State University, Logan, Utah, USA.

Mathwig, H. J. 1973. Food and population characteristics of Iowa coyotes. Iowa State Journal of Research 47:167–189.

Meinzer, W. P., and F. S. Guthery. 1980. Age distributions and weights of coyotes in northwestern Texas. Southwestern Naturalist 25:275–278.

Mitchell, B. R., M. M. Jaeger, and R. H. Barrett. 2004. Coyote depredation management: current methods and research needs. Wildlife Society Bulletin 32:1209–1218.

Mitchell, C. D. 1979. Some demographic characteristics of a coyote population in southwestern New Mexico. Thesis, New Mexico State University, Carlsbad, New Mexico, USA.

Nellis, C. H., and L. B. Keith. 1976. Population dynamics of coyotes in central Alberta, 1964-68. Journal of Wildlife Management 40:389–399.

Nelson, T. A., and D. M. Lloyd. 2005. Demographics and condition of coyotes in Illinois. American Midland Naturalist 153:418–427.

Nevada Department of Wildlife. 2011. Predator management plan FY11 report and FY12 project proposals. Reno, Nevada, USA.

Prism Climate Group. 2014. Prism climate data. Northwest Alliance for Computational Science and Engineering, Oregon State University, Corvallis, Oregon, USA, <www.prism.oregonstate.edu>. Accessed July 10, 2014.

Pruss, S. 2002. Ecology of coyotes (*Canis latrans*) in Elk Island National Park. Dissertation, University of Alberta. Edmonton, Alberta, Canada.

Pyrah, D. 1984. Social distribution and population estimates of coyotes in north-central Montana. Journal of Wildlife Management 48:679–690.

Sacks, B. N., M. M. Jaeger, J. C. Neale, and D. R.

McCullough. 1999. Territoriality and breeding status of coyotes relative to sheep predation. Journal of Wildlife Management 63:593–605.

Schmidt, R. H. 1986. Community-level effects of coyote population reduction. Pages 49–65 *in* J. J. Cairns, editor. Community toxicity testing. American Society for Testing and Materials, Philadelphia, Pennsylvania, USA.

Skogland, T. 1991. What are the effects of predators on large ungulate populations? Oikos 61:401–411.

Smith, R. H., D. J. Neff, and N. G. Woolsey. 1986. Pronghorn response to coyote control: a benefit: cost analysis. Wildlife Society Bulletin 14:226–231.

Tzilkowski, W. 1980. Mortality patterns of radiomarked coyotes in Jackson Hole, Wyoming. Dissertation, University of Massachusetts, Amherst, Massachusetts, USA.

Tzilkowski, W. M., and F. F. Knowlton. 1979. Mancaused mortality of coyotes marked in Grand Teton National Park. Pages 164–168 *in* Recreational Impact on Wildlands. Seattle, Washington, USA.

Van Ballenberghe, V., and W. B. Ballard. 1994. Limitation and regulation of moose populations: the role of predation. Canadian Journal of Zoology 72:2071–2077.

Van Deelen, T. R., and T. E. Gosselink. 2006. Coyote survival in a row-crop agricultural landscape. Canadian Journal of Zoology 84:1630–1636.

Voigt, D. R., and W. E. Berg. 1987. Coyote. Pages 345–357 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ashton-Potter, Concord, Ontario, Canada.

Wetmore, S. P., C. H. Nellis, and L. B. Keith. 1969. A study of winter coyote hunting in Alberta with emphasis on use of snowmobiles. Fish and Wildlife Division, Department of Lands and Forests, Alberta, Canada.

Wilson, P. J., S. Grewal, T. McFadden, R. C. Chambers, and B. N. White. 2003. Mitochondrial DNA extracted from eastern North American wolves killed in the 1800s is not of gray wolf origin. Canadian Journal of Zoology 81:936–940.

Windberg, L. A. 1995. Demography of a high-density coyote population. Canadian Journal of Zoology 73:942–954.

Windberg, L. A., H. L. Anderson, and R. M. Engeman. 1985. Survival of coyotes in southern Texas. Journal of Wildlife Management 49:301–307.

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