12-1-2009

Effectos of Coyote Removal on Pronghorn and Mule Deer Populations in Wyoming

Dylan Earl Brown
Utah State University

EFFECTS OF COYOTE REMOVAL ON PRONGHORN AND MULE DEER

POPULATIONS IN WYOMING

by

Dylan E. Brown

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Biology

Approved:

Michael R. Conover Major Professor	Terry A. Messmer Committee Member
John A. Shivik Committee Member	Byron R. Burnham Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2009

ABSTRACT

Effects of Coyote Removal on Pronghorn and Mule Deer

Populations in Wyoming

by

Dylan E. Brown, Master of Science

Utah State University, 2009

Major Professor: Dr. Michael R. Conover
Department: Wildland Resources

I studied the relationship between coyote (*Canis latrans*) removal and pronghorn (*Antilocapra americana)* and mule deer (*Odocoileus hemionus*) density and fawn:doe ratios in southwest Wyoming and northeast Utah in 2007 and 2008. Coyote removal variables studied included the number of coyotes removed, ground hours worked, total hours worked, coyotes removed/aerial gunning hour, coyotes removed/ground work hour, and coyotes removed/total effort hour. None of the variables explained changes observed in fawn:doe ratios of pronghorn or mule deer. The number of coyotes removed, ground hours worked, total hours worked, and coyotes removed/aerial gunning hour were positively correlated with pronghorn density. However, none of the coyote removal variables were correlated with mule deer density. Coyote removal conducted in the winter and spring explained more variation and had a stronger positive correlation with fawn survival and ungulate density than removal conducted in the summer or fall. My results suggest that coyote removal conducted over large areas may increase density of pronghorn. However, coyote removal did not appear to increase mule deer fawn survival or density.

(64 pages)

ACKNOWLEDGMENTS

Funding was provided by the Predator Management Districts of Lincoln and Sweetwater counties of Wyoming. I thank my advisor, Dr. Michael Conover, for this opportunity and advice given throughout my graduate career, and my committee members, Dr. Terry Messmer and Dr. John Shivik, for their support and feedback. I would like to thank all the graduate students in the Conover and Messmer labs, in particular Josh Vest, for his help in editing and his input on many aspects of the project. Thanks go to all Wyoming Game and Fish employees who helped with the project, especially Mark Zornes and Tim Woolley. I thank USDA Wildlife Services for providing coyote removal data, in particular Rod Merrell as well as the National Wildlife Research Center and Dr. John Shivik for the use of a camp trailer and pickup during the second year of the project. This project would not have been a success without the help of Joe Barnett, who assisted with ungulate and scat counts. Vic Dana helped me learn the country during my first field season and provided a place to stay. Finally, I thank Jody McLeod for supporting me throughout the process.

Dylan Earl Brown

CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Mule deer (*Odocoileus hemionus*) population numbers in the western United States have exhibited wide fluctuations over the past century. However, recent declines in the 1980s and 1990s have prompted state wildlife agencies to reexamine contemporary deer management strategies (Ballard et al. 2001, deVos et al. 2003). Because mule deer are an important big-game species generating both hunting opportunities and agency revenue, both hunters and managers have expressed concern about these declines (deVos et al. 2003). Factors identified as likely contributors to these declines include severe winters, drought, habitat loss, competition with elk (*Cervus elephus*), and predation (deVos et al. 2003).

The fact that mule deer inhabit an assortment of very different habitat types throughout the West complicates the issue by preventing a single factor from being implicated as the driving force behind these declines (deVos et al. 2003). Thus, identifying factors contributing to these declines within specific habitat types or regions is of importance. Of these factors, research is limited regarding the effect of predation and few predator removal studies, which can be applied to management, have been performed.

Mule deer predators include the coyote (*Canis latrans*), golden eagle (*Aquila* chrysaetos), gray wolf (*Canis lupus*), bobcat (*Lynx rufus*), mountain lion (*Puma concolor*), black bear (*Ursus americanus*), and grizzly bear (*Ursus arctos*) (Lingle 2000, Ballard et al. 2001, Ballard et al. 2003, Zimmer 2004, White and Garrott 2005, Zager and Beecham 2006).

Pronghorn population numbers have not exhibited the same range-wide fluctuations as mule deer. However, pronghorn population declines have been documented in some areas (Smith et al. 1986, Dunbar and Giordano 2002, Jacques et al. 2007). Drought, severe winters with deep crusted snow, malnutrition, disease, hunter harvest, poisonous plants, and coyote predation have been identified as limiting factors affecting pronghorn survival. Although the decline in pronghorn populations has been less dramatic and more isolated than the decline seen in mule deer, these localized declines merit research because pronghorn managers need to know the cause of these localized declines to make sound management decisions.

Effects of Predation on Ungulates

Determining the effect of predation on native ungulates is complicated. Factors such as alternate prey species abundance, the ungulate population's relationship to habitat carrying capacity (K), the type and density of predator, weather, and habitat condition have all been suggested to affect the role predation has on native ungulate populations (Hamlin et al. 1984, Bartmann et al. 1992, Ballard et al. 2001, deVos et al. 2003, Hurley and Zager 2007). These factors likely influence both predation rate and to what degree mortality due to predation is either compensatory or additive. Predation would be considered compensatory mortality if the animals taken would have succumbed to another form of mortality even if they were not killed by predators. It would be considered additive if the animals taken would have survived had they not been killed by predators (Ballard et al. 2001).

Currently, the effect that predation has on ungulate populations is thought to be best explained by 4 models. These models include low-density equilibria, multiple stable states, stable limit cycles, and recurrent fluctuations (Ballard et al. 2001, Ballard et al. 2003). The low-density equilibria model contends that ungulates are regulated by density-dependent predation at low densities until predation pressure is reduced, either by predator control or natural occurrence. Ungulate densities increase, but do not reach carrying capacity (K); when predator populations recover, ungulate densities return to their former level. The multiple stable states model contends that ungulates are regulated by density dependent predation at low densities until predation pressure is reduced. Ungulate densities then increase until they reach K where they remain even after predator populations recover. The stable-limit cycle model contends that ungulate density is cyclical with a full cycle taking 30–40 years. Ungulate densities increase during periods of good weather where predation is density independent and decline during periods of poor weather where predation is inversely density dependent. The recurrent fluctuations model contends that ungulate densities exhibit fluctuations but are not in equilibrium. Ungulate density is affected by changes in weather, forage quality and human harvest, but predation is the primary limiting factor. When ungulates are at high densities, predation is inversely density dependent. It is important to note that none of the models have successfully explained ungulate-predator relationships under all conditions and have only been tested in caribou (*Rangifer tarandus*) and moose (*Alces alces*) populations in areas largely unaffected by humans. They have not by tested with mule deer or pronghorn populations (Ballard and Van Ballenberghe 1998, Ballard et al. 2001).

Connolly (1978) reviewed articles addressing the effects of predation on native ungulates. He reported that 31 studies indicated predation was a limiting factor and 27 studies did not. He drew no definitive conclusion on the effects of predation on ungulates, although he suggested predation could have an important effect on ungulate numbers if coupled with inclement weather, disease, or habitat change. A more recent review on the effects of predation on mule deer produced similar findings with some studies indicating that predator control improved deer populations and others indicating that it did not (Ballard et al. 2001).

Coyotes are the most widely documented predator of mule deer and pronghorn fawns. Since Connolly's (1978) review, lethal control of coyote populations has decreased throughout the West. Reasons for this decrease include the ban on broad-based poisons after 1972, substantial decreases in fur prices that occurred in the late 1980s, and increased public opposition to lethal control (R. Merrell and S. Shwiff, Wildlife Services, unpublished report).

Coyote density is positively correlated with predation intensity (Knowlton et al. 1999, Stoddart et al. 2001, Sacks and Neale 2007) and recent research indicates that increased predator densities in the northern Yellowstone ecosystem are likely tied to decreases in overall abundance and calf survival in elk (Barber-Meyer et al. 2008). It is possible that increased coyote densities due to decreased lethal control over the past decades could contribute to increased predation rates on pronghorn and mule deer fawns.

Most mule deer studies that either employed the use of radiotelemetry or manipulated predator populations reported coyote predation to be a major cause of fawn mortality (Ballard et al. 2001). However, many deer studies have not found predation to limit recruitment in mule deer and found other factors such as extreme winter and range condition to contribute more to lack of recruitment (Bartmann et al. 1992, Ballard et al. 2001, Ballard et al. 2003).

In parts of the West, the greatest source of mortality for pronghorn fawns is coyote predation (Barrett 1984, Smith et al. 1986, Gregg et al. 2001, Zimmer 2004, Jacques et al. 2007). Coyote removal has coincided with an increase in fawn survival and pronghorn density in some studies (Smith et al. 1986, Phillips and White 2003, Harrington and Conover 2007). However, Beale and Smith (1973) found coyote predation was not an important factor affecting pronghorn fawn survival in Utah.

Even given the mixed results of previous studies regarding the benefits of coyote removal on pronghorn recruitment some western states have contracted with the United States Department of Agriculture, Animal Plant Health Inspection Service, Wildlife Services (WS) to remove coyotes for the benefit of pronghorn (Harrington and Conover 2007). The debate remaining is whether current coyote removal programs can increase fawn survival and density. Until recently, studies examining the effects of predator control were conducted in areas $< 1{,}000$ km^2 (Ballard et al. 2001, Ballard et al. 2003). The size of the area in which predators are removed is important because efforts to reduce wildlife numbers are usually more successful when conducted over large areas (Conover 2002). However, in their review on deer-predator relationships Ballard et al. (2001) stated that case studies where predator control appeared to be effective generally were small scale and cases where predator control appeared to be ineffective involved large scale areas.

To date only 2 large-scale studies on the effect of predator removal on mule deer and pronghorn have been conducted. Harrington and Conover (2007) conducted a study in Utah and Colorado that encompassed an area >1,900 km^2. They did not find a relationship between coyote removal and fawn:doe ratios, but found a correlation between the level of coyote removal and pronghorn and mule deer densities. Hurley and Zager (2007) conducted a 14,700 km^2 study on mule deer in southeast Idaho. They found that coyote removal did not increase fawn or adult survival during winter and that coyote removal did not increase the population growth rate. However, coyote removal increased fawn survival under specific coyote-prey ratios and it had a positive, but weak, effect on fawn:doe ratios.

Given these variable results, it is unclear if removal of coyotes can improve fawn survival, and thus growth rate of pronghorn and mule deer populations. Objectives of my research were to determine if coyote removal increased pronghorn and mule deer fawn survival, and pronghorn and mule deer densities. Additionally I evaluated if coyote removal conducted at a large scale would decrease coyote populations. This research may help managers better address stakeholder concerns and questions regarding the role of predation in mule deer and pronghorn recruitment. My thesis was written in monograph format. I followed editorial guidelines as recommended by the Journal of Wildlife Management.

STUDY AREA

This study was conducted during 2007 and 2008 on 12 study sites located throughout southwest Wyoming and northeast Utah (Fig. 1). Much of southwest Wyoming and part of northeast Utah can be categorized as high desert. Winter conditions are often extreme with temperatures dropping well below -20° C and snow accumulating within many of the study sites. Much of the area receives very little rainfall in the summer. Elevation of the study sites ranged from 1,800–2,750 m. Average annual precipitation within the study sites varied from 15–30 cm. Predominant land use within the study sites included livestock grazing and oil and gas development. Pronghorn, mule deer and coyotes were hunted within all study sites. Wildlife Services management units were used as study sites to allow the collection of coyote removal data. I paired study sites together on the basis of habitat type. One study-site in each pair was subjected to coyote removal and the other was not.

The 10 study sites in Wyoming and 2 study sites in Utah made up an area of 10,518 km^2. Flat Top Mountain (821 km^2), Kinney Rim (407 km^2), Delaney Rim (1,761 km^2), Sand Butte (649 km^2), Hay Reservoir (1,403 km^2), and Bush Creek (710 km^2) all were located within the Red Desert of Wyoming and contained similar habitat. Common vegetation occurring within these sites includes big sagebrush (*Artemisia tridentata*), black sagebrush (*Artemisia nova*), salt sage (*Atriplex nuttallii*), greasewood (*Sarcobatus vermiculatus*), rubber rabbitbrush (*Chrysothamnus nauseosus*), western wheatgrass (*Agropyron smithii*), and Indian ricegrass (*Oryzopsis hymenoides*) (Alldredge et al. 1991). Aspen

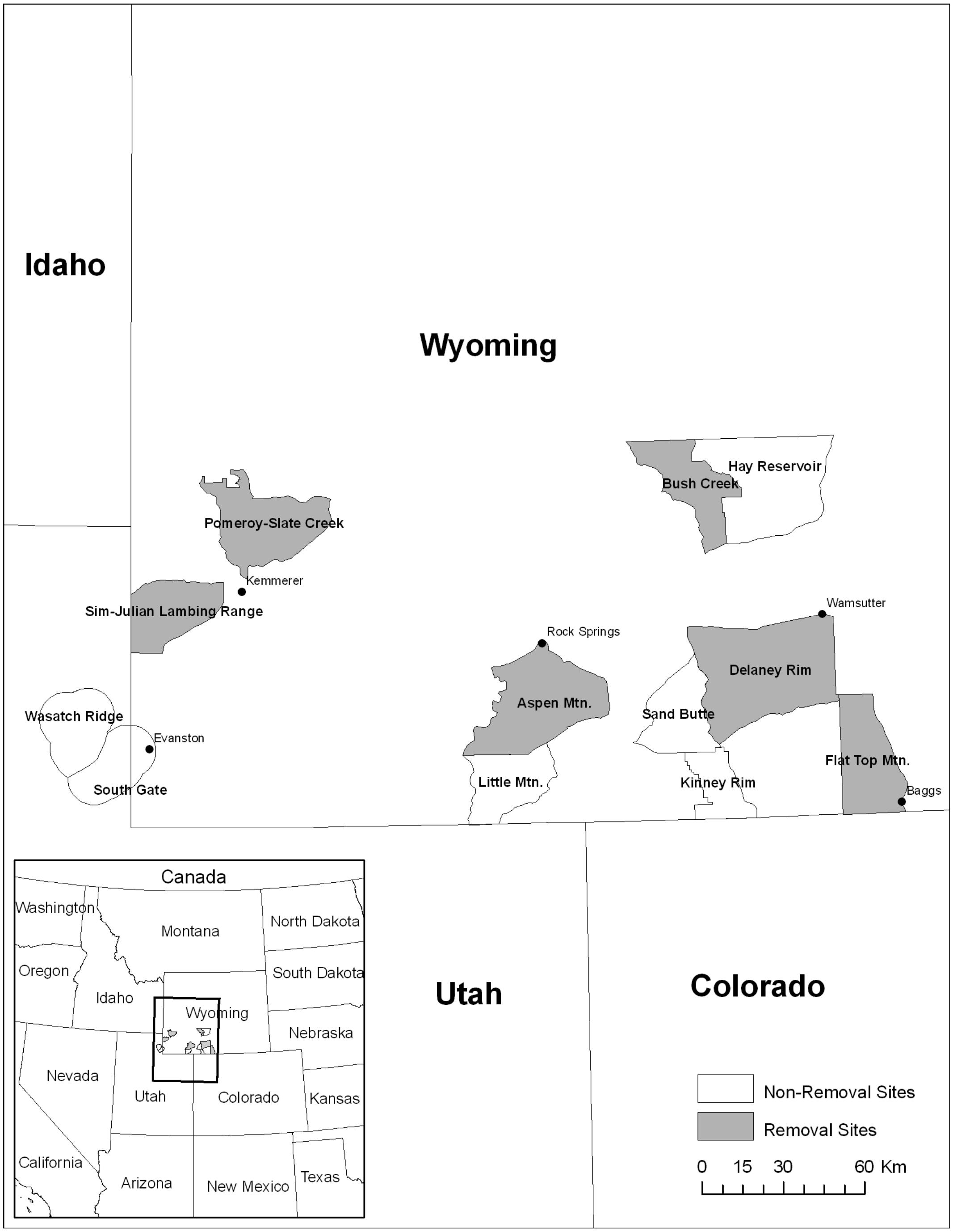

Figure 1. Study sites in Wyoming and Utah where I studied the effects of coyote removal on pronghorn and mule deer populations in 2007 and 2008, Wyoming Coyote Predation Study, 2008.

Mountain (1,261 km^2) and Little Mountain (643 km^2) were located south of Rock Springs, WY, and contained similar habitat. Common vegetation occurring within Aspen Mountain and Little Mountain includes big sagebrush (*Artemisia tridentata*), black sagebrush (*Artemisia nova*) Utah serviceberry (*Amelanchier utahensis*), mountain mahogany (*Cercocarpus montanus*), aspen (*Populus tremuloides*) and antelope bitterbrush (*Purshia tridentata*). Pomeroy-Slate Creek (978 km^2), and South Gate (564 km^2) were located north of Kemmer, WY and west of Evanston, WY, respectively. Habitat within Pomeroy-Slate Creek and South Gate was similar. Common vegetation includes big sagebrush (*Artemisia tridentata*), black sagebrush (*Artemisia nova*), western wheatgrass (*Agropyron smithii*), needle-and-thread grass (*Stipa comata*) and Indian ricegrass (*Oryzopsis hymenoides*) (Bromley and Gese 2001). Sim-Julian Lambing Range (681 km^2), and Wasatch Ridge were located southwest of Kemmer, WY and northwest of Evanston, WY, respectively. Habitat within Sim-Julian Lambing Range and Wasatch Ridge was similar. Common vegetation includes big sagebrush (*Artemisia tridentata*), aspen (*Populus tremuloides*), Utah serviceberry (*Amelanchier utahensis*), mountain mahogany (*Cercocarpus montanus*) and antelope bitterbrush (*Purshia tridentata*).

METHODS

Coyote Removal

Wildlife Services personnel conducted most (>90%) of the coyote removals. Several private contractors also removed coyotes within some of the study sites. These contractors were all experienced at removing coyotes and collected data in the same format as WS.

Removals were accomplished primarily by aerial gunning from a fixed-wing aircraft and helicopter, although some trapping and ground shooting occurred. One site from each pair was subjected to intense coyote removals and the other was not. I define intense coyote removal as an area where >25 hours/1,000 km^2 are spent aerial gunning within the 12 month period leading up to ungulate parturition. Coyote removal data were standardized in two ways for each study-site. The first standardization was performed by calculating the number of coyotes removed and hours of effort spent per 1,000 km^2. Data were also standardized by calculating the number of coyotes removed per hour of effort per 1,000 km^2. This was done to attain a more accurate measure of the intensity which coyotes were being removed. Two of the coyote removal sites had a history of intense coyote removal prior to this study. In 2007, intense coyote removal occurred prior to ungulate parturition on the Pomeroy-Slate Creek and Sim-Julian Lambing Range study sites. The rest of the sites did not receive intense coyote removal prior to ungulate parturition in 2007. In 2008, all coyote removal sites (Aspen Mountain, Bush Creek, Delaney Rim, Flat Top Mountain, Pomeroy-Slate Creek, Sim-Julian Lambing Range) received intense coyote removal prior to ungulate parturition and all non-removal sites did not. Four sites where removal was initiated during this study had not been subjected to intense coyote removal for > 8 years prior to this study (R. Merrell, USDA APHIS Wildlife Services, personal communication). I collected baseline data for 4 of the 6 pairs during the first year. Removal efforts where initiated in late July 2007 and continued through March 2008. Wildlife Services and private contractors provided coyote removal data for all 12 study sites. These data consisted of the number of coyotes removed, number of hours spent aerial gunning, number of hours spent hunting or trapping coyotes on the ground, and total number of hours spent removing coyotes.

To examine the influence of timing on the effectiveness of removals, I classified coyote removal data into 3 time periods: long, intermediate and short. The long period included coyote removal conducted during the 12–month period prior to ungulate parturition (June–May), the intermediate period included coyote removal conducted within 8 months of ungulate parturition (October–May), and the short period included coyote removal conducted within 5 months of ungulate parturition (January–May).

Ungulate Counts

Ungulate counts were conducted similar to the methods described by Connolly (1981), Lopez et al. (2004), and Harrington and Conover (2007). Each study-site was surveyed weekly during July–August and bi-weekly during September 2007–2008. One permanent transect was placed in the middle of each study-site along roads. All of the roads used as transects were dirt or gravel and few other vehicles were encountered during the surveys. Transect length varied from 17–27 km depending upon availability of roads. The location of transects were not changed during the study, and all were surveyed by the same person. Surveys were conducted from the same start position each time using a pickup truck traveling 25 km/hr during the first 2 hours after sunrise or the last 2 hours prior to sunset. Surveys were conducted regardless of weather conditions. All ungulates observed within 1,600 m were identified to species (mule deer, pronghorn), sex, and age (fawn, adult) using binoculars and a spotting scope. I estimated the ungulate's perpendicular distance from the transect using a laser rangefinder and recorded the group size. I estimated fawn survival for each study-site by calculating fawn:doe ratios from my survey data (Harrington and Conover 2007). Ungulate density indices for each site were calculated as the number of ungulates seen per km of transect.

Pronghorn and mule deer data were collected for Aspen Mountain, Little Mountain, Delaney Rim and Sand Butte. Only pronghorn data were collected for Bush Creek, Hay Reservoir, Flat Top Mountain, Kinney Rim, Pomeroy-Slate Creek, and South Gate. Only mule deer data were collected for Sim-Julian Lambing Range and Wasatch Ridge. Pretreatment data (2007) were collected for 4 of the 5 pairs of sites where pronghorn occurred and 2 of the 3 pairs of sites where mule deer occurred. Pretreatment data were unavailable for one pair of sites where pronghorn occurred and one pair of sites where mule deer occurred because these sites had a history of intense coyote removal.

Coyote Density Index

Coyote scat counts have been found to be highly correlated with coyote density and thus provide a good index for comparing coyote density between areas (Knowlton 1984). Coyote relative abundance was estimated for each site in 2008 using coyote scat counts (Clark 1972, Andelt and Andelt 1984, Knowlton 1984). Scat counts were not conducted in 2007 due to a lack of resources. I systematically placed 10 transects, each 1 km in length, along dirt roads within the boundaries of each study-site. I walked transects once in each direction and all scats were counted and removed. I sampled all sites once every 14 days from June–August. Numbers of scats counted were standardized by the number of days between surveys and transect length.

Statistical Analysis

I analyzed pronghorn and mule deer data separately. Data for the 2 pairs of sites where mule deer occurred were averaged monthly to create 3 separate sampling periods (July, August, and September). This was done to account for low numbers of mule deer seen on the Delaney Rim study-site. Data for the 4 pairs of sites where pronghorn occurred were adequate to use observations from each week as the sampling period.

Sites were compared between years. Presence or absence of intense coyote removals was the independent variable used in this analysis. Dependent variables included fawn survival measured as fawn:doe ratios, the number of fawns, number of does, and total number of ungulates seen per km of transect.

I compared the change in fawn:doe ratios and relative ungulate density indices between 2007 and 2008 to test whether fawn survival and relative ungulate density were different between coyote removal and non-removal sites. Data for each individual year (2007 and 2008) were also compared between coyote removal and non-removal sites. I used a repeated-measures ANOVA (PROC MIXED; SAS Institute 2003) to test the results for statistical significance ($P \leq 0.05$).

I compared fawn:doe ratios, and the relative density of ungulates to coyote removal data using simple linear regressions (PROC REG; SAS Institute 2003) to determine if any differences were observed in treatment and control sites. Regressions were run using 3 separate periods of coyote removal data to determine if any differences could be related to temporal effects. I made the assumption that coyote removals performed during 1 year would not affect coyote densities or predation rates the following year (Knowlton et al. 1999, Wagner and Conover 1999, Harrington and Conover 2007). Thus, I considered the experimental unit for this analysis to be a site-year.

Pronghorn and mule deer densities were estimated for each study-site using program DISTANCE (Thomas et al. 2006). I collected line transect data consisting of the distance that each observed ungulate was located perpendicular to the transect and cluster size during ungulate counts. I modeled detection functions, g(y), using program DISTANCE (Thomas et al. 2006). Information provided in Buckland et al. (2001), Buckland et al. (2004), and Thomas et al. (2006) was used to determine detection functions during modeling and in the model selection process. Detection functions considered for use during modeling included a half-normal key function with a cosine series expansion, a half-normal key function with a hermite polynomial series expansion, a hazard-rate key function with a cosine series expansion, a hazard-rate key function with a simple polynomial series expansion, a uniform key function with a cosine series expansion, and a uniform key function with a simple polynomial series expansion. Assessment of the shape criterion, Chi-square goodness of fit test, and AIC values were used to select the best model. Data were combined across sampling periods occurring in the months of July–September and densities were estimated for both pronghorn and mule deer for each site for 2007 and 2008. I was unable to calculate ungulate densities for each sampling period due to a lack of data. Thus, I combined data for the sampling periods, and calculated a density estimate each year for all study sites. I ran 4 separate DISTANCE analyses for pronghorn and mule deer. These 4 analyses were broken down for each year and type of management (2007 removal sites, 2007 non-removal sites, 2008 removal sites, 2008 non-removal sites). Thus, ungulate density was not included as a variable in the analysis using the repeated-measures ANOVA (PROC MIXED; SAS Institute 2003) but was including in the analysis using simple linear regressions (PROC REG; SAS Institute 2003).

Coyote density indices were used to test if coyote density differed between coyote removal and non-removal sites. The experimental unit for this analysis was the study-site, and I used a repeated-measures ANOVA to test the results for statistical significance ($P \leq 0.05$).

RESULTS

Coyote Removal Indices

A total of 1,219 coyotes and mean of 203 coyotes (SE = 44) were removed from each of the 6 coyote removal sites in the 12–month period leading up to ungulate parturition in 2008. A total of 1,879 hours and mean of 313 hours (SE = 78) of effort were spent by WS and private contractors removing coyotes from each removal site. These included a total of 273 hours and mean of 45 hours (SE = 9) spent aerial gunning at each removal site. The rest of the hours were spent on the ground shooting and trapping coyotes.

A mean of 195 coyotes/1,000 km^2 (SE = 38) were removed from each treatment site during the 12–month period leading up to ungulate parturition in 2008. A mean of 329 hours/1,000 km^2 (SE = 96) were spent by WS and private contractors removing coyotes from each removal site. These included a mean of 46 hours/1,000 km^2 (SE = 10) spent aerial gunning at each removal site. The rest of the hours were spent on the ground shooting and trapping coyotes. A mean of 5.56 coyotes/aerial gunning hour/1,000 km^2 (SE = 2.12), 0.55 coyotes/ground work hour/1,000 km^2 (SE = 0.18), and 1.18 coyotes/total effort hour/1,000 km^2 (SE = 0.62) were removed from each removal site during the 12–month period leading up to ungulate parturition in 2008.

Effects of Coyote Removal on Coyote Density

A total of 1,406 coyote scats were observed during 2008. A mean of 0.05 scats/km/day (SE = 0.01) were observed across all study sites. Scats observed within coyote removal sites ($\bar{x}$ = 0.04 scats/km/day, SE = 0.01) was lower (F = 9.76; df = 1, 10; P =0.01) than that for non-removal sites ($\bar{x}$ = 0.07 scats/km/day, SE = 0.02).

Pronghorn Density Estimates

Pooled estimates of pronghorn density were higher for the coyote removal sites than the non-removal sites during 2007 and 2008 (Fig. 2 and 3). Increases in pronghorn density were recorded in 4 of the 5 coyote removal sites between 2007 and 2008, whereas a decrease in pronghorn density was recorded in 4 of the 5 non-removal sites. The pooled estimates of pronghorn density across coyote removal sites increased by 0.75 pronghorn/km^2. In contrast, the pooled estimate of pronghorn density across non-removal sites decreased by 0.5 pronghorn/km^2.

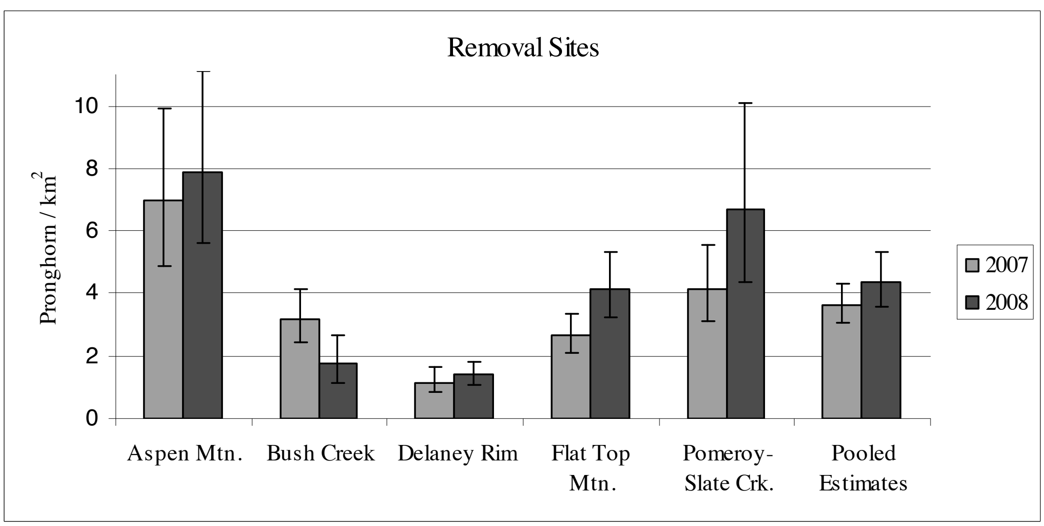

Figure 2. Density estimates of pronghorn within coyote removal sites for 2007 and 2008. Error bars represent 95% confidence intervals, Wyoming Coyote Predation Study, 2008.

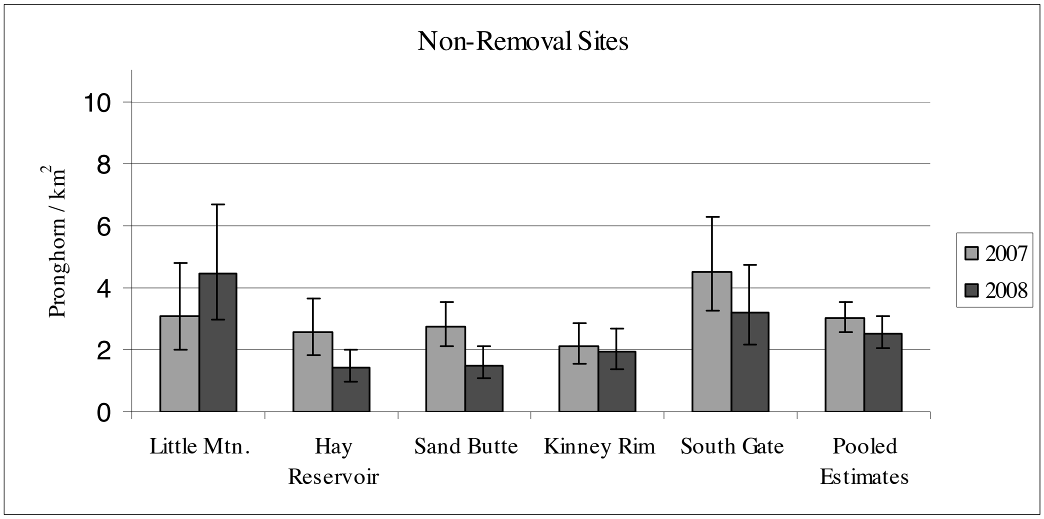

Figure 3. Pronghorn density estimates within non-removal sites during 2007 and 2008. One site (South Gate) received some coyote removal in 2007 and 2008. Coyotes were not removed on any of the other sites in 2007 and 2008. Error bars represent 95% confidence intervals, Wyoming Coyote Predation Study, 2008.

Mule Deer Density Estimates

Pooled estimates of mule deer density were higher for the non-removal sites than the coyote removal sites during 2007 and 2008 (Fig. 4 and 5). Increases in mule deer density were recorded on 2 of the 3 coyote removal sites between 2007 and 2008, whereas a decrease in mule deer density was recorded on all 3 non-removal sites. The pooled estimate of mule deer density decreased between 2007 and 2008 for both the coyote removal and non-removal sites. A decrease of 0.41 mule deer/km^2 was recorded within the coyote removal sites. A decrease of 1.41 mule deer/km^2 was recorded within the non-removal sites.

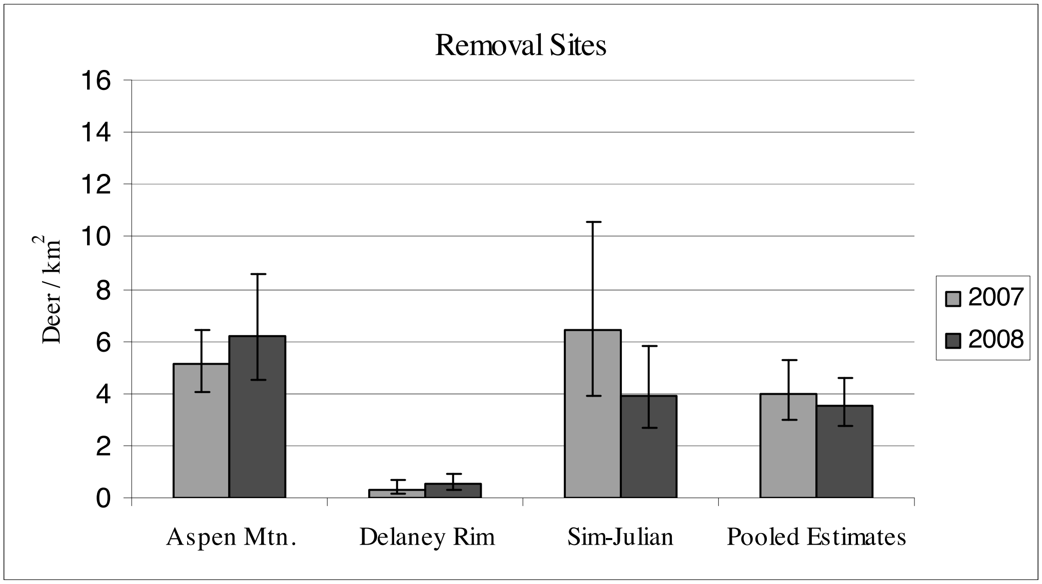

Figure 4. Mule deer density estimates within coyote removal sites during 2007 and 2008. One site (Sim-Julian Lambing Range) received intensive coyote removal in 2007. All sites received intensive coyote removal in 2008. Error bars represent 95% confidence intervals, Wyoming Coyote Predation Study, 2008.

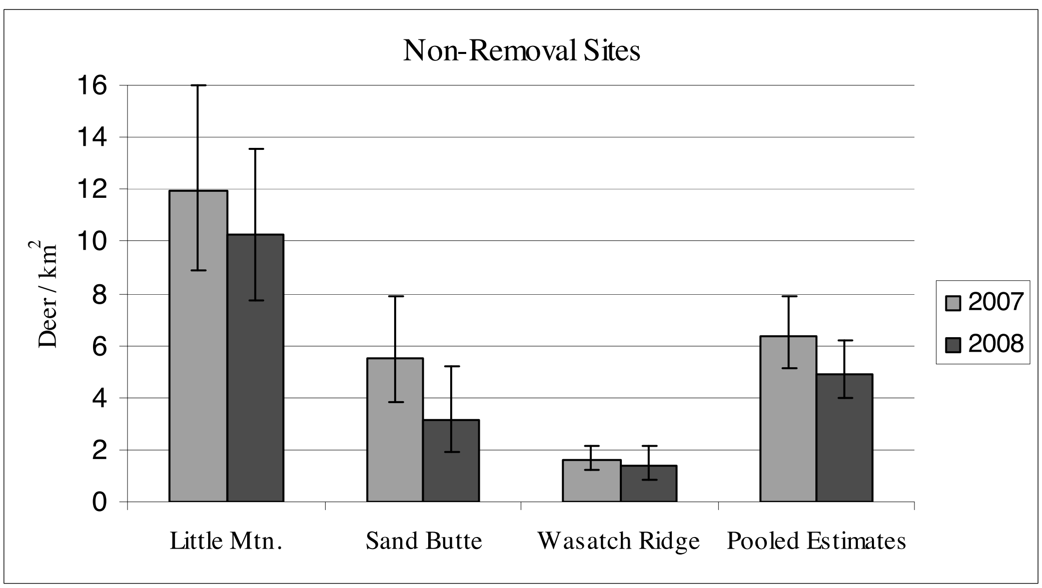

Figure 5. Mule deer density estimates within non-removal sites during 2007 and 2008. One site (Wasatch Ridge) received some coyote removal in 2007 and 2008. Coyotes were not removed on any of the other sites in neither 2007 or 2008. Error bars represent 95% confidence intervals, Wyoming Coyote Predation Study, 2008.

Relationship of Coyote Removal to Pronghorn

Fawn:Doe Ratios and Density Indices

I observed a mean of 2.0 does per km (SE = 0.2), 1.0 fawn per km (SE = 0.2), 4.0 total pronghorn per km (SE = 0.4) and 50 fawns per 100 does (SE = 7) at all sites where pronghorn occurred. No difference in the change in number of fawns per 100 does between years existed between coyote removal sites and non-removal sites ($P = 0.06$). No differences in treatment effect were seen between the removal and non-removal sites in the number of does ($P = 0.54$), fawns ($P = 0.09$) or total pronghorn seen per km (Table 1). There were no differences between coyote removal and non-removal sites during the pretreatment year, 2007 (Table 2). However, in 2008 the number of does ($P = 0.01$), fawns ($P = 0.01$), and total pronghorn ($P < 0.01$) seen per km were all higher in the coyote removal sites than non-removal sites (Table 3).

Table 1. Effect of management type (coyote removal vs. non-removal) on change in number of does per km, fawns per km, total pronghorn per km, and fawns per 100 does between 2007 (pre-treatment year) and 2008 (treatment year), Wyoming Coyote Predation Study, 2008.

	Manangement Type						
	Coyote removal		Non-removal				
Variable	$\bar{x}$	SE	$\bar{x}$	SE	*df*	*F*	*P*
Does per km	0.39	0.25	0.16	0.37	1,6	0.42	0.539
Fawns per km	0.03	0.07	-0.31	0.11	1,6	4.13	0.088
Pronghorn per km	0.58	0.46	-0.10	0.48	1,6	1.02	0.352
Fawns per 100 does	-6.50	5.70	-21.90	13.22	1,6	5.45	0.058

Table 2. Effect of management type (coyote removal vs. non-removal) on number of pronghorn does per km, pronghorn fawns per km, total pronghorn per km, and pronghorn fawns per 100 does for 2007 (pre-treatment year), Wyoming Coyote Predation Study, 2008.

	Manangement Type						
	Coyote removal		Non-removal				
Variable	$\bar{x}$	SE	$\bar{x}$	SE	*df*	*F*	*P*
Does per km	2.07	0.57	1.50	0.14	1,6	3.11	0.128
Fawns per km	1.03	0.52	0.75	0.22	1,6	1.28	0.301
Pronghorn per km	4.23	1.17	2.83	0.34	1,6	5.09	0.065
Fawns per 100 does	43.58	8.85	50.80	15.78	1,6	1.11	0.332

Table 3. Effect of management type (coyote removal vs. non-removal) on number of pronghorn does per km, pronghorn fawns per km, total pronghorn per km, and pronghorn fawns per 100 does for 2008 (treatment year), Wyoming Coyote Predation Study, 2008.

	Manangement Type						
	Coyote removal		Non-removal				
Variable	$\bar{x}$	SE	$\bar{x}$	SE	*df*	*F*	*P*
Does per km	2.17	0.48	1.80	0.19	1,8	10.8	0.011
Fawns per km	1.04	0.55	0.65	0.31	1,8	11.14	0.01
Pronghorn per km	4.23	1.02	3.10	0.36	1,8	17.88	0.003
Fawns per 100 does	42.04	16.40	38.97	20.50	1,8	0.46	0.518

Three separate regression analyses were performed using the 3 coyote-removal periods (long, intermediate, and short). Analysis using the short period of coyote-removal best explained the variation among sites where pronghorn occurred. Thus, the following results were derived using values from the short time period of coyote removal as independent variables. Pronghorn fawn:doe ratios were unrelated to the number of coyotes removed (R^2= 0.16, F = 3.35, P = 0.08), number of ground hours worked (R^2 = 0.18, F = 3.83, P = 0.07), number of total hours worked (R^2 = 0.2, F = 4.37, P = 0.05), coyotes/aerial gunning hour (R^2 = 0.1, F = 1.95, P = 0.18), coyotes/ground work hour (R^2 = 0.12, F = 2.35, P = 0.14), and coyotes/total effort hour (R^2 = 0.12, F = 2.52, P = 0.13).

The number of pronghorn does, pronghorn fawns, total pronghorn, and pronghorn density were unrelated to the number of coyotes/ground work hour, and coyotes/total effort hour (Tables 4 and 5). However, the number of coyotes removed, coyotes/aerial gunning hour, ground hours worked, and total hours worked were all positively correlated with pronghorn density estimates as well as the number of pronghorn does, pronghorn fawns, and total number of pronghorn seen per km (Tables 4 and 5).

Table 4. Correlations between variables monitoring the intensity of coyote removal with number of pronghorn does observed per km of transect and pronghorn fawns observed per km during 2007 and 2008 at the 10 sites where pronghorn occurred, Wyoming Coyote Predation Study, 2008.

	Pronghorn does per km			Pronghorn fawns per km		
Variable	R^2	F	P	R^2	F	P
Coyotes/aerial gunning hour	0.24	5.6	0.029	0.22	5.1	0.037
Coyotes/ground work hour	0.07	1.45	0.244	0.1	1.89	0.186
Coyotes/ total effort hour	0.07	1.37	0.257	0.09	1.87	0.188
Coyotes removed	0.57	24.28	<0.001	0.46	15.20	0.001
Ground hours worked	0.32	8.41	0.01	0.40	11.76	0.003
Total hours worked	0.34	9.24	0.007	0.43	13.70	0.002

Table 5. Correlations between variables monitoring the intensity of coyote removal with total number of pronghorn observed per km of transect and pronghorn density estimates during 2007 and 2008 at the 10 sites where pronghorn occurred, Wyoming Coyote Predation Study, 2008.

	Total pronghorn per km			Pronghorn density		
Variable	R^2	F	P	R^2	F	P
Coyotes/aerial gunning hour	0.28	7.13	0.016	0.2	4.55	0.047
Coyotes/ground work hour	0.13	2.62	0.123	0.06	1.08	0.312
Coyotes/ total effort hour	0.12	2.55	0.128	0.05	1.05	0.32
Coyotes removed	0.64	32.18	<0.001	0.48	16.85	<0.001
Ground hours worked	0.42	12.99	0.002	0.25	6.04	0.024
Total hours worked	0.45	14.75	0.001	0.28	7.08	0.016

Relationship of Coyote Removal to Mule

Deer Fawn:Doe Ratios and Density Indices

A mean of 0.9 does per km (SE = 0.2), 0.6 fawns per km (SE = 0.1), 1.8 total mule deer per km (SE = 0.4), and 56 fawns per 100 does (SE = 5) were observed for all sites where mule deer occurred. No differences were recorded between the removal and non-removal sites in the number of does ($P = 0.82$), fawns ($P = 0.5$), or total deer ($P = 0.69$) seen per km (Table 6). No differences in does per km ($P = 0.33$), fawns per km ($P = 0.36$), total deer per km ($P = 0.42$), or fawns per 100 does ($P = 0.29$) were recorded during 2007 (pre-removal year) (Table 7). No differences in does per km ($P = 0.88$), fawns per km ($P = 0.90$), total deer per km ($P = 0.99$), or fawns per 100 does ($P = 0.39$) were recorded during 2008 (Table 8). The number of coyotes removed, ground hours worked, total hours worked , coyotes/ground work hour, coyotes/aerial gunning hour, and coyotes/total effort hour were unrelated to mule deer fawn:doe ratios, mule deer density, the number of mule deer does, mule deer fawns, and total number of mule deer seen per km (Tables 9 and 10).

Table 6. Effect of management type (coyote removal vs. non-removal) on change in number of mule deer does per km, mule deer fawns per km, total mule deer per km, and mule deer fawns per 100 does between 2007 (pre-treatment year) and 2008 (treatment year), Wyoming Coyote Predation Study, 2008.

	Management Type						
	Coyote removal		Non-removal				
Variable	$\bar{x}$	SE	$\bar{x}$	SE	*df*	*F*	*P*
Does per km	0.14	0.13	0.19	0.23	1,2	0.07	0.818
Fawns per km	0.16	0.13	0.07	0.06	1,2	0.67	0.499
Mule deer per km	0.43	0.32	0.32	0.13	1,2	0.21	0.691
Fawns per 100 does	19.80	11.68	0.40	15.06	1,2	2.52	0.254

Table 7. Effect of management type (coyote removal vs. non-removal) on number of mule deer does per km, mule deer fawns per km, total mule deer per km, and mule deer fawns per 100 does for 2007 (pre-treatment year), Wyoming Coyote Predation Study, 2008.

	Management Type						
	Coyote removal		Non-removal				
Variable	$\bar{x}$	SE	$\bar{x}$	SE	*df*	*F*	*P*
Does per km	0.67	0.60	1.19	0.36	1,2	1.64	0.329
Fawns per km	0.39	0.37	0.76	0.38	1,2	1.38	0.361
Mule deer per km	1.34	1.21	2.21	0.85	1,2	1.04	0.416
Fawns per 100 does	39.43	20.91	60.44	13.62	1,2	2.07	0.287

Table 8. Effect of management type (coyote removal vs. non-removal) on number of mule deer does per km, mule deer fawns per km, total mule deer per km, and mule deer fawns per 100 does for 2008 (treatment year), Wyoming Coyote Predation Study, 2008.

	Management Type						
	Coyote removal		Non-removal				
Variable	$\bar{x}$	SE	$\bar{x}$	SE	*df*	*F*	*P*
Does per km	0.91	0.43	0.97	0.53	1,4	0.03	0.876
Fawns per km	0.56	0.29	0.59	0.30	1,4	0.02	0.9
Mule deer per km	1.82	0.89	1.83	0.89	1,4	<0.01	0.99
Fawns per 100 does	55.96	6.26	61.88	1.33	1,4	0.93	0.389

Table 9. Correlations between variables monitoring the intensity of coyote removal with the number of mule deer fawns per 100 does, mule deer does observed per km of transect, and mule deer fawns observed per km during 2007 and 2008 at the 6 sites where mule deer occurred, Wyoming Coyote Predation Study, 2008.

	Mule deer fawn:doe ratios			Mule deer does per km			Mule deer fawns per km		
Variable	R^2	*F*	*P*	R^2	*F*	*P*	R^2	*F*	*P*
Coyotes/aerial gunning hour	0.03	0.32	0.581	0.11	1.22	0.294	0.08	0.91	0.363
Coyotes/ground work hour	0.08	0.88	0.37	<0.01	0.0	0.999	0.01	0.08	0.785
Coyotes/ total effort hour	0.08	0.82	0.387	<0.01	0.01	0.906	<0.01	0.02	0.882
Coyotes removed	0.19	2.37	0.155	0.18	2.14	0.174	0.24	3.17	0.106
Ground hours worked	0.13	1.44	0.258	0.11	1.27	0.285	0.16	1.97	0.191
Total hours worked	0.14	1.56	0.240	0.13	1.47	0.254	0.19	2.28	0.162

Table 10. Correlations between variables monitoring the intensity of coyote removal with the total number of mule deer observed per km of transect and mule deer density estimates during 2007 and 2008 at the 6 sites where mule deer occurred, Wyoming Coyote Predation Study, 2008.

	Mule deer per km			Mule deer density		
Variable	R^2	F	P	R^2	F	P
Coyotes/aerial gunning hour	0.1	1.11	0.318	0.08	0.85	0.377
Coyotes/ground work hour	<0.01	<0.01	0.984	0.02	0.17	0.689
Coyotes/ total effort hour	<0.01	0.2	0.895	0.02	0.25	0.629
Coyotes removed	0.24	3.22	0.103	0.02	0.17	0.691
Ground hours worked	0.12	1.30	0.280	<0.01	0.05	0.834
Total hours worked	0.13	1.54	0.243	<0.01	0.07	0.797

Effects of Timing on Efficacy of Coyote Removal

The number of coyotes removed January–May 2007 and 2008 (Short Period) explained more variation and was positively correlated with pronghorn density (R^2 = 0.48, F = 16.85, P < 0.001; Fig. 6) than the number of coyotes removed October–May 2007 and 2008 (Intermediate Period) (R^2 = 0.35, F = 9.68, P = 0.006; Fig. 7) or the number of coyotes removed July–May 2007 and 2008 (Long Period) (R^2 = 0.22, F = 5.06, P = 0.037; Fig. 8). This trend was present during analysis of both pronghorn and mule deer data and was consistent across all coyote-removal variables (number of coyotes removed, ground hours worked, total hours worked, coyotes/ground work hour, coyotes/aerial gunning hour, and coyotes/total effort hour).

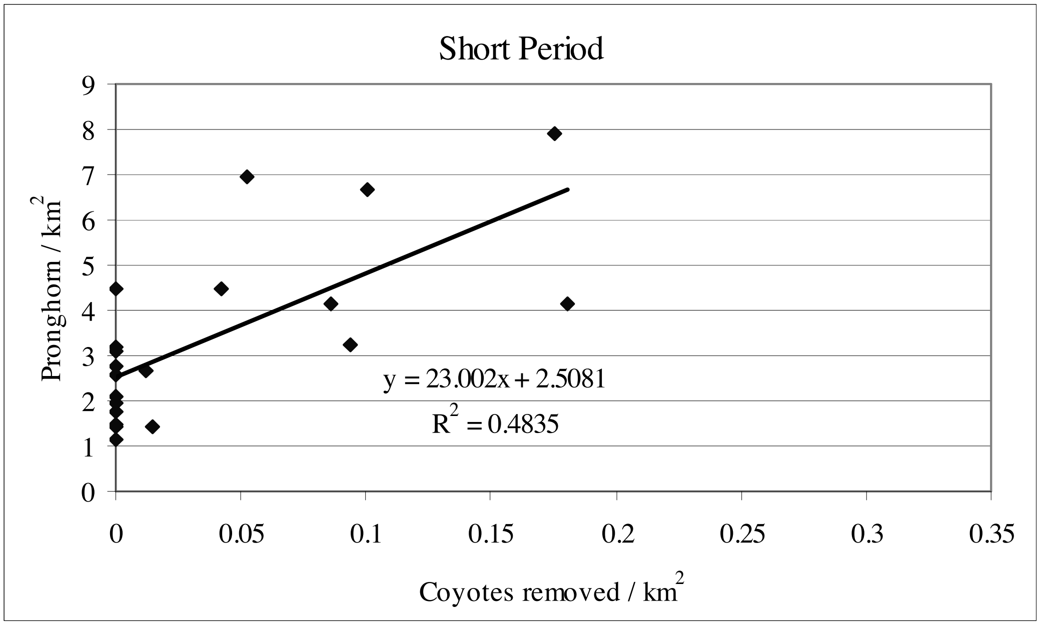

Figure 6. Pronghorn per km² against level of coyote removal during the short period (January–May) measured as number of coyotes removed per km², Wyoming Coyote Predation Study, 2008.

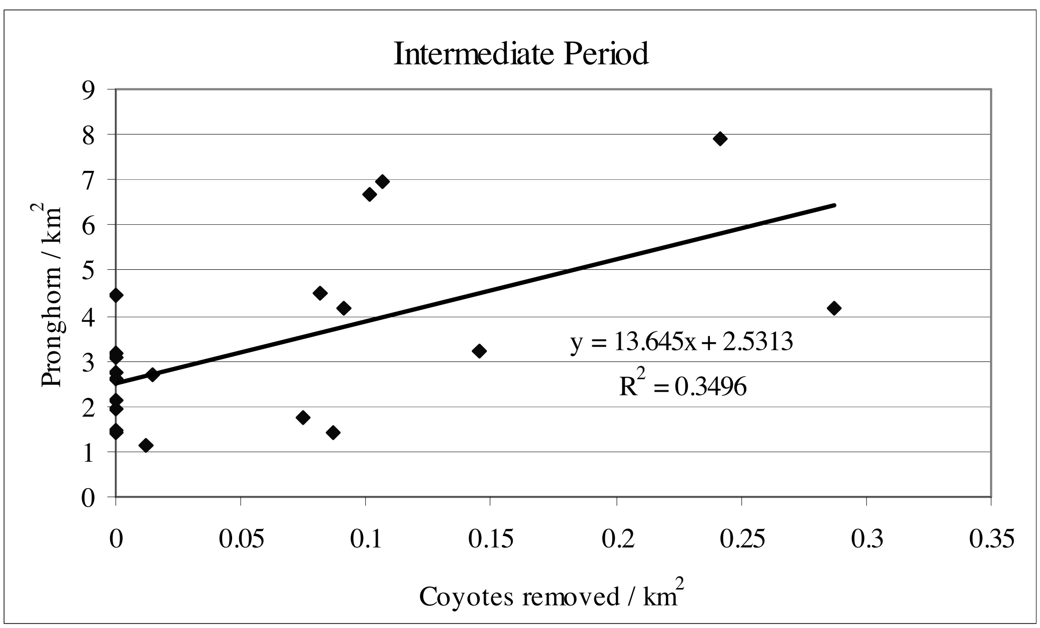

Figure 7. Pronghorn per km² against level of coyote removal during the intermediate period (October – May) measured as number of coyotes removed per km², Wyoming Coyote Predation Study, 2008.

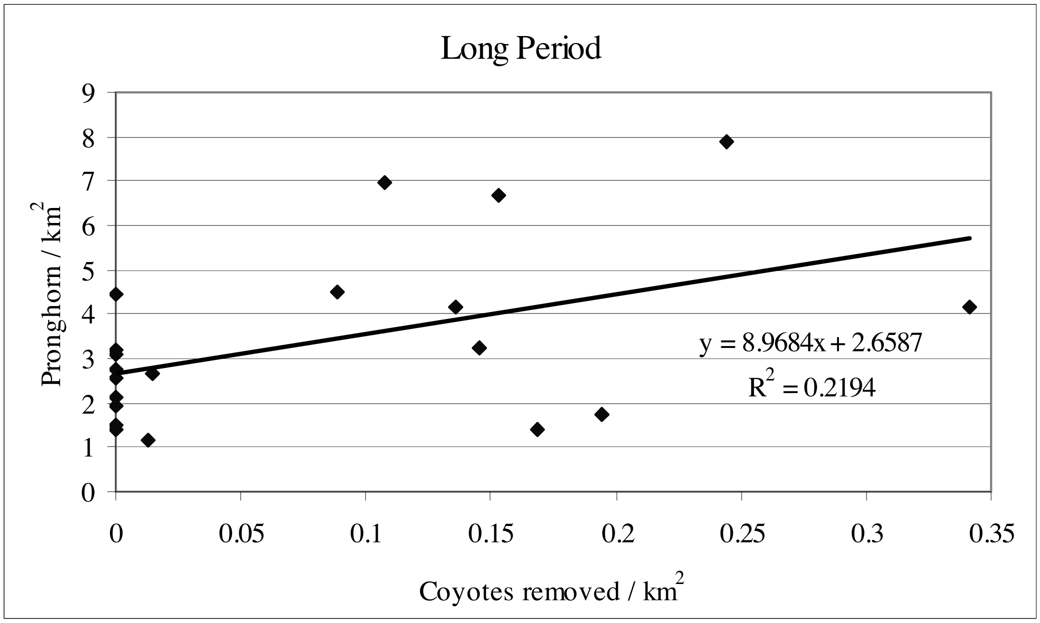

Figure 8. Pronghorn per km² against level of coyote removal during the long period (June–May) measured as number of coyotes removed per km², Wyoming Coyote Predation Study, 2008

DISCUSSION

Impact of Coyote Removal on Coyote Density

Preventive coyote removal has been defined as a management action where coyotes are removed from an area prior to the occurrence of damage such as a calf or lamb depredation (Wagner 1997, Conner et al. 1998, Knowlton et al. 1999, Wagner and Conover 1999, Mitchell et al. 2004, Harrington and Conover 2007). Published results regarding the effectiveness of preventive coyote removal on coyote populations and depredation on livestock and wildlife have been mixed.

I conducted scat counts from June until late August, the time period when ungulate fawns are most susceptible to coyote predation (Hamlin et al. 1984, Zimmer 2004, Jacques et al. 2007). I found that coyote scat indices were lower within coyote removal sites than non-removal sites. These data suggest that coyote removal during the desired time period reduced coyote density.

One difference between my study and earlier studies was the size of area over which coyotes were removed. Reducing coyote populations across large areas is usually more effective than over small areas due to the greater distances immigrating individuals have to travel and the high number of immigrants required to repopulate an area to pre-removal levels (Sargeant et al. 1995, Garrettson and Rohwer 2001, Conover 2002, Karki et al. 2007). This likely contributed to the lower coyote densities found within the coyote removal sites. My study comprised an area of 10,517 km^2, with mean size of the 6 coyote removal sites of 1,035 km^2. In contrast, most of the prior research on coyote removal has been conducted on areas < 1,000 km^2 (Ballard et al. 2001). These studies often lacked indices of coyote density within coyote removal and reference sites and when available these indices frequently were based on differing methods or sampling techniques.

Impact of Coyote Removal on Pronghorn

Populations

I found no difference in fawn:doe ratios, or pronghorn density indices between the pre-removal period (2007) and when coyotes were removed (2008). However, it appears that percentage of change in fawn:doe ratios between coyote removal and non-removal sites may have had some biological importance. Between 2007 and 2008, fawn:doe ratios decreased by a mean of 7 fawns per 100 does (15%) within coyote removal sites and 22 fawns per 100 does (43%) within the non-removal sites. Although the observed difference in fawn:doe ratios was not statistically significant ($P = 0.06$), the fact that the percentage of decline differed between the removal and non-removal sites suggests a density dependent effect. The 2007–2008 winter was extreme with heavier than average snowfall throughout southwest Wyoming (M. Zornes, Wyoming Game and Fish Department, personal communication). These extreme conditions likely contributed to the decrease in productivity during 2008.

Fawn:doe ratios were not correlated with the number of coyotes removed, ground hours worked, total hours worked, coyotes removed/aerial gunning hour, coyotes removed/ground work hour, or coyotes removed/total effort hour. This suggests that coyote removal did not affect fawn:doe ratios. Pronghorn density, number of does per km, number of fawns per km, and total number of pronghorn per km were also unrelated to coyotes removed/ground work hour, and coyotes removed/total effort hour. However, pronghorn density, number of does per km, number of fawns per km, and total number of pronghorn per km were positively correlated with the number of coyotes removed, ground hours worked, total hours worked, and coyotes removed/aerial gunning hour. This suggests that coyote removal may benefit pronghorn populations even though fawn:doe ratios appeared to be unrelated to coyote removal variables.

It is unclear why all pronghorn density measurements were positively correlated with the majority of coyote removal variables, but fawn:doe ratios were unrelated. Harrington and Conover (2007) found a similar result and suggested that pronghorn may have moved to areas where coyotes had been removed to avoid adjacent areas with higher coyote densities. This is possible, however, I propose another explanation, that coyote removal may have reduced coyote populations during the winter and increased winter survival of adults and fawns. Adult pronghorn are more vulnerable to coyote predation in the winter, especially in deep crusted snow (Barrett 1982, Gese and Grothe 1995). If coyote predation was an important mortality factor during the 2007–2008 winter coyote removal may have increased winter survival. This increase in winter survival could have resulted in increased pronghorn density.

Differences in overwinter survival of pronghorn between study sites could have biased the outcome of my study. Variation between the study sites in temperature and snowfall could affect the number of animals that survived until the summer. This could have affected the number of animals I recorded during my surveys and potentially biased my results.

Impact of Coyote Removal on Mule Deer

Populations

Fawn:doe ratios, and mule deer density indices between the pre-treatment year (2007) and the year coyotes were removed (2008) did not differ. Mule deer populations did not exhibit the same drop in productivity following the severe winter of 2007–2008, as observed in the pronghorn populations. Between 2007 and 2008, mule deer fawn:doe ratios increased by a mean of 20 fawns per 100 does (50%) within the coyote removal sites and remained constant within the non-removal sites.

It is unclear why mule deer populations examined during this study did not experience the same overall drop in productivity during 2008 as seen in pronghorn. Possible reasons for this could be due to differences in mule deer and pronghorn foraging behavior, winter habitats, or differences in physiological response to nutritional stress. Pronghorn have the ability to resorb fetuses during times of nutritional stress, unlike mule deer which generally give birth to smaller fawns when under nutritional stress (Barrett 1982, Andelt et al. 2004). This difference in physiology between pronghorn and mule deer may have affected fawn:doe ratios following the hard winter of 2007–2008.

Coyote removal variables were unrelated to mule deer fawn:doe ratios, mule deer density, number of does per km, number of fawns per km, and total number of mule deer per km. This suggests that coyote removal did not benefit mule deer in my study. However, it is important to note that fewer replicates for mule deer (6 sites) were available for analysis than for pronghorn (10 sites). Differences in the results between pronghorn and mule deer, may be due to actual differences in the effect coyote predation has on these 2 species, differences in habitat types that affect the ability of WS to effectively remove coyotes (removing coyotes in broken country with heavy brush is more difficult), or the lower number of replicates and thus reduced statistical power available during the mule deer analysis. Harrington and Conover (2007) found that coyote removal intensity was positively correlated with density of pronghorn and mule deer. It is remains unclear why Harrington and Conover (2007) detected an increase in density of mule deer, yet mule deer did not appear to increase in density during my study.

Impact of Timing on Efficacy of Coyote Removal

Coyote removal occurred over a broad range of time during this study. I found that coyote removal conducted in the late summer and fall was less beneficial to pronghorn than removal conducted in the winter and spring. Coyote removal conducted January–May (Short Period) explained more variation and was more positively correlated with fawn survival and ungulate density than coyote removal occurring October–May (Intermediate Period) or July–May (Long Period). This general trend was seen during the regression analyses for both pronghorn and mule deer and was consistent across all coyote removal variables (number of coyotes removed, ground hours worked, total hours worked, coyotes removed/aerial gunning hour, coyotes removed/ground work hour, coyotes removed/total effort hour). This indicates that coyote removals performed in the winter and spring benefit ungulates more than removals performed in the fall or summer.

Wagner and Conover (1999) reported the optimal time to remove coyotes for the benefit of livestock is during winter and spring. Removing coyotes during the winter and spring allows aerial gunners to take advantage of snow cover, is the period of time when coyote populations are at or near their lowest point of the year, is the time of year when breeding pairs of coyotes are particularly vulnerable and allows less time for transient coyotes to replace coyotes that were killed when removal efforts take place just prior to ungulate parturition (Knowlton 1972, Knowlton et al. 1999, Wagner and Conover 1999, Conover 2002, Harrington and Conover 2007).

Till and Knowlton (1983), Wagner and Conover (1999), and Harrington and Conover (2007) proposed an alternate hypothesis that removing coyotes during winter and spring may reduce predation on large herbivores by reducing the number of pairs with pups rather than reducing coyote density. Their hypothesis is based on the finding that most predation on sheep is caused by coyotes that have pups (Till and Knowlton 1983).

Results of my study support the hypothesis that the winter and spring is the optimal time to remove coyotes for the benefit of pronghorn. This is in agreement with the findings of several studies (Knowlton 1972, Knowlton et al. 1999, Wagner and Conover 1999, Conover 2002, Harrington and Conover 2007). However, other studies indicated coyote removal was not effective at either reducing coyote numbers or reducing depredations on livestock or wild ungulates (Conner et al. 1998, Mitchell et al. 2004, Hurley and Zager 2007). Results of my study do not agree with these previous studies and instead suggest that coyote removal did reduce coyote populations and likely benefited pronghorn.

MANAGEMENT IMPLICATIONS

The long term benefits of large scale predator removal on wildlife productivity continues to interest as populations decline. The results of my study suggest predator removal may benefit pronghorn populations, but the effects are subject to environmental factors.

I observed an increase in pronghorn density as the intensity of coyote removal increased. Coyote removal appeared to benefit pronghorn populations within my study sites, but not mule deer populations. I found that pronghorn density increased as the intensity of coyote removal increased. I also observed that coyote removal conducted in the winter and spring increased pronghorn productivity. Coyote removal had no observed effect on mule deer productivity.

If managers decide to use coyote removal as a management tool, efforts should be concentrated in the winter and spring to maximize the benefits pronghorn receive. Monitoring fawn:doe ratios and overall density of pronghorn before and during coyote removal efforts can help managers make better decisions regarding the use of coyote removal as a management tool.

LITERATURE CITED

Alldredge, W. A., R. D. Deblinger, and J. Peterson. 1991. Birth and fawn bed site selection by pronghorns in a sagebrush-steppe community. Journal of Wildlife Management 55:222–227.

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

Andelt, W. F., T. M. Pojar, and L. W. Johnson. 2004. Long-term trends in mule deer pregnancy and fetal rates in Colorado. Journal of Wildlife Management 68:542–549.

Ballard, W. B., and V. Van Ballenberghe. 1998. Moose-predator relationships: research and management needs. Alces 34:91–105.

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.

Ballard W. B., D. Lutz, T. W. Keegan, L. H. Carpenter, and J. C. deVos, Jr. 2003. Deer-predator relationships. Pages 177–218 *in* Mule deer conservation: issues and management strategies. Berryman Institute Press, Utah State University, Logan, USA.

Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs 169.

Barrett, M. W. 1982. Distribution, behavior, and mortality of pronghorns during a severe winter in Alberta. Journal of Wildlife Management 46:991–1002

Barrett, M. W. 1984. Movements, habitat use, and predation on pronghorn fawns in Alberta. Journal of Wildlife Management 48:542–550.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monograph 121:1–39.

Beale, D. M., and A. D. Smith. 1973. Mortality of pronghorn antelope fawns in western Utah. Journal of Wildlife Management 37:343–352.

Bromley, C., and E. M. Gese. 2001. Surgical sterilization as a method of reducing coyote predation on domestic sheep. Journal of Wildlife Management 65:510–519.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York, New York, USA.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2004. Advanced distance sampling: estimating abundance of biological populations. Oxford University Press, New York, New York, USA.

Clark, F. W. 1972. Influence of jackrabbit density on coyote population change. Journal of Wildlife Management 36:343–356.

Conner, M. M., M. M. Jaeger, T. J. Weller, and D. R. McCullough. 1998. Effect of coyote removal on sheep depredation in northern California. Journal of Wildlife Management 62:690–699.

Connolly, G. E. 1978. 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. 1981. Limiting factors and population regulation. Pages 245–285 *in* O.C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska, Lincoln, USA.

Conover, M. R. 2002. Resolving human-wildlife conflicts: the science of wildlife damage management. CRC, Boca Raton, Florida, USA.

deVos, J. C., Jr., M. R. Conover, and N. E. Headrick. 2003. Mule deer conservation: issues and management strategies. Jack H. Berryman Institute Press, Utah State University, Logan, USA.

Dunbar, M. R., and M. R. Giordano. 2002. Abundance and condition indices of coyotes on Hart Mountain National Antelope Refuge, Oregon. Western North American Naturalist 62:341–347.

Garrettson, P. R., and F. C. Rohwer. 2001. Effects of mammalian predator removal on production of upland-nesting ducks in North Dakota 65:398–405.

Gese, E. M., and S. Grothe. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. American Midland Naturalist 133:36–43.

Gregg, M. A., M. Brady, K. M. Kilbride, and M. R. Dunbar. 2001. Birth synchrony and survival of pronghorn fawns. Journal of Wildlife Management 65:19–24.

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.

Hurley, M., and P. Zager. 2007. Southeast mule deer ecology. Idaho Department of Fish and Game Project W-160-R-33, Subproject 51, Boise, Idaho, USA.

Jacques, C. N., J. A. Jenks, J. D. Sievers, D. E. Roddy, and F. G. Lindzey. 2007. Survival of pronghorns in western South Dakota. Journal of Wildlife Management 71:737–743.

Karki, S. M., E. M. Gese, and M. L. Klavetter. 2007. Effects of coyote population reduction on swift fox demographics in southeastern Colorado. Journal of Wildlife Management 71:2707–2718

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

Knowlton, F. F. 1984. Feasibility of assessing coyote abundance on small areas. U.S. Fish and Wildlife Service, Denver Wildlife Research Center, Logan, Utah, 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.

Lingle, S. 2000. Seasonal variation in coyote feeding behaviour and mortality of white-tailed deer and mule deer. Canadian Journal of Zoology 78:85–99.

Lopez, R. R., N. J. Silvy, B. L. Pierce, P. A. Frank, M. T. Wilson, and K. M. Burke. 2004. Population density of the endangered Florida Key deer. Journal of Wildlife Management 68:570–575.

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.

Phillips, G. E., and G. C. White. 2003. Pronghorn population response to coyote control: modeling and management. Wildlife Society Bulletin 31:1162–1175.

Sacks, B. N., and J. C. C. Neale. 2007. Coyote abundance, sheep predation, and wild prey correlates illuminate Mediterranean trophic dynamics. Journal of Wildlife Management 71:2404–2411.

Sargeant, A. B., M. A. Sovada, and T. L. Shaffer. 1995. Seasonal predator removal relative to hatch rate of duck nests in waterfowl production areas. Wildlife Society Bulletin 23:507–513

SAS Institute. 2003. Version 9.1.3. SAS Institute, Cary, North Carolina, USA.

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.

Stoddart, C. L., R. E. Griffiths, and F. F. Knowlton. 2001. Coyote responses to changing jackrabbit abundance affect sheep predation. Journal of Range Management 54:15–20

Thomas, L., J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, J. R. B. Bishop, and

T. A. Marques. 2006. Distance 5.0. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, St. Andrews, United Kingdom.

Till, J. A., and F. F. Knowlton. 1983. Efficacy of denning in alleviating coyote depredation upon domestic sheep. Journal of Wildlife Management 47:1018–1025.

Wagner, K. K. 1997. Preventive predation management: an evaluation using winter aerial coyote hunting in Utah and Idaho. Dissertation, Utah State University, Logan. USA.

Wagner, K. K., and M. R. Conover. 1999. Effect of preventive coyote hunting on sheep losses to coyote predation. Journal of Wildlife Management 63:606–612.

White, P. J., and R. A. Garrott. 2005. Yellowstone's ungulates after wolves – expectations, realizations and predictions. Biological Conservation 125:141–152.

Zager, P., and J. Beecham. 2006. The role of American black bears and brown bears as predators on ungulates in North America. Ursus 17:95–108.

Zimmer, J. E. 2004. Pronghorn productivity and fawn survival in central and southeastern Wyoming. Thesis, University of Wyoming, Laramie, USA.

APPENDICES

APPENDIX A. COMBINED COYOTE REMOVAL DATA

Total Coyotes Removed By Wildlife Services and Private Contractors

	Coyotes removed		
Site-year	Short period	Intermediate period	Long period
2007			
Aspen Mountain	66	134	136
Bush Creek	0	0	0
Delaney Rim	0	21	22
Flat Top Mountain	10	12	12
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	84	89	133
Sand Butte	0	0	0
Sim-Julian Lambing Range	77	77	88
South Gate	24	46	50
Wasatch Ridge	1	1	7
2008			
Aspen Mountain	221	305	308
Bush Creek	0	53	138
Delaney Rim	26	153	297
Flat Top Mountain	148	236	280
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	98	99	150
Sand Butte	0	0	0
Sim-Julian Lambing Range	39	46	46
South Gate	53	82	82
Wasatch Ridge	16	16	30

Total Hours Spent Removing Coyotes

	Total hours worked		
Site-year	Short period	Intermediate period	Long period
2007			
Aspen Mountain	124.4	258.3	300.3
Bush Creek	0	0	0
Delaney Rim	0	4.1	4.1
Flat Top Mountain	4.5	9.5	9.5
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	344.6	348	536.7
Sand Butte	0	0	0
Sim-Julian Lambing Range	228.1	228.1	296.7
South Gate	43.7	148.5	179.3
Wasatch Ridge	8	8	80
2008			
Aspen Mountain	125.7	240	244.6
Bush Creek	0	12.9	49.8
Delaney Rim	19.5	102.8	263.5
Flat Top Mountain	116.2	234.5	532
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	142	180	544.3
Sand Butte	0	0	0
Sim-Julian Lambing Range	142.6	215.2	244.7
South Gate	26.2	186.2	186.2
Wasatch Ridge	34	34	136

Ground Hours Spent Removing Coyotes

	Ground hours worked		
Site-year	Short period	Intermediate period	Long period
2007			
Aspen Mountain	122	254	296
Bush Creek	0	0	0
Delaney Rim	0	0	0
Flat Top Mountain	3	8	8
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	292	292	461
Sand Butte	0	0	0
Sim-Julian Lambing Range	192	192	257
South Gate	36	140	168
Wasatch Ridge	8	8	80
2008			
Aspen Mountain	82	194.5	198.5
Bush Creek	0	0	4
Delaney Rim	17	88.5	212
Flat Top Mountain	101.5	213	510.5
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	100.5	138.5	460
Sand Butte	0	0	0
Sim-Julian Lambing Range	122.5	191.5	221
South Gate	20	180	180
Wasatch Ridge	33	33	135

Aerial Hours Spent Removing Coyotes

	Aerial hours worked		
Site-year	Short period	Intermediate period	Long period
2007			
Aspen Mountain	2.4	4.3	4.3
Bush Creek	0	0	0
Delaney Rim	0	4.1	4.1
Flat Top Mountain	1.5	1.5	1.5
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	52.6	56	75.7
Sand Butte	0	0	0
Sim-Julian Lambing Range	36.1	36.1	39.7
South Gate	7.7	8.5	11.3
Wasatch Ridge	0	0	0
2008			
Aspen Mountain	43.7	45.5	46.1
Bush Creek	0	12.9	45.8
Delaney Rim	2.5	14.3	51.5
Flat Top Mountain	14.7	21.5	21.5
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	41.5	41.5	84.3
Sand Butte	0	0	0
Sim-Julian Lambing Range	20.1	23.7	23.7
South Gate	6.2	6.2	6.2
Wasatch Ridge	1	1	1

APPENDIX B. WILDLIFE SERVICES COYOTE REMOVAL DATA

Coyotes Removed by Wildlife Services

	Coyotes removed		
Site-year	Short period	Intermediate period	Long period
2007			
Aspen Mountain	66	134	136
Bush Creek	0	0	0
Delaney Rim	0	21	22
Flat Top Mountain	10	12	12
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	50	50	94
Sand Butte	0	0	0
Sim-Julian Lambing Range	28	28	39
South Gate	24	26	30
Wasatch Ridge	1	1	7
2008			
Aspen Mountain	65	149	152
Bush Creek	0	53	138
Delaney Rim	26	153	297
Flat Top Mountain	148	236	280
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	26	27	78
Sand Butte	0	0	0
Sim-Julian Lambing Range	21	28	28
South Gate	33	37	37
Wasatch Ridge	16	16	30

Total Hours Worked by Wildlife Services

	Total hours worked		
Site-year	Short period	Intermediate period	Long period
2007			
Aspen Mountain	124.4	258.3	300.3
Bush Creek	0	0	0
Delaney Rim	0	4.1	4.1
Flat Top Mountain	4.5	9.5	9.5
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	333.1	333.1	521.8
Sand Butte	0	0	0
Sim-Julian Lambing Range	209.8	209.8	278.4
South Gate	7.7	16.5	47.3
Wasatch Ridge	8	8	80
2008			
Aspen Mountain	87.4	201.7	206.3
Bush Creek	0	12.9	45.8
Delaney Rim	19.5	102.8	263.5
Flat Top Mountain	116.2	234.5	532
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	124	162	526.3
Sand Butte	0	0	0
Sim-Julian Lambing Range	130.2	202.8	232.3
South Gate	14.2	78.2	78.2
Wasatch Ridge	34	34	136

Ground Hours Worked by Wildlife Services

	Ground hours worked		
Site-year	Short period	Intermediate period	Long period
2007			
Aspen Mountain	122	254	296
Bush Creek	0	0	0
Delaney Rim	0	0	0
Flat Top Mountain	3	8	8
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	302	302	471
Sand Butte	0	0	0
Sim-Julian Lambing Range	192	192	257
South Gate	0	8	36
Wasatch Ridge	8	8	80
2008			
Aspen Mountain	82	194.5	198.5
Bush Creek	0	0	0
Delaney Rim	17	88.5	212
Flat Top Mountain	101.5	213	510.5
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	117	155	476.5
Sand Butte	0	0	0
Sim-Julian Lambing Range	122.5	191.5	221
South Gate	8	72	72
Wasatch Ridge	33	33	135

Aerial Hours Worked by Wildlife Services

	Aerial hours worked		
Site-year	Short period	Intermediate period	Long period
2007			
Aspen Mountain	2.4	4.3	4.3
Bush Creek	0	0	0
Delaney Rim	0	4.1	4.1
Flat Top Mountain	1.5	1.5	1.5
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	31.1	31.1	50.8
Sand Butte	0	0	0
Sim-Julian Lambing Range	17.8	17.8	21.4
South Gate	7.7	8.5	11.3
Wasatch Ridge	0	0	0
2008			
Aspen Mountain	5.4	7.2	7.8
Bush Creek	0	12.9	45.8
Delaney Rim	2.5	14.3	51.5
Flat Top Mountain	14.7	21.5	21.5
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	7	7	49.8
Sand Butte	0	0	0
Sim-Julian Lambing Range	7.7	11.3	11.3
South Gate	6.2	6.2	6.2
Wasatch Ridge	1	1	1

APPENDIX C. PRIVATE CONTRACTOR COYOTE REMOVAL DATA

Coyotes Removed by Private Contractors

	Coyotes removed		
Site-year	Short period	Intermediate period	Long period
2007			
Aspen Mountain	0	0	0
Bush Creek	0	0	0
Delaney Rim	0	0	0
Flat Top Mountain	0	0	0
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	34	39	39
Sand Butte	0	0	0
Sim-Julian Lambing Range	49	49	49
South Gate	0	20	20
Wasatch Ridge	0	0	0
2008			
Aspen Mountain	156	156	156
Bush Creek	0	0	0
Delaney Rim	0	0	0
Flat Top Mountain	0	0	0
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	72	72	72
Sand Butte	0	0	0
Sim-Julian Lambing Range	18	18	18
South Gate	20	45	45
Wasatch Ridge	0	0	0

Total Hours Worked by Private Contractors

	Total hours worked		
Site-year	Short period	Intermediate period	Long period
2007			
Aspen Mountain	0	0	0
Bush Creek	0	0	0
Delaney Rim	0	0	0
Flat Top Mountain	0	0	0
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	11.5	14.9	14.9
Sand Butte	0	0	0
Sim-Julian Lambing Range	18.3	18.3	18.3
South Gate	36	132	132
Wasatch Ridge	0	0	0
2008			
Aspen Mountain	38.3	38.3	38.3
Bush Creek	0	0	4
Delaney Rim	0	0	0
Flat Top Mountain	0	0	0
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	18	18	18
Sand Butte	0	0	0
Sim-Julian Lambing Range	12.4	12.4	12.4
South Gate	12	108	108
Wasatch Ridge	0	0	0

Ground Hours Worked by Private Contractors

	Ground hours worked		
Site-year	Short period	Intermediate period	Long period
2007			
Aspen Mountain	0	0	0
Bush Creek	0	0	0
Delaney Rim	0	0	0
Flat Top Mountain	0	0	0
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	0	0	0
Sand Butte	0	0	0
Sim-Julian Lambing Range	0	0	0
South Gate	36	132	132
Wasatch Ridge	0	0	0
2008			
Aspen Mountain	0	0	0
Bush Creek	0	0	4
Delaney Rim	0	0	0
Flat Top Mountain	0	0	0
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	0	0	0
Sand Butte	0	0	0
Sim-Julian Lambing Range	0	0	0
South Gate	12	108	108
Wasatch Ridge	0	0	0

Aerial Hours Worked by Private Contractors

	Aerial hours worked		
Site-year	Short period	Intermediate period	Long period
2007			
Aspen Mountain	0	0	0
Bush Creek	0	0	0
Delaney Rim	0	0	0
Flat Top Mountain	0	0	0
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	21.5	24.9	24.9
Sand Butte	0	0	0
Sim-Julian Lambing Range	18.3	18.3	18.3
South Gate	0	0	0
Wasatch Ridge	0	0	0
2008			
Aspen Mountain	38.3	38.3	38.3
Bush Creek	0	0	0
Delaney Rim	0	0	0
Flat Top Mountain	0	0	0
Hay Reservoir	0	0	0
Kinney Rim	0	0	0
Little Mountain	0	0	0
Pomeroy-Slate Creek	34.5	34.5	34.5
Sand Butte	0	0	0
Sim-Julian Lambing Range	12.4	12.4	12.4
South Gate	0	0	0
Wasatch Ridge	0	0	0

APPENDIX D. UNGULATE SURVEY DATA

Pronghorn Dependent Variables

Site-year	Does / km	Fawns / km	Deer / km	Fawns / 100 does	Deer density
2007					
Aspen Mountain	3.55	2.54	7.39	69.34	6.97
Bush Creek	1.72	0.50	3.34	28.94	3.20
Delaney Rim	0.79	0.27	1.83	37.83	1.16
Flat Top Mountain	2.23	0.80	4.37	38.22	2.68
Hay Reservoir	1.77	0.82	3.31	50.22	2.58
Kinney Rim	1.18	0.15	1.88	12.36	2.11
Little Mountain	1.37	1.19	2.80	89.67	3.09
Pomeroy-Slate Creek	2.66	2.02	6.05	77.85	4.15
Sand Butte	1.68	0.84	3.31	50.94	2.74
South Gate	1.72	1.65	4.66	97.24	4.49
2008					
Aspen Mountain	4.04	2.68	8.61	70.14	7.90
Bush Creek	1.42	0.39	2.66	31.96	1.76
Delaney Rim	1.27	0.20	2.30	15.71	1.42
Flat Top Mountain	3.12	0.96	5.67	30.50	4.17
Hay Reservoir	0.97	0.61	2.36	56.72	1.41
Kinney Rim	1.57	0.09	2.56	5.19	1.93
Little Mountain	2.35	0.80	3.60	37.73	4.46
Pomeroy-Slate Creek	2.85	2.62	6.31	89.99	6.66
Sand Butte	1.74	0.25	2.40	15.96	1.48
South Gate	1.54	1.46	3.85	97.02	3.22

Mule Deer Dependent Variables

Site-year	Does / km	Fawns / km	Deer / km	Fawns / 100 does	Deer density
2007					
Aspen Mountain	1.27	0.77	2.55	60.35	5.12
Delaney Rim	0.07	0.02	0.12	18.52	0.31
Little Mountain	1.54	1.14	3.06	74.06	11.92
Sand Butte	0.83	0.38	1.36	46.82	5.50
Sim-Julian Lambing Range	1.53	1.21	2.95	74.58	6.45
Wasatch Ridge	0.17	0.08	0.50	46.53	1.62
2008					
Aspen Mountain	1.54	1.05	3.30	68.47	6.20
Delaney Rim	0.08	0.04	0.23	50.00	0.51
Little Mountain	1.97	1.15	3.50	59.40	10.27
Sand Butte	0.79	0.51	1.55	62.28	3.17
Sim-Julian Lambing Range	1.10	0.58	1.94	49.42	3.94
Wasatch Ridge	0.17	0.12	0.44	63.95	1.37