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Using sterilization to change predation rates of wild coyotes: A test case involving pronghorn fawns

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ABSTRACT

Surgical sterilization of coyotes (Canis latrans) reduced their predation rate on domestic sheep. We investigated whether sterilizing coyotes would similarly change coyote predation rates on pronghorn antelope (Antilocapra americana) neonates. From May 2006 to March 2008, we radio-collared 71 pronghorn fawns to determine survival rates in southeast Colorado, USA. During the first year of the study, all coyotes were reproductively intact. During the second year, we surgically sterilized 15 coyotes from 10 packs in the southern half of the study area, while nine coyotes from seven packs in the northern half were given sham sterilizations (i.e., remained reproductively intact). In addition, we estimated the availability of alternative prey and coyote density on both areas to evaluate predator–prey factors that could interact with the sterilization treatment. Using the known fate model in Program Mark, we constructed models with and without a treatment effect, plus year, area, individual covariates, alternative prey indices, and predator density to estimate pronghorn fawn survival rates. Results from model averaged parameter estimates and cumulative summer survival indicated coyote sterilization increased survival rates of pronghorn fawns by reducing predation rates of fawns. While fawn survival was higher overall in the north area, after treatment was applied, cumulative pronghorn fawn survival during the summer of 2007 in the south area was 242% higher for pronghorn fawns captured in sterile coyote territories (0.44; 79-day interval survival rate) compared to fawns captured in intact coyote territories (0.18). There was also a significant local area effect, but no relationship between fawn survival and individual fawn covariates of sex, birth weight, birth date, or age. No relationship was detected between fawn survival and lagomorph abundance index, rodent abundance index, or coyote density. Surgical sterilization of coyotes was useful in reducing predation rates on pronghorn fawns.

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1. Introduction

Coyotes (Canis latrans) are considered an abundant and expanding native species in North America. Their population expansion has been enhanced by altered landscapes and the loss of top carnivores (Gompper, 2002; Berger and Gese, 2007). One concern with the expansion of native predators is their impact on prey species. In North America, predation of ungulate neonates can be the primary cause of mortality (Linnell et al., 1995). Coyotes are especially adept at killing pronghorn (Antilocapra americana) fawns (Byers, 1997). Studies have shown coyote-caused mortality of pronghorn neonates exceeds 75% of total mortality (Gerlach and Vaughan, 1990; Dunbar and Giordano,

2003) and can lead to fawn:doe ratios <1:100 (Dunbar and Giordano, 2003). Where ungulate populations are declining or critically low, limited fawn recruitment can affect the persistence of local populations (Bright and Hervert, 2005; Berger et al., 2008). Under these circumstances, coyote management may be required to sustain ungulate populations. Coyote control in areas of fawn birthing could increase chances of fawn recruitment into the population (Smith et al., 1986; Bright and Hervert, 2005).

Management of coyote predation for domestic animals is complex and involves using several techniques (Knowlton et al., 1999). There are added challenges for coyote management for wild ungulate populations, such as pronghorn or mule deer (*Odocoileus hemionus*), due to unrestricted animal movements, extent of the landscape, cost of the effort, and lack of public support. Non-lethal management techniques for domestic animals, such as animal husbandry, guard animals, repellents, or aversive conditioning, are impractical for wildlife management. Habitat management is often the most obvious non-lethal method by which to influence ungulate population dynamics (Gaillard et al., 2000; Ballard et al., 2001; Forrester and Wittmer, 2013) with the interaction of forage quality and predation often being mediated by climate (Hopcraft et al., 2010). Lethal control of coyotes is frequently the only method available for managers to cope with predation. However, lethal control is a source of controversy to the public (Kellert, 1985; Messmer et al., 2001) and in some cases may not be biologically effective, particularly in cases where predation is not a limiting factor to the ungulate population (Ballard et al., 2001; Hurley et al., 2011; Forrester and Wittmer, 2013).

One non-lethal method to control coyote predation is changing predatory behavior through reproductive interference (i.e., reduce the energetic demands of provisioning pups). Till and Knowlton (1983) showed removing coyote pups from a den reduced predation on domestic sheep and hypothesized that the absence of pups reduced energetic needs of the pack, thus reducing predation on larger food items. Sacks et al. (1999) found offending coyotes responsible for sheep predation were the breeding, territorial animals and recommended that control efforts focus on these individuals. Zemlicka (1995) demonstrated sterilization of captive coyotes did not affect social or territorial behaviors. Bromley and Gese (2001a) found surgical sterilization of coyotes resulted in an eight-fold reduction of predation on lambs. In addition, results from a modeling study comparing sterilization and other lethal strategies, indicated sterilization offered the most lasting impact on coyote population dynamics (Conner et al., 2008). Surgical sterilization is less objectionable to the public and has the potential to be more successful biologically because it can persist for several years, whereas lethal control generally is applied annually. In addition, sterilized wild coyote pairs continued to defend their territory against neighboring coyotes and maintain pair bonds (Bromley and Gese, 2001b; Seidler and Gese, 2012).

Since coyote predation on lambs can be reduced using sterilization (Bromley and Gese, 2001a), then it may work in a wildlife application as well. In this study,

we tested the hypothesis that surgical sterilization of coyotes would increase survival rates of pronghorn fawns by decreasing coyote predation rates on fawns, using a Before-After-Control-Impact paired (BACIP) field study design (Stewart-Oaten et al., 1986; Smith, 2002; Gotelli and Ellison, 2004). To evaluate factors impacting coyote predation on pronghorn fawns, we also examined levels of alternative prey availability and coyote density, as well as individual fawn covariates of sex, birth weight, and birth date. Our study is the first to examine the use of sterilization on coyotes as a non-lethal management tool to reduce predation on wild neonates.

2. Methods

2.1. Description of study area

We conducted this research on the 1,040 km^2 Piñon Canyon Maneuver Site (PCMS) in Las Animas County, Colorado, USA. The study area encompassed the home-range boundaries of radio-collared coyotes and the locations of radio-collared fawns involved in the study (approximately 350 km^2). Average elevation on the PCMS was 1520 m, mean temperatures ranged from 1 °C in January to 24 °C in July (Shaw and Diersing, 1990), and mean annual precipitation was 305 mm (Milchunas et al., 1999). Harvest of coyotes was not permitted for the duration of the study. Nearly 60% of the PCMS was identified as short-grass prairie dominated by blue grama (*Bouteloua gracilis*), galleta (*Hilaria jamesii*), and western wheatgrass (*Agropyron smithii*) (Shaw et al., 1989). Many shrub communities occurred within the grassland communities along alluvial fans, waterways, and slopes. These were characterized by black greasewood (*Sarcobatus vermiculatus*), fourwing saltbush (*Atriplex canescens*), Bigelow sagebrush (*Artemisia bigelovii*), winterfat (*Krascheninnikovia lanata*), small soapweed (*Yucca glauca*), and tree cholla (*Opuntia imbricata*). Woodland communities were composed primarily of oneseed juniper (*Juniperus monsperma*) and pinyon pine (*Pinus edulis*) mixed with grassland or shrubland species. Woodlands dominated the canyons and breaks. Areas that were defined as burned had natural or prescribed fires during or after 2004.

2.2. Description of study design

This study was designed to test the prediction that fawns born in territories of sterile coyotes (i.e., no pups) would have higher survival rates than fawns born in territories of intact coyotes (i.e., with pups). Using a Before-After-Control-Impact paired (BACIP) field study design (Stewart-Oaten et al., 1986; Smith, 2002; Gotelli and Ellison, 2004), the first year of the study was a baseline year in which no treatment (i.e., sterilization) was applied. We captured and radio-collared fawns in two sites (north, south) and determined survival rates in both sites for the baseline survival rate estimates. During the second year of the study, we sterilized coyotes in the south area, while sham-operating coyotes in the north area (i.e., remained reproductively intact). To maintain hormone levels, female coyotes were tubal ligated and males were vasectomized,

thereby insuring maintenance of territorial boundaries and pair bonds (Bromley and Gese, 2001a; Seidler and Gese, 2012). However, some fawns in the south were captured outside the territorial boundaries of our sterile packs and these fawns were considered to be within the range of intact packs. Therefore our comparisons were across two areas (north, south) and two treatments (sterile, intact). To evaluate additional factors impacting survival rates other than sterilization, we also included variables that measured levels of prey availability, coyote density, as well as individual pronghorn fawn covariates of sex, birth weight, and birth date.

2.3. Capture and monitoring of pronghorn fawns

We observed solitary pronghorn does during the fawning season (mid-May through early June) with spotting scopes to locate hidden fawns (Autenrieth and Fichter, 1975). Newborn fawns were permitted to bond with their mother for >4 h before capture. We captured fawns by hand or with a long-handled salmon net, then blindfolded and handled them with latex gloves. We outfitted fawns with ≤75 g expandable radio-collars with a 6 h mortality mode and precise event transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). The transmitter was programmed to convey the amount of time elapsed post-mortality mode. We measured fawn mass, and noted the presence and state of the umbilicus (Byers and Moodie, 1990), sex, and health of fawns. Research protocols were approved by the Institutional Animal Care and Use Committees at the National Wildlife Research Center and Utah State University.

We monitored fawns daily from the ground with telemetry from mid-May through July, weekly through August, and monthly through March of the following year. We located mortalities immediately and the body, if present, and surrounding area was carefully examined. We classified predation events as coyote, eagle (*Aquila chrysaetos*), or unknown, based upon tracks, scat, hair, hemorrhage patterns, and caching characteristics (O'Gara, 1978; Wade and Bowns, 1984; Acorn and Dorrance, 1998). We collected DNA evidence from fatal puncture wounds on carcasses that had evidence of hemorrhaging (Blejwas et al., 2006). When in doubt about the species of predator responsible for the mortality, we attempted to identify the species through genotyping (Wildlife Genetics International, Nelson, British Columbia, Canada). Unless otherwise noted, all statistics were calculated in SPSS 10.0.5 (SPSS Inc., Chicago, IL).

2.4. Capture and monitoring of coyotes

We selected a contiguous area to treat as opposed to randomizing our treatment area based on coyote home ranges. If the treatment had been randomly applied at the scale of the home range we would have had the issue of radio-collared fawns moving across the landscape through treated and non-treated areas. In addition, a broad spectrum application of coyote sterilization best simulated what would be conducted in a true management setting. Coyotes were sterilized in December 2006 in half of the study site in a BACIP study design. We attempted to capture all coyotes present in the study area with a net-gun fired from a helicopter (Barrett et al., 1982; Gese et al., 1987). We sterilized animals captured in the southern portion of the study area (treated), while animals captured in the northern portion were sham-operated (i.e., remained intact). We transported captured animals by vehicle or helicopter to a central processing location. A veterinarian sterilized females by tubal ligation and males by vasectomy, thereby allowing hormonal systems and social behaviors to remain unaffected (Asa, 1995; Zemlicka, 1995). All animals otherwise received the same treatment: they were anesthetized, incised and sutured, radio-collared, allowed to recover, and released at the capture site within 24 h. Effects of surgical sterilization on coyote social and spatial ecology (pair bonds, territory maintenance, space use, and survival rates) are addressed in Seidler and Gese (2012).

To determine with greater certainty that treated coyote packs were indeed sterile, we conducted howling surveys (Harrington and Mech, 1982; Fuller and Sampson, 1988) and searched for dens and pups of radio-collared individuals. Howling surveys were conducted from 4 June 2007 to 13 August 2007, with one to two field teams going to high points, howling, and recording whether the response included pups or not. Concurrently, all radio-collared individuals in the pack were detected with telemetry. Packs with pups were considered intact. Visual observations of radio-collared individuals allowed us to gain information on pup presence as well as minimum group sizes. We conducted these surveys from 8 June 2007 to 5 December 2007. One to two people would home in on a radio-collared coyote on foot. We attempted to approach animals from downwind in a stealthy manner to reduce disturbance of pack members. We noted coyote group size, location, and the presence of pups. We estimated pre-whelping coyote density by dividing the minimum pack size observed by the pack's home-range size (Gese et al., 1989; Gese, 2001).

2.5. Home range analysis

We monitored coyotes with telemetry from December 2006 to March 2008, primarily at dawn and dusk to obtain locations during the highest activity periods (Andelt and Gipson, 1979). Telemetry locations were attempted every 2 days. We calculated locations using ≥3 bearings in Program Locate II (Pacer, Ltd., Truro, Nova Scotia, Canada). To reduce estimation errors when assigning fawn capture locations to specific coyote home ranges, we only used locations with 95% error areas ≤0.10 km². We used data locations gathered from April 2007 to September 2007 to define seasonal pack home ranges used in assigning pronghorn fawns to sterile or intact coyote packs. We chose this time period to include the coyote pup-rearing season when energetic needs for the pack were highest and pronghorn fawns were vulnerable to predation. We used observation-area curves (Odum and Kuenzler, 1955) to determine whether we collected enough locations to adequately estimate seasonal home ranges for radio-collared coyotes.

We plotted home ranges of coyote packs with the ArcMap (ArcGIS 9.2, Environmental Systems Research Institute, Inc., Redlands, California, USA) extension,

Hawth's Tools 3.27. We used the fixed kernel density estimator (Worton, 1989) with point locations to describe resident pack home ranges because it is less biased to small sample sizes and outliers (Millspaugh and Marzluff, 2001). We used a 95% contour to describe a pack's home range (Shivik and Gese, 2000). To determine bandwidths, we adapted an *ad hoc* method which prevents undersmoothing, is relatively unaffected by sample size, and reduces Type I errors. Initially, we plotted home ranges using *h* (bandwidth) = 1000 and then incrementally reduced the bandwidth by 10% until we had the smallest bandwidth that did not create disjoint polygons.

We calculated the amount of each habitat type present in each coyote pack home range to compute indices for alternative prey available to each coyote pack. Vegetation layers were provided by the Directorate of Environmental Compliance and Management, Fort Carson, Colorado, USA. These layers were merged into four habitat types: grassland, shrubland, woodland, or burned area. Coyote pack home ranges were overlaid with the habitat layers to estimate the amount of each habitat type present within each pack's home range.

2.6. Estimates of prey availability

We conducted surveys to determine the relative abundance of rodents (trapping grids) and lagomorphs (spotlight surveys) available within each coyote pack home range (Bromley and Gese, 2001a) during June and July of both years. We used $7.6 \times 7.6 \times 25.4$ cm Sherman live traps (H.B. Sherman Traps, Tallahassee, Florida, USA) baited with chicken–scratch–grain mix and peanut butter to capture small mammals. Traps were set in a 5×7 grid design with 10 m spacing across all four different habitats in a nested design of three replicates per habitat in both the sterile (treated) and intact (sham) areas; traps were run for three consecutive nights (Valone et al., 2002; Thibault et al., 2010; Allington et al., 2013). We checked the traps each morning and captured animals were marked, recorded, and released. To calculate the rodent index, all catchable species were grouped by genus and the median mass for each species (Fitzgerald et al., 1994) was then averaged across all species captured in that genus. The average mass was then multiplied by the total number of unique individuals of that genus captured on each grid. A rodent index value was assigned to each habitat type as rodent kg/km^2. We then extrapolated the rodent index to each coyote home range based upon the amount of habitat type in the home range (Bromley and Gese, 2001a).

Lagomorph spotlight surveys (Smith and Nydegger, 1985) were conducted in replicates of three per habitat type over three consecutive nights in both the sterile and intact areas. Cottontail (*Sylvilagus audubonii*) and black-tailed jackrabbit (*Lepus californicus*) numbers were counted for each habitat and replicates were averaged together. The mean number of lagomorphs/km was multiplied by the average mass of the species and used to assign a lagomorph index value to each habitat type. These index values were then extrapolated into each coyote home range (Bromley and Gese, 2001a).

2.7. Pronghorn fawn survival analyses

We estimated semi-monthly fawn survival rates over five time intervals (14 May–31 July) using known fate models in Program MARK (White and Burnham, 1999). Survival rates for unequal time intervals (18, 15, 15, 15, 16 days) were standardized to semi-monthly rates for comparison (White and Burnham, 1999) and encounter histories were censored for the year the fawn was not monitored. We compared models using the Akaike Information Criteria corrected for small sample size (AICc; Burnham and Anderson, 2002).

Due to small sample sizes, *a priori* models were carefully designed to avoid detection of spurious correlations (Burnham and Anderson, 2002). We grouped the data by area (north or south). Our models included eight covariates: fawn sex, birth weight (kg), estimated age at capture (days), birth date, treatment (captured in an intact or sterile coyote home range), relative coyote density, lagomorph abundance index, and rodent abundance index. We assigned values for the last four covariates based upon the coyote home range in which the fawn was captured. We did not use a fawn's mortality location to test the effects of the covariates because not all fawns died. Fawns captured outside of a known coyote home range were classed as intact and assigned an average coyote density, rodent abundance, and lagomorph abundance value.

The primary goal of our study was to estimate the effect of coyote sterilization on pronghorn fawn survival. Therefore, we examined a dual model set with and without the treatment effect (Bishop et al., 2008) allowing us to use model averaging (White et al., 1999); that is, each model had a structure with and without a treatment effect. If there was no treatment effect, then there would be no difference in the model averaged fawn survival estimates on intact and sterile coyote home ranges; that is, the model-averaged estimated effect-size would be small and the confidence interval would cover 0. To minimize the number of models, we constructed models of fawn survival in a three-phase process. First, we constructed models with only temporal effects (Table 1, models 1a,b–6a,b). We predicted survival of fawns over a 79-day period would be variable because their vulnerability to predation changes as they develop (Barrett, 1978; Von Gunten, 1978). To model these hypothesized temporal differences in survival, we ran the following four models: (1) a linear time trend model based on the hypothesis that fawn survival increases after birth; (2) a non-linear time trend model (i.e., a threshold model using the natural logarithm) based on the hypothesis that fawn survival increases to a maximum value then plateaus; (3) a model which held the first three and the last two time intervals equal based on the hypothesis that survival increases in stages as fawns age; and (4) a model which allowed the first three time intervals to vary but held the last two intervals constant based on the hypothesis that survival is variable when fawns are the youngest and most vulnerable to predation (Table 1, models 3a,b–6a,b). We then combined the best time model of fawn survival with area and year effects (Table 1, models 7a,b–9a,b). Area was different from treatment because, although we attempted to capture and sterilize coyote packs throughout the entire

Table 1

Models used to evaluate the influence of coyote sterilization and other covariates on pronghorn fawn survival (*S*), Piñon Canyon Maneuver Site, Colorado, USA, May 2006–March 2008.

Model no.	Model structure	Model hypothesis
1a	$S(\text{area} \times \text{time}) + \text{treatment}$	Survival varied by an interactive effect of area and time, plus treatment
1b	$S(\text{area} \times \text{time})$	Survival varied by an interactive effect of area and time
2a	$S(\text{treatment})$	Survival varied only by treatment
2b	$S(.)$	Survival was constant
3a	$S(\text{time} + \text{treatment})$	Survival varied by a linear trend in time, plus treatment
3b	$S(\text{time})$	Survival varied by a linear trend in time
4a	$S(\ln(\text{time}) + \text{treatment})$	Survival varied by a nonlinear trend in time, plus treatment
4b	$S(\ln(\text{time}))$	Survival varied by a nonlinear trend in time
5a	$S((t1 = t2 = t3, t4 = t5) + \text{treatment})$[a]	Survival was constant in time intervals 1, 2, and 3 and constant in intervals 4 and 5, plus treatment
5b	$S(t1 = t2 = t3, t4 = t5)$	Survival was constant in time intervals 1, 2, and 3 and constant in intervals 4 and 5
6a	$S((t4 = t5) + \text{treatment})$	Survival was constant in time intervals 4 and 5, plus treatment
6b	$S(t4 = t5)$	Survival was constant in time intervals 4 and 5
7a	$S((t4 = t5) + \text{area} + \text{treatment})$	Survival was constant in time intervals 4 and 5 but varied by area (north and south) and treatment
7b	$S((t4 = t5) + \text{area})$	Survival was constant in time intervals 4 and 5 but varied by area (north and south)
8a	$S((t4 = t5) + \text{year} + \text{treatment})$	Survival was constant in time intervals 4 and 5 but varied by year (2006 and 2007) and treatment
8b	$S((t4 = t5) + \text{year})$	Survival was constant in time intervals 4 and 5 but varied by year (2006 and 2007)
9a	$S((t4 = t5) + \text{area} + \text{year} + \text{treatment})$	Survival was constant in time intervals 4 and 5 but varied by area, year, and treatment
9b	$S((t4 = t5) + \text{area} + \text{year})$	Survival was constant in time intervals 4 and 5 but varied by area and year
10a	$S((t4 = t5) + \text{area} + \text{sex} + \text{treatment})$	Survival was constant in time intervals 4 and 5 but varied by area, fawn sex, and treatment
10b	$S((t4 = t5) + \text{area} + \text{sex})$	Survival was constant in time intervals 4 and 5 but varied by area and fawn sex
11a	$S((t4 = t5) + \text{area} + \text{birth weight} + \text{treatment})$	Survival was constant in time intervals 4 and 5 but varied by area, fawn birth weight, and treatment
11b	$S((t4 = t5) + \text{area} + \text{birth weight})$	Survival was constant in time intervals 4 and 5 but varied by area and fawn birth weight
12a	$S((t4 = t5) + \text{area} + \text{age} + \text{treatment})$	Survival was constant in time intervals 4 and 5 but varied by area, fawn age, and treatment
12b	$S((t4 = t5) + \text{area} + \text{age})$	Survival was constant in time intervals 4 and 5 but varied by area and fawn age
13a	$S((t4 = t5) + \text{area} + \text{birth date} + \text{treatment})$	Survival was constant in time intervals 4 and 5 but varied by area, fawn birth date, and treatment
13b	$S((t4 = t5) + \text{area} + \text{birth date})$	Survival was constant in time intervals 4 and 5 but varied by area and fawn birth date
14a	$S((t4 = t5) + \text{area} + \text{coyote} + \text{treatment})$	Survival was constant in time intervals 4 and 5 but varied by area, coyote density, and treatment
14b	$S((t4 = t5) + \text{area} + \text{coyote})$	Survival was constant in time intervals 4 and 5 but varied by area and coyote density
15a	$S((t4 = t5) + \text{area} + \text{year} + \text{lago} + \text{treatment})$	Survival was constant in time intervals 4 and 5 but varied by area, year, lagomorph density, and treatment
15b	$S((t4 = t5) + \text{area} + \text{year} + \text{lago})$	Survival was constant in time intervals 4 and 5 but varied by area, year, and lagomorph density
16a	$S((t4 = t5) + \text{area} + \text{year} + \text{rodent} + \text{treatment})$	Survival was constant in time intervals 4 and 5 but varied by area, year, rodent density, and treatment
16b	$S((t4 = t5) + \text{area} + \text{year} + \text{rodent})$	Survival was constant in time intervals 4 and 5 but varied by area, year, and rodent density

[a] *t* = time interval.

For each model structure, two versions of the model were run; one with a treatment effect (a) and one without a treatment effect (b), for a total of 32 models.

southern portion of the study site, some fawns in the south were not captured within a radio-collared coyote home range and could not be assigned to the treatment group.

For the last phase of model building, we added all other covariates to the best model from phase one and two. We included sex, birth weight, age at capture, and birth date to account for potentially important sources of individual variation of fawn survival (Fairbanks, 1993; Byers, 1997;

Table 1, models 10–13), and coyote density, lagomorph abundance index, and rodent abundance index to account for predator–prey factors (Table 1, models 14a,b–16a,b).

Age at capture was estimated using a constant for growth rate derived from Byers (1997). Mean known birth weight was estimated from fawns known to have been born the day of capture. We knew <1-day-old fawns because either we witnessed their birth or they had a wet umbilicus

(Byers and Moodie, 1990). Because there was a difference between prey index estimates in the 2 years, we always included year in models with an alternative prey covariate. Using model averaged estimates, we performed a Z-test for differences in survival rates to compare survival between areas and years. A Wald's test (Agresti, 1990) was used to determine significance of covariates.

We estimated model averaged cumulative summer survival (White et al., 1999) to evaluate the overall impact of sterilization on fawn survival over the 79-day study period. We estimated overall summer survival from the five semi-monthly model averaged survival estimates ($\hat{s}_1 - \hat{s}_5$) as $\hat{s}_1 \times \hat{s}_2 \times \cdots \times \hat{s}_5$ and used the delta method to estimate its variance (on the natural-log scale; Franklin et al., 2004).

3. Results

3.1. Coyote home range and density

We captured 30 coyotes: nine coyotes from seven resident home ranges in the north were captured and sham-operated (i.e., intact), while we sterilized 15 coyotes from 10 resident home ranges in the south; although two of the sterile packs were later assigned to intact due to suspected presence of pups. Four radio-collared coyotes (two intact and two sterile) were transient (their home range encompassed multiple resident home ranges) and one sterile and two intact resident coyotes began dispersing in the summer of 2007. One intact coyote could not be accurately tracked due to her home range being on private land.

We used 485 locations ($\bar{x} = 28.5$, 95% CI = 23.5–33.5 per home range) to define seasonal pack home ranges. The mean telemetry error was 328 m (95% CI = 231–425) based on 14 blind tests of randomly placed transmitters. The total area considered sterile was 125.1 km². Mean home range size of all radio-collared coyotes was 16.1 km² (95% CI = 12.7–19.5) and the mean minimum pack size was 2.2 coyotes (95% CI = 2.0–2.4). Coyote density was not different in the north (0.15 coyotes/km², 95% CI = 0.10–0.20, $n = 9$) and south (0.18 coyotes/km², 95% CI = 0.14–0.22, $n = 8$; $t_{14} = -0.816$, $P = 0.428$) areas.

3.2. Alternative prey indices

The lagomorph abundance index was 22.7 kg/km (95% CI = 18.0–27.4) in 2006, and 5.0 kg/km (95% CI = 3.4–6.6) in 2007 ($t_{20} = 7.034$, $P < 0.001$). The rodent abundance index was 1235.2 kg/km² (95% CI = 1,007.1–1,463.3) in 2006, and 282.2 kg/km² (95% CI = 211.4–353.0) in 2007 ($t_{20} = 7.819$, $P < 0.001$). We detected no difference in overall availability of alternative prey between the north and south areas (lagomorph index, $t_{32} = -0.349$, $P = 0.730$; rodent index, $t_{32} = 0.038$, $P = 0.970$).

3.3. Pronghorn fawn survival

We captured and radio-collared 31 fawns in 2006 and 40 fawns in 2007. Coyote predation was the primary cause of death in both years. In 2006, 26 of 31 fawns died by July; 16 (61.5%) fawns were killed by coyotes, one mortality was due to eagle predation, and nine mortalities were

by unknown predators; DNA analysis attributed the cause of death to coyote predation in one out of two questionable mortalities. In 2007, 25 of 40 fawns died by July. In both sterile and intact areas, deaths were primarily due to coyote predation (76%) while six mortalities were due to unknown causes. DNA analysis attributed cause of death to coyote predation in five out of six questionable mortalities. A simple determination of the 78-day survival rate (Heisey and Fuller, 1985) using accumulated radio-days and the number of deaths (Trent and Rongstad, 1974) showed that during 2006, the 78-day interval survival rate was 0.04 (10 of 14 fawns died) and 0.01 (16 of 17 fawns died) for the north and south areas, respectively (both areas contained intact coyote packs). In 2007, the 78-day interval survival rate was 0.25 in the north area (again all coyotes were intact in the north). However, in the south area, the interval fawn survival rate was 0.07 in the intact coyote home ranges, but 0.24 in the sterile home ranges, generating over a 3× increase in fawn survival in the sterile home ranges compared to the intact ranges in the southern study site.

The best model of fawn survival, $S(t4 = t5) + area + year$, was only slightly better than the model $S(t4 = t5) + area + treatment$ (Table 2, models 9 and 7). Based upon a criterion of $\Delta AICc < 2$ (Burnham and Anderson, 2002), 11 models were competitive (Table 2). All competing models included area and semi-monthly time interval (modeled as varying in the first three intervals but constant in the last two; Table 2). Based on model averaged parameter estimates, there was a significant treatment effect at $\alpha = 0.10$ ($\beta_{treat} = 0.543$, 90% CI = −0.361–1.447, 1-sided Wald test, $P = 0.098$; Fig. 1A and B), which suggested fawn survival was higher for fawns captured in treated (sterile) coyote home ranges when compared to fawns captured in untreated (intact) coyote home ranges in the south area. Overall survival differences were consistent between years (Fig. 1A and B); model averaged parameter estimates of fawn survival in 2006 were similar to 2007 ($\beta_{year} = 0.135$, 90% CI = −0.673–0.397, 1-sided Wald test, $P = 0.289$). Overall, survival was higher in the north control than in the south control area ($\beta_{area} = 0.763$, 90% CI = 0.023–1.549, 1-sided Wald test, $P = 0.018$). In spite of this area difference, the treatment effect was evidenced by increased survival on the south treatment area (sterile) compared to the south control area (intact) in 2007 (Fig. 1B). None of the other model covariates (i.e., lagomorph index, rodent index, fawn sex, fawn birth weight, fawn birth date, fawn age at capture) were significant ($P > 0.110$ for all tests, 1-sided Wald test).

The treatment effect was also manifested in model averaged cumulative summer survival rates (Fig. 2). In 2007, cumulative summer survival for the north area was 2.4× higher than for the south control area, while cumulative survival on the south sterile area was 2.4× higher than for the south intact area ($P = 0.032$ and $P = 0.068$, respectively; Table 3). After accounting for treatment, model averaged cumulative survival of fawns differed by area (Table 3). Fawn survival showed the same pattern for years, areas, and treatment groups; after declining over the first two time intervals, the probability of fawn survival stabilized in the third week of June (Fig. 2).

Table 2

Model selection results for pronghorn fawn survival (S) with five semi-monthly time (t) intervals, Piñon Canyon Maneuver Site, Colorado, USA, May 2006–March 2008.

Model no.	Model structure	K[a]	ΔAICc[b]	AICc Weights	Deviance
9b	$S((t4 = t5) + area + year)$	6	0.00	0.12	173.06
7a	$S((t4 = t5) + area + treatment)$	6	0.40	0.10	173.47
9a	$S((t4 = t5) + area + year + treatment)$	7	0.67	0.08	171.58
10a	$S((t4 = t5) + area + sex + treatment)$	7	1.06	0.07	171.97
8b	$S((t4 = t5) + year)$	5	1.64	0.05	176.84
10b	$S((t4 = t5) + area + sex)$	6	1.74	0.05	174.80
11a	$S((t4 = t5) + area + birthweight + treatment)$	7	1.80	0.05	172.71
7b	$S((t4 = t5) + area)$	5	1.82	0.05	177.02
16b	$S((t4 = t5) + area + year + rodent)$	7	1.88	0.05	172.79
13a	$S((t4 = t5) + area + birthdate + treatment)$	7	1.92	0.05	172.83
15b	$S((t4 = t5) + area + year + lago)$	7	1.94	0.04	172.84
13b	$S((t4 = t5) + area + birthdate)$	6	2.34	0.04	175.41
16a	$S((t4 = t5) + area + year + rodent + treatment)$	8	2.45	0.03	171.17
12a	$S((t4 = t5) + area + age + treatment)$	7	2.53	0.03	173.43
15a	$S((t4 = t5) + area + year + lago + treatment)$	8	2.55	0.03	171.27
14a	$S((t4 = t5) + area + coyote + treatment)$	7	2.56	0.03	173.46
6b	$S((t4 = t5))$	4	3.28	0.02	180.59
11b	$S((t4 = t5) + area + birthweight)$	6	3.41	0.02	176.48
8a	$S((t4 = t5) + year + treament)$	6	3.63	0.02	176.70
14b	$S((t4 = t5) + area + coyote)$	6	3.69	0.02	176.75
12b	$S((t4 = t5) + area + age)$	6	3.89	0.02	176.95
6a	$S((t4 = t5) + treatment)$	5	4.35	0.01	179.55
5b	$S((t1 = t2 = t3, t4 = t5))$	2	4.69	0.01	186.16
5a	$S((t1 = t2 = t3, t4 = t5) + treatment)$	3	5.89	0.01	185.29
3b	$S(T)$	2	20.73	0.00	202.19
3a	$S(T + treatment)$	3	21.88	0.00	201.27
1b	$S(area \, x \, t)$	20	25.94	0.00	166.44
4b	$S(\ln(T))$	2	26.89	0.00	208.35
1a	$S(area \, x \, t) + treatment$	21	27.34	0.00	165.31
4a	$S(\ln(T) + treatment)$	3	27.98	0.00	207.37
2b	$S(.)$	1	32.36	0.00	215.86
2a	$S(treatment)$	2	33.20	0.00	214.66

[a] Number of estimable parameters.
[b] Minimum AICc = 185.53.

Table 3

Difference in model-averaged cumulative pronghorn fawn summer survival rates (interval: May 14–31 July; 79 days), based on five semi-monthly intervals, Piñon Canyon Maneuver Site, Colorado, USA.

Year	Area	Treatment	Cumulative $\hat{s}$	SE	Diff $(\hat{s}_{intact} - \hat{s}_{intact})$	SE	P	Diff $(\hat{s}_{sterile} - \hat{s}_{intact})$	SE	P
2006	North	Intact	0.416	0.129	0.243	0.152	0.055	–	–	–
–	South	Intact	0.173	0.081	–	–	–	–	–	–
2007	North	Intact	0.439	0.105	0.250	0.135	0.032	0.254	0.170	0.068
–	South	Intact	0.183	0.085	–	–	–	–	–	–
–	South	Sterile	0.443	0.147	–	–	–	–	–	–

Models with no treatment effect were used for model averaged survival estimates in 2006 and for north and south intact in 2007. Models with a treatment effect were used for model averaged survival estimates for south sterile in 2007.

4. Discussion

Our results from model averaged parameter estimates and cumulative summer survival indicated coyote sterilization changed the predatory behavior of coyotes as evidenced by reducing predation rates on pronghorn fawns. While fawn survival was higher overall in the north area, after treatment was applied, cumulative pronghorn fawn survival during the summer of 2007 was $2.42\times$ higher for fawns captured in sterile packs compared to fawns captured in intact packs in the southern area. Indeed, despite the fact that pronghorn fawn survival was $2.40\times$ higher in the north area than the south area during pre-treatment in 2006, the treatment effect was evidenced by increased

survival in sterile packs compared to no increase in intact packs in 2007, nor any increase on the north intact area from 2006 to 2007. That is, cumulative fawn survival in the sterile packs on the south was raised to northern levels, while remaining low in southern intact packs. For wildlife managers seeking an alternative to lethal removal of coyotes, acquiring a 242% increase in pronghorn fawn survival by using coyote sterilization is biologically significant and relevant for management actions in areas where lethal control is undesirable.

None of the individual covariates we tested (fawn sex, birth weight, birth date, age at capture) were statistically important. The lack of difference between male and female fawn survival was similar to other studies (Fairbanks, 1993;
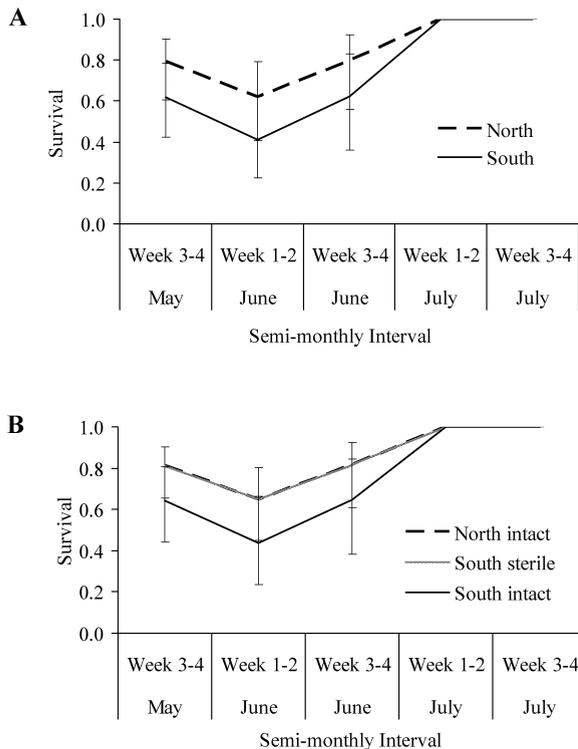
Fig. 1. Model averaged pronghorn fawn survival rates (±95% CI) in semi-monthly intervals, 14 May–31 July (79 days), (A) before treatment in 2006, and (B) after treatment in 2007, Piñon Canyon Maneuver Site, Colorado, USA. Models with no treatment effect were used for model averaged survival estimates in 2006 and for north and south intact in 2007. Models with a treatment effect were used for model averaged survival estimates for south sterile in 2007. Note in (B) that three survival curves are present.
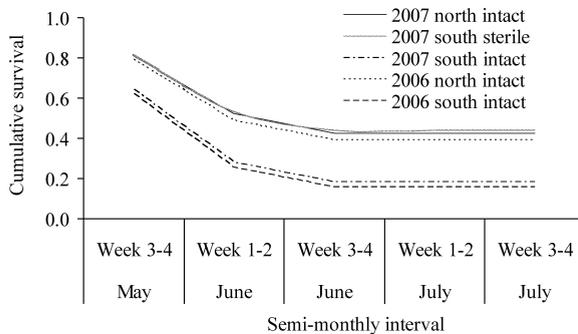

Fig. 2. Model averaged estimates of cumulative summer pronghorn fawn survival, 14 May–31 July (79 days), for north and south study areas in 2006 and 2007, Piñon Canyon Maneuver Site, Colorado, USA. Models with no treatment effect were used for model averaged survival estimates in 2006 and for north and south intact in 2007. Models with a treatment effect were used for model averaged survival estimates for south sterile in 2007.

Byers, 1997). However, this pattern may be variable; in the Greater Yellowstone Ecosystem, female fawn survival was higher than males (Berger et al., 2008). We found fawn survival was lowest in the second semi-monthly time interval, and after the first 6 weeks of life the probability of fawn survival increased to 100%. This is similar to results from

previous studies (Barrett, 1978; Von Gunten, 1978; Byers, 1997).

While we found no significant individual covariates, there were large survival differences between the local areas (i.e., between the north and south), and this difference was as large as the treatment difference (i.e., intact versus sterile in the south). We attempted to account for these differences by including prey abundance and coyote density in the models. However, these relationships were not significant. The lack of significance in these results may be due to small sample sizes of small mammals or differences in detection probability for lagomorph surveys in the second year that resulted from dramatically different weather conditions (higher winter and spring precipitation) and the consequent increase in vegetation height and density.

The north and south sites were close enough so that average precipitation amounts were similar (approximately 27.5 and 30.2 cm for north and south sites, respectively; Stevens et al., 2008); in accordance with the requirement that sites for BACIPs need to be close enough to be influenced by the same range of environmental phenomena (Stewart-Oaten et al., 1986). Besides similar environmental conditions, the north and south were comprised primarily of grassland species. However, distributions of vegetation types within the grasslands in the two areas were different, which may explain the differences in survival between the two areas. Predominant species in the north (i.e., western wheatgrass and needle-and-thread (*Stipa comata*)) tend to grow taller than predominant species in the south (i.e., grama species), potentially providing more escape cover for fawns in the northern area. In addition, a recent burn regime had been used in the southern part of the study area in 2004–2006, and not in the north. Although fires are often used to improve shortgrass prairie habitats to benefit species such as pronghorn (Yoakum, 1979; Wright and Bailey, 1982; Courtney, 1989), recent burns could compromise immediate fawn survival by reducing cover. Cover has been shown to be an important correlate in fawn survival (Barrett, 1984; Alldredge et al., 1991). It is possible that higher fawn survival in the north resulted from its higher vegetation height and the escape cover it provided.

In addition to survival differences by area, there were slight differences between years. The winter of 2006–2007 was the second highest total winter snowfall on record since 1947 (Western Regional Climate Center, Reno, Nevada). Although extreme winter weather can adversely affect fawn survival by affecting the condition of the doe (Verme, 1977), the extreme snowfalls of 2006–2007 did not reduce fawn survival on the PCMS. In fact, fawn survival following the winter of 2006–2007 was slightly higher than the previous year for the entire study area (although not statistically significant). It is possible that winter snowfall and spring precipitation (in 2007, heavier rain patterns occurred in April, May, and June) boosted fawn survival in 2007 by increasing vegetation biomass. Anecdotally, we noted an increase in vegetative cover across the study area in 2007. Coyotes are reported to use visual cues to detect pronghorn fawns (Wells, 1978), so high vegetation would make it difficult for them to find fawns (Barrett, 1981).

Additionally, increased vegetation would provide important forage for lactating does, subsequently increasing fawn survival.

We recommend coyote sterilization be considered as a non-lethal tool to boost pronghorn fawn survival in pronghorn populations where predation is a limiting factor. This non-lethal tool is applicable where lethal management of coyotes is controversial, unacceptable, or not an option (i.e., national parks, sites near urban areas). Costs to perform this technique (helicopter captures + sterilization = $900/coyote) were approximately 12% higher than cost estimates to trap and kill coyotes ($805; Wagner and Conover, 1999). Adjusting the cost from Smith et al. (1986) to current rates for helicopter flying ($1100/h), we estimated aerial gunning would cost $600/coyote. The fact that surgical sterilization will last for many years (Bromley and Gese, 2001a, b) offers promise of lower long-term costs than lethal control and is considered to be economically feasible.

5. Conclusion

Pronghorn have been present in North America since the Pleistocene and have been sympatric with coyotes since the evolution of *Canis latrans* (Kurtén and Anderson, 1980). Because coyote predation on pronghorn reflects an evolved relationship unlike the predatory relationship with domestic sheep, we were concerned that sterilization of coyotes may not decrease ungulate neonate predation as it did in sheep. However, we observed a substantial effect (Figs. 1 and 2) which was significant at $\alpha = 0.10$, even with the number of parameters included in our models and the relatively small sample size. Certainly, these results indicate biological significance (i.e., a 242% increase in fawn survival in sterile packs compared to intact packs in the south area). In addition, our estimates of fawn survival reflect biologically relevant population changes (i.e., cumulative fawn survival rates in the south more than doubled from 0.18 to 0.44 for fawns captured in sterile coyote home ranges); an increase which could influence fawn recruitment and provide important demographic changes for a pronghorn population, particularly in areas where coyote predation is a limiting factor on population growth and predation is additive to natural mortality.

Acknowledgments

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