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Territory fidelity, space use, and survival rates of wild coyotes following surgical sterilization

Renee G. Seidler · Eric M. Gese

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Abstract Sterilization of wild canids is being used experimentally in many management applications. Few studies have clearly demonstrated vasectomized and tubal-ligated canids will retain pair-bonding and territorial behaviors. We tested whether territory fidelity, space use, and survival rates of surgically sterilized coyote (*Canis latrans*) packs were different from sham-operated coyote packs. We captured and radio-collared 30 coyotes in December 2006. Sixteen of these animals were sterilized via vasectomy or tubal ligation, and 14 were given sham-surgeries (i.e., remained intact). We monitored these animals using telemetry and visual observations through 2 breeding seasons and 1 pup-rearing season from December 2006 to March 2008. Mean pack size was not significantly different between sterile and intact coyote packs. We found no difference in home range size between sterile and intact coyotes. We found differences in home range and core area overlap between sterile and intact coyote packs in some seasons; however, this difference may have existed prior to sterilization. Home range fidelity was not significantly different between sterile and intact coyotes. All coyotes had higher residency rates during the breeding season, with no differences between sterile and intact coyotes. Survival rates were correlated with biological season, but there were no differences in survival rates between sterile and intact coyotes. We concluded that surgical sterilization of coyotes

did not affect territory fidelity, survival rates, or home range maintenance.

Keywords Carnivore · Coyotes · Home range · Sterilization · Survival · Territory fidelity

Introduction

Sterilization of canids is being tested for various management purposes including population control of native and non-native species, predation control, and to reduce genetic introgression with other canids (Haight and Mech 1997; Kelly et al. 1999; Spence et al. 1999; Bromley and Gese 2001a; Saunders et al. 2002). Surgical sterilization in particular is a promising management approach for these objectives because hormonal systems remain intact with vasectomy and tubal ligation. Canid reproductive strategies (e.g., monogamy and pseudopregnancy in subordinate pack members) and physiology (e.g., monestrum and prolonged proestrus and estrus) favor pair and pack cohesion (Asa 1997). Without hormonal signals, these characteristics may not be preserved (Asa 1995). For most management purposes, retaining social structure of the pack is critical (Bromley and Gese 2001a, b). If the social structure of a sterilized pack fails, then a vacant territory becomes open to colonization by intact animals (Asa 1995; Mech et al. 1996; DeLiberto et al. 1998; Gese 1998).

Mech et al. (1996) vasectomized 5 wolves (*Canis lupus*) to determine if sterilization was a viable method for controlling population size. They determined the vasectomized wolves' social behaviors were not altered (i.e., the males maintained pair bonds and territories). Due to the success (i.e., pack size remained the same or decreased) of this study, sterilization is one of several proposed methods to

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control wolf populations (Haight and Mech 1997). In Canada, wolves had been implicated in the decline of caribou (*Rangifer tarandus*) and moose (*Alces alces*) calf survival (Spence et al. 1999). Due to public concern of the use of lethal control, fertility control was tested as an alternative to manage wolves (Spence et al. 1999). To determine the applicability of such a tool, territorial behaviors were examined. They found sterilized wolves maintained pair bonds and remained in their territories (Spence et al. 1999).

The sheep industry in the United States has a long history of conflict with coyotes (*Canis latrans*) preying on domestic livestock (Wagner 1988). Ranchers and wildlife management agencies utilize various lethal methods to reduce coyote predation on livestock and wildlife species (Knowlton et al. 1999). The public repeatedly is concerned over the use of lethal management (Arthur 1981; Kellert 1985; Andelt 1987; Messmer et al. 2001). One alternative to reduce predation on sheep is surgical sterilization of coyotes (Knowlton et al. 1999). Bromley and Gese (2001a) sterilized coyotes and found an eight-fold reduction in coyote predation on domestic sheep. This technique is effective because it reduces the energetic needs of the pack during pup rearing (Bromley and Gese 2001a). Bromley and Gese (2001b) further demonstrated the sterile coyotes' territorial and pack affiliative behaviors were not modified.

Coyotes are considered a social canid (Bekoff and Gese 2003; Gese 2004). The basic social unit is the adult, heterosexual pair, referred to as the alpha pair. Coyotes form heterosexual pair bonds that may persist for several years, but not necessarily for life. Courtship behavior begins 2–3 months before copulation. Coyotes may maintain pair bonds and whelp or sire pups up to 10–12 years of age (Gese 1990). Associate animals may remain in the pack and possibly inherit or displace members of the breeding pair and become alphas themselves. Associates participate in territorial maintenance and pup rearing, but not to the extent of the alpha pair (Gese 2004). Other coyotes exist outside the resident packs as transient or nomadic individuals. Transients travel alone over larger areas and do not breed, but will move into territories when vacancies occur. One factor that may affect coyote sociality is prey size or prey biomass. In populations where rodents are the major prey, coyotes tend to be in pairs or trios (Bekoff and Gese 2003). In populations where ungulates are available, large packs of up to 10 individuals may form (Gese et al. 1996a, b, c). Coyotes are territorial with a dominance hierarchy within each resident pack (Gese et al. 1996a, c; Gese 2004). Territoriality mediates the regulation of coyote numbers as packs space themselves across the landscape in relation to available food and habitat. The dominance hierarchy influences access to food resources within the pack (Gese et al. 1996a, b, c). Resident coyotes actively defend

territories with direct confrontation, and indirectly with scent marking and howling (Gese 2001, 2004). Only packs maintain and defend territories (Gese 2001, 2004; Bekoff and Gese 2003). Fidelity to the home range area is high and may persist for many years (Kitchen et al. 2000). Shifts in territorial boundaries may occur in response to loss of one or both of the alpha pair (Gese 1998). Dispersal of coyotes from the natal site may be into a vacant or occupied territory in an adjacent area, or they may disperse long distances. Generally, pups, yearlings, and non-breeding adults of lower social rank disperse (Gese et al. 1996a). Dispersal seems to be voluntary as social and nutritional pressures intensify during winter when food becomes limited (Gese et al. 1996a). Dispersal by juveniles usually occurs during autumn and early winter.

Although sterilization has been used in a few canids, only Bromley and Gese's (2001b) study has demonstrated that free-ranging coyotes maintained territorial and breeding-pair behaviors. If coyote sterilization continues to be used as a management tool, it is important to validate that territorial maintenance and pair-bonding behaviors are retained across various circumstances (Asa 1995) and environments. Without this assurance, intact animals could displace sterile packs and threaten the success of the management action (Till and Knowlton 1983; Asa 1995; Mech et al. 1996; DeLiberto et al. 1998). As part of a study to test whether coyote sterilization could increase pronghorn (*Antilocapra americana*) fawn survival (Seidler 2009), we also tested the hypothesis that sterilization would not affect territory fidelity, survival rates, and home range maintenance of coyotes. Using similar methodologies, we examined the same parameters as Bromley and Gese (2001b), including home range size, home range and core area overlap, home range fidelity, pack size, and survival rates of sterile versus intact coyotes. Scientific theory is advanced through repeated studies (Ford 2000; Gauch 2003). Since Bromley and Gese (2001b) was the only study examining the effects of sterilization on coyote behavior and survival rates, additional studies in different environments are needed to increase our understanding of the effects of reproductive control on coyote behavior and broaden our scope of inference. Our study was conducted in a shortgrass prairie and native prey ecosystem, while the study by Bromley and Gese (2001b) was conducted in the sage-brush steppe with a mixture of domestic livestock and native prey species.

Materials and methods

Study area

We conducted this study on the 1,040-km² Piñon Canyon Maneuver Site (PCMS) in Las Animas County, Colorado.

The study area within the PCMS was defined by the home range boundaries of the radio-collared coyotes. Mean elevation on the PCMS was 1,520 m, mean temperature 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 during the study. Nearly 60 % of the PCMS was shortgrass 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, and included 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 dominated the canyons and breaks, and were composed of one-seeded juniper (*Juniperus monosperma*) and pinyon pine (*Pinus edulis*).

Capture and monitoring of coyotes

We captured coyotes using aerial net-gunning (Barrett et al. 1982; Gese et al. 1987). Animals captured in the southern portion of the study area were sterilized, while animals captured in the northern portion of the study area were sham-sterilized (i.e., animals were sham-operated but remained intact). The boundaries of the two areas were 4 km apart and both areas were similar in climate, topography, vegetation, and prey availability. We used this clustered experimental design in an effort to swamp a single area with the treatment simulating actual management practices. Due to the uncertainty of capturing the breeding individuals, we sterilized both males and females from each pack.

Captured animals were blind-folded and muzzled, then transported to a licensed veterinarian. Animals were sexed and weighed with a spring scale to the nearest 0.1 kg to determine the initial drug dosage and then sedated with a combination of tiletamine and zolazepam (dosage 10 mg/kg). Continued anesthesia to maintain the anesthesia plane during surgery and processing were with a combination of tiletamine and zolazepam plus xylazine (dosage 2 mg/kg). Temperature, pulse, and respiration were monitored every 10 min. The surgical procedure for the tubal ligation (Howe 2006) involved a 2- to 3-cm incision along the midline of the abdomen, exposing the horns of the uterus, and locating the ovary and oviduct. The oviduct was clamped and then tied off 1 cm either side of the clamp. A 1-cm section of the oviduct was then cut and removed. The ovary and uterus were then returned to the normal positions in the body cavity. The incision was then closed via three separate suturing procedures involving the peritoneum, subcutaneous tissues, and skin.

Surgical vasectomy involved bilateral removal or occlusion of the portion of the ductus deferens (Howe 2006). The vasectomy was performed through a 1- to 2-cm incision located in the inguinal area. Following skin and subcutaneous incision, the spermatic cords were identified, separated, and exteriorized. Manipulation of the testicle identified the spermatic cord and ductus deferens. Following isolation of the ductus deferens, a segment of the ductus was then removed and both of the severed ends of the ductus ligated. The incision was then closed via three separate suturing procedures involving the peritoneum, subcutaneous tissues, and skin.

Following the surgical procedure, each coyote was aged by visual inspection of tooth wear (Gier 1968), ear-tagged, and radio-collared. We reversed the effects of the xylazine with the antagonist yohimbine (dosage 0.15 mg/kg) after the surgery was completed. An analgesic (butorphanol; dosage 0.4 mg/kg) was administered immediately following surgery for post-operative pain management. We applied ophthalmic ointment to prevent corneal desiccation. Animals held overnight were monitored for any post-operative complications. The following morning, animals were inspected and then returned to their respective sites of capture. Control animals (intact coyotes) underwent a sham surgery following the exact same procedures without the final tying of the tubes (thereby remaining reproductively intact), so that all else (including the surgery) was controlled. This method (sterile vs. control) has previously been documented to show no impact to subsequent survival, dispersal, and behaviors of surgically sterilized coyotes (Bromley and Gese 2001b). Close monitoring of all animals released into the wild following surgery showed no complications or deaths due to the surgical procedures. Research protocols were approved by the Institutional Animal Care and Use Committees at the USDA/National Wildlife Research Center (QA-1350) and Utah State University (IACUC #1269).

To determine with greater certainty that treated coyote packs were sterile (i.e., we captured and sterilized one or both of the breeding pair), 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 during June to mid-August, with personnel going to high points, howling, and recording whether the response included pups. In addition, visual observations of radio-collared individuals allowed us to gain information on pup presence. Any pack found to have pups was considered intact.

Determination of pack size

We compared pack sizes between sterile and intact packs using the observed minimum pack size. We made multiple

visual observations of radio-collared individuals to count associated pack members. Field personnel would home-in on a radio-collared animal, attempting to approach animals from downwind in a stealthy manner to reduce disturbance of additional pack members that may be present. Group size, location, and pup presence were noted. We did not include pups in pack size estimations, but estimated pre-whelping pack size (Gese et al. 1989).

Home range size and overlap

We acquired telemetry locations primarily at dawn and dusk to obtain point locations during the highest activity periods (Andelt and Gipson 1979). We attempted to locate animals every 2 days. We calculated locations using ≥ 3 compass bearings in Program LOCATE (Pacer, Truro, Nova Scotia, Canada). All home ranges were computed using only locations with an error polygon $< 0.10 \text{ km}^2$. We calculated home range size using the 95 % fixed kernel (FK) density estimator and core area with the 50 % FK density estimator in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA, USA) with the Hawth's Tools extension (Hawth's Analysis Tools); bandwidth was set to $h = 1,000$. We calculated home range estimates (home range size and overlap) for two breeding seasons (breeding season 1: December 2006–March 2007; breeding season 2: October 2007–March 2008), and one pup-rearing season (April–September 2007).

We compared percent overlap among adjacent packs for the 95 and 50 % FK contours using analysis of variance (ANOVA). We used only adjacent packs to calculate percent overlap, including adjacent packs with zero overlap. Packs were considered adjacent if their home range boundaries were $< 2 \text{ km}$ apart; this figure represents the radius of the smallest home range and was the minimum area we used to exclude the potential presence of a home range in which the pack members were not radio-collared. We made comparisons of home range overlap among adjacent sterile–sterile packs, intact–intact packs, and sterile–intact packs. Tests for differences between each pair were performed with a Tukey's Honestly Significant

Difference (HSD) test. All statistical tests were performed using SPSS 10.0.5 (SPSS, Chicago, IL, USA).

Home range fidelity

Familiarity of the home range, and therefore territory fidelity, is important in reducing the vulnerability of coyotes to human persecution (Knowlton et al. 1999). We tested home range fidelity of resident coyotes using known fate models in Program MARK (White and Burnham 1999); animals were censored after dispersal. We defined dispersal as the movement of an animal from its point of origin to where it reproduces or would have reproduced if it had survived and found a mate (Howard 1960). We compared models of residency rates between sterile and intact coyotes with Akaike's Information Criterion (AIC; Akaike 1973) corrected for small sample size bias (ΔAICc ; Burnham and Anderson 2002). We grouped coyotes by treatment (sterile or intact) and encounter occasions were expressed as 15 1-month intervals. Because treatment was of primary interest, all models included this variable. Hypotheses tested included residency varying by treatment alone, treatment and 4-month season, or treatment and 1-month time interval (Table 1: models 1, 2, 3). For examining home range fidelity, we used 4-month seasons based on biological changes in coyote behavior, including the breeding season (December–March), pup-rearing season (April–July), and dispersal season (August–November; adapted from Gese and Ruff 1998). We also tested a model which examined the interactive effect between treatment and time (the most parameterized model, Table 1: model 4). We censored transient animals from the analysis unless and until they became established as residents later in the study.

Survival rates

We examined survival rates of intact and sterile coyotes because, if sterilization changed coyote behavior and they dispersed, these animals would become more vulnerable to human persecution (Windberg and Knowlton 1990;

Table 1 Model selection for residency rates of sterile ($n = 15$) and intact ($n = 12$) coyotes, Piñon Canyon Maneuver Site, Colorado, December 2006–March 2008

Model no.	Model structure	AICc	ΔAICc	AICc weights	Model likelihood	K^a	Deviance	Evidence ratio (w_1/w_i)
2	{R(treatment + season)}	62.583	0.000	0.686	1.000	5	14.630	1.00
1	{R(treatment)}	64.151	1.568	0.313	0.457	2	22.344	2.19
3	{R(treatment + time)}	76.242	13.659	0.001	0.001	16	4.761	927.04
4	{global R(treatment \times time)}	103.889	41.306	0.000	0.000	30	0.000	NA ^b

^a Number of parameters

^b Evidence ratios could not be calculated because model weight was = 0

Table 2 Model selection for survival rates of sterile and intact coyote ($n = 30$), Piñon Canyon Maneuver Site, Colorado, December 2006–March 2008

Model no.	Model	AICc	Delta AICc	AICc weights	Model likelihood	K^a	Deviance	Evidence ratio
1	{S(treatment)}	47.907	0.000	0.336	1.000	2	43.876	1.00
5	{S(treatment + season)}	48.377	0.471	0.266	0.790	5	38.224	1.27
3	{S(treatment + age)}	49.536	1.629	0.149	0.443	3	43.474	2.26
4	{S(treatment + kg)}	49.871	1.965	0.126	0.374	3	43.810	2.67
2	{S(treatment + sex)}	49.923	2.016	0.123	0.365	3	43.861	2.74
6	{S(treatment + time)}	65.058	17.151	0.000	0.000	15	33.795	5,606.83
7	{global S(treatment \times time)}	94.335	46.429	0.000	0.000	30	29.239	NA

^a Number of parameters

Windberg 1996; Harris and Knowlton 2001). We compared estimates of survival rates between sterile and intact coyotes in Program MARK using known fate analysis (White and Burnham 1999). We compared models of survival rates using ΔAICc (Akaike 1973; Burnham and Anderson 2002). Coyotes were grouped by treatment and models included three covariates: gender, age class, and weight. We analyzed survival over 15 1-month occasions. We created models based on gender, age class, weight, coyote season, or monthly time interval and always included the variable treatment since this was our variable of interest (Table 2: models 1–6). Except a global model (Table 2: model 7), all hypothesized models were restricted to additive models due to limited sample size.

Results

Pack size

We captured and radio-collared 30 coyotes. We sterilized 16 (mean age 3.3 years, range 1–8 years old) animals from the southern portion of the study area and sham-operated 14 (mean age 2.5 years, range 1–8 years old) coyotes from the northern portion; ages were not different between the two areas ($P = 0.12$). Defined home ranges contained 1–2 radio-collared individuals. During the first breeding season, we documented 8 sterile and 10 intact home ranges. During the subsequent pup-rearing season, we defined 8 sterile and 9 intact home ranges. We documented 6 sterile and 8 intact home ranges during the second breeding season. Mean pack size of sterile packs (2.3 ± 0.3 ; 95 % CI) was not significantly different than intact coyote packs (2.10 ± 0.3 ; $t_9 = 0.607$, $P = 0.554$).

Home range size and overlap

Home range sizes were not different between sterile and intact coyote packs during any of the three seasons. During

the first breeding season, mean home range sizes of intact ($n = 10$) and sterile ($n = 8$) coyote packs were 24.0 ± 3.8 (95 % CI) and $22.3 \pm 3.9 \text{ km}^2$, respectively ($t_{16} = 0.601$, $P = 0.556$; Fig. 1a). During the pup-rearing season, home range sizes of intact ($n = 9$) and sterile ($n = 8$) coyote packs were $26.4 \pm 6.8 \text{ km}^2$ and $24.7 \pm 4.4 \text{ km}^2$, respectively ($t_{15} = 0.405$, $P = 0.692$; Fig. 1b). During the second breeding season, home range sizes of intact ($n = 7$) and sterile ($n = 6$) coyote packs were 20.6 ± 4.9 and $22.0 \pm 4.0 \text{ km}^2$, respectively ($t_{11} = -0.421$, $P = 0.682$; Fig. 1c).

Home range overlap was expressed as a proportion of total home range area. During the first breeding season, mean overlap between adjacent sterile home ranges was 0.251 ± 0.081 (95 % CI) and mean overlap between adjacent intact home ranges was 0.139 ± 0.076 . Mean overlap between adjacent sterile and intact home ranges was 0.060 ± 0.069 . During the first breeding season, core areas of adjacent sterile home ranges had a mean overlap of 0.033 ± 0.032 (SD). Core areas of adjacent intact home ranges overlapped by 0.001 ± 0.001 and core areas of adjacent sterile–intact home ranges had no overlap. We found differences in overlap of adjacent sterile core areas compared to adjacent intact core areas ($P = 0.020$). This relationship appeared to be mainly due to the overlap of core areas between only 2 sets of sterile home range pairs (Fig. 1a). We did not find any other differences in overlap during the first breeding season (Table 3a).

Mean home range overlap during the pup-rearing season among adjacent sterile home ranges (0.266 ± 0.073 95 % CI) was different from the mean overlap among adjacent intact home ranges (0.113 ± 0.061 ; $P = 0.006$). Differences in overlap among adjacent sterile home ranges and adjacent sterile–intact home ranges were also significant (0.057 ± 0.074 , $P = 0.007$). However, there was no evidence of difference in the overlap among adjacent intact home ranges and adjacent sterile–intact home ranges ($P = 0.639$). Core area overlap during the pup-rearing season was also different among adjacent sterile home

Fig. 1 Plots of 95 and 50 % fixed kernel estimates of individual coyote home ranges during **a** breeding season 2006–2007, **b** pup-rearing season 2007, and **c** breeding season 2007–2008, Piñon Canyon Maneuver Site, Colorado. Sterile home ranges are represented by cross-hatching

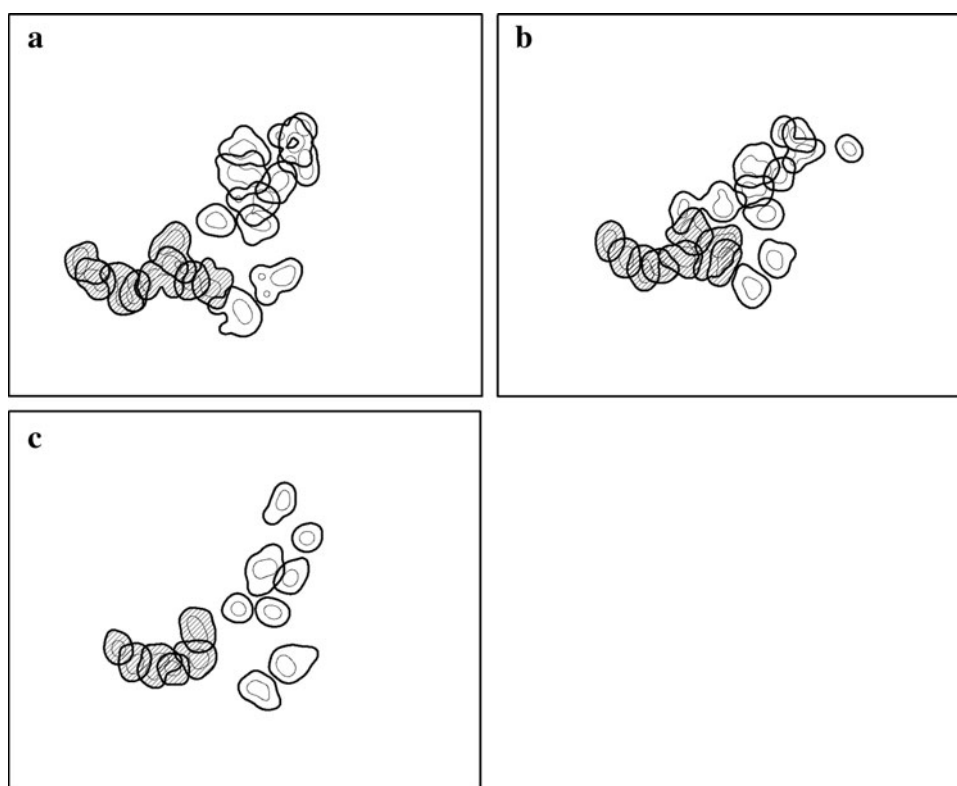


Table 3 Tukey's Honestly Significant Difference comparison of home range and core area overlap between sterile and intact coyote home ranges during the first breeding season, pup-rearing season, and second breeding season, Piñon Canyon Maneuver Site, Colorado, December 2006–March 2008

Season	Area	Group comparison	<i>P</i>
1st breeding	95 % home range	Sterile–intact	0.118
		Sterile–sterile	0.181
		Intact–intact	0.734
	50 % core	Sterile–intact	0.020
		Sterile–sterile	0.343
		Intact–intact	0.999
Pup-rearing	95 % home range	Sterile–intact	0.006
		Sterile–sterile	0.007
		Intact–intact	0.639
	50 % core	Sterile–intact	0.043
		Sterile–sterile	0.200
		Intact–intact	0.999
2nd breeding	95 % home range	Sterile–intact	<0.001
		Sterile–sterile	0.011
		Intact–intact	0.982
	50 % core area	Sterile–intact	0.312
		Sterile–sterile	0.733
		Intact–intact	0.999

ranges (0.028 ± 0.030) and adjacent intact home ranges (no overlap, $P = 0.043$). No other differences in core area overlap were found (Table 3b).

Mean overlap of adjacent sterile home ranges (0.208 ± 0.074 95 % CI) during the second breeding season was different from adjacent intact home ranges (0.012 ± 0.017 , $P < 0.001$). We also found a difference among mean overlap of adjacent sterile home ranges and adjacent sterile–intact home ranges (no overlap). We found no differences in overlap during the second breeding season (Table 3c).

Because age could affect overlap, we tested for differences in ages between sterile and intact coyotes. We found no difference in mean age between sterile and intact coyotes ($t_{28} = -0.976$, $P = 0.337$). We found no differences between sample sizes used to define home ranges for sterile and intact coyotes (first breeding season: $t_{16} = -0.429$, $P = 0.674$; pup-rearing season: $t_{15} = -0.249$, $P = 0.807$; second breeding season: $t_{13} = -0.147$, $P = 0.885$) which may also influence home range overlap. We also found no correlation between location sample sizes used to determine home range and percent overlap of home ranges (first breeding season: $R^2 = 0.013$, $F_{53} = 0.676$, $P = 0.415$; pup-rearing season: $R^2 = 0.013$, $F_{45} = 0.601$, $P = 0.442$; second breeding season: $R^2 = 0.017$, $F_{29} = 0.480$, $P = 0.494$).



Fig. 2 Coyote residency rates ($\pm 95\%$ CI) from the top model, $\{R(\text{treatment} + \text{season})\}$, in 4-month seasonal increments for sterile and intact coyotes, Piñon Canyon Maneuver Site, Colorado, December 2006–March 2008

Home range fidelity

Six radio-collared coyotes (20 %) dispersed during the study. Three of these dispersals occurred during the pup-rearing season and 3 during the dispersal season. No radio-collared coyotes dispersed during the breeding seasons. The best model for coyote residency was $\{R(\text{treatment} + \text{season})\}$ (Table 1: model 2). This model was 2.2 times as plausible as the second-best model $\{R(\text{treatment})\}$ (Table 1: model 1). Models 3 $\{R(\text{treatment} + \text{time})\}$ and 4 $\{R(\text{treatment} \times \text{time})\}$ were not well supported by the data (evidence ratios 927.04 and NA, respectively; Table 1). Residency was highest during the breeding seasons and dropped during the pup-rearing and dispersal season (Fig. 2). Model averaging showed that derived residency rates (the probability of remaining a resident through the duration of the study) were not different between sterile ($\hat{r} = 0.779$, 95 % CI 0.496–0.927) and intact ($\hat{r} = 0.738$, 95 % CI 0.432–0.913) coyotes ($z = 0.239$, $P = 0.406$).

Survival rates

We analyzed survival rates of 17 male and 13 female coyotes; 8 males and 8 females were sterilized. Four coyotes perished during the study: 3 due to gunshot wounds, 1 due to unknown causes. Many of the models used to analyze coyote survival rates were competitive. The first 5 models were within <2.016 ΔAICc values from each other, indicating that all 5 were plausible (Burnham and Anderson 2002). The best-fit model, $\{S(\text{treatment})\}$ (Table 2: model 1), suggested sterile coyotes had lower survival rates than intact coyotes (sterile: $\hat{s} = 0.805$, 95 % CI 0.540–0.936; intact: $\hat{s} = 0.923$, 95 % CI 0.608–0.989). The second-ranked model, $\{S(\text{treatment} + \text{season})\}$ (Table 2: model 5), showed an increasing trend in survival over the seasons and higher survival in intact coyotes, but the confidence intervals

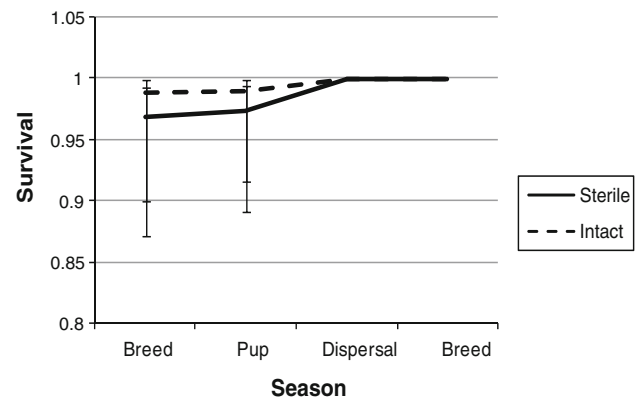


Fig. 3 Coyote survival rates ($\pm 95\%$ CI) from the second-ranked model, $\{S(\text{treatment} + \text{season})\}$, in 4-month seasonal increments for sterile and intact coyotes, Piñon Canyon Maneuver Site, Colorado, December 2006–March 2008

between the groups overlapped (Fig. 3). Model averaged derived estimates of survival rates (i.e., probability of surviving the duration of the study) of sterile and intact coyotes were not different (sterile: $\hat{s} = 0.809$, 95 % CI 0.544–0.938; intact: $\hat{s} = 0.924$, 95 % CI 0.611–0.990). When we calculated statistics for the third-, fourth-, and fifth-ranked models, $\{S(\text{treatment} + \text{age})\}$, $\{S(\text{treatment} + \text{weight})\}$, and $\{S(\text{treatment} + \text{sex})\}$, we found the covariates were not significant ($P > 0.280$). Other models had ΔAICc values >2.016 . In a post hoc analysis, $\{S(\cdot)\}$ (coyote survival rate is not influenced by any variables) was ranked as the top model and $\{S(\text{season})\}$ was ranked second.

Discussion

As sterilization becomes more widely used in canid research and management practices, we must confirm territorial maintenance and pair-bonding behaviors are being retained. Without these behaviors, the social structure of the pack will dissolve leading to an unguarded, open territory, and management efforts could fail. We found no evidence to suggest territorial behaviors among coyotes were altered by sterilization. Pack size, home range size, home range fidelity, and coyote survival rates were not significantly different between sterilized and sham-operated coyotes. We did find sterile packs exhibited greater home range overlap than intact packs, but it is unknown whether this was due to the effects of sterilization.

Similar to our results, sterile red fox vixens had increased home range overlap compared to non-sterile vixens (Saunders et al. 2002). In contrast, coyotes in Utah did not display differences in home range overlap between sterile and intact packs (Bromley and Gese 2001b). Average overlap between coyote territories in Utah was 21 %, greater than the overall average overlap in our study (14 %). Possibly, sterile coyote

packs on the PCMS were more tolerant of overlap than intact coyote packs. We also tested for age and location sample size differences between the sterile and intact packs to account for the differences in overlap. Younger, low-ranking pack members disperse when resources are not abundant (Gese et al. 1996a). If coyotes in the sterile group were younger than coyotes in the intact group, and location sample sizes were not large enough to accurately detect pre-dispersal forays, then we might mistake these forays for home range overlap. However, we did not find differences in age classes, dispersal rates, or location sample sizes between the groups suggesting that pre-dispersal forays were not occurring differentially between sterile and intact coyotes. Varying location sample sizes were also not correlated to the degree of overlap.

Additionally, 2 dispersers in the second breeding season of previously resident coyotes in the intact area may account for differences observed between home range overlap in this season. One of the dispersers was an adult male coyote located in the center of the intact part of the study area. His initial home range had contributed to overlap in previous seasons. His dispersal coincided with the expansion of adjacent coyote pack home ranges into his previous home range area and may have been the result of displacement (Carbyn 1981). However, the expansion of the neighboring pack's home range was not enough to compensate for the lost overlap. Given consistently high overlap in the sterile home ranges and dispersal events which reduced overlap in the intact home ranges, we believe the disparity in home range overlap was not prompted by sterilization, but most likely had high pre-existing overlap among home ranges in that area.

Home range fidelity of coyotes varied by season and declined during the pup-rearing and dispersal seasons. Pack sizes gradually decline after whelping due to dispersals of non-breeding associated pack members (Bekoff and Gese 2003). We found no evidence that dispersal rates were influenced by sterilization. This corroborates with Bromley and Gese's (2001b) results; they found no difference between residency rates of sterile and sham-operated animals.

Although our results suggested many variables were important to coyote survival rates, sterilization had no significant influence. In addition, a post hoc analysis incorporating the model {S(·)} (coyote survival rate was not influenced by any of the variables), ranked this model at the top when run with the previously described models, further suggesting none of the other variables explained the true effects. Indeed, a Wald's test confirmed them as not significant. Season, as modeled as a coyote biological interval, may have been influential on coyote survival rates. An additional post hoc analysis ranked the model {S(season)} as second only to {S(·)}. However, we must also consider confounding variables such as human persecution.

Three of 4 coyote mortalities were caused by gunshot and the fourth mortality suggested human involvement (i.e., the carcass was found <4 m from a gravel road). Although shooting of coyotes was not permitted during the study, 3 of these mortalities were detected during or shortly after military maneuvers involving armed personnel.

Results from this study add to the small body of knowledge we have regarding the effects of sterilization on wild canids. We did not find any results that were in contradiction to other studies on coyotes or wolves. One component lacking in all peer-reviewed studies of coyote sterilization is an assessment of the long-term stability of territorial and social behaviors following sterilization. Mech et al. (1996) monitored vasectomized wolves for 7 years, but the sample size was small and females were not sterilized. Zemlicka (1995) monitored sterilized captive coyotes for 1 year, while Bromley and Gese (2001b) followed the sterile coyotes for 3 years. Despite functioning endocrine systems, after multiple years of no reproductive success sterile coyotes could sever their pair-bond and search for a more successful mate. Hence, we recommend a study of sterile free-ranging coyotes following treated and untreated animals into senescent years. With a long-term study, dispersal by "breeding" individuals (dominant animals which had been sterilized) due to a lack of reproductive success may be detected. Also, by following sterile and intact coyotes to senescence, changes in survival rates may be detected. Because home range overlap of red fox vixens was reported (Saunders et al. 2002) and this study found possible pre-existing home range overlap in sterile coyotes, disruption of territory boundaries may warrant further exploration. Tolerance of trespassers into territories may complicate interpretation of experimental results and could result in failed measures for canid management.

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