DOES SPATIAL STRUCTURE PERSIST DESPITE RESOURCE AND POPULATION CHANGES? EFFECTS OF EXPERIMENTAL MANIPULATIONS ON COYOTES

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We tested the influence of a change in food resource distribution on space use and diet of coyotes (*Canis latrans*). We focused on 2 facets of space use: maintenance of home ranges by residents, and establishment of home ranges by immigrants after a coyote removal program. The study was conducted on 2 populations of coyotes in southern Texas. In both populations, a clumped, high-quality food source was added to randomly selected feeding stations to measure the influence of food distribution and abundance on home-range patterns, trespassing rates, and consumption of native prey. In established home ranges, coyotes visited and foraged at stations regularly and were found closer to stations during the treatment period. Although there was no overall treatment effect on home-range size ($F = 1.66$, *d.f.* = 5, $P = 0.15$), home ranges without supplemental food remained stable in size, whereas home ranges that had received supplemental food increased during the posttreatment period ($t = 2.09$, *d.f.* = 1, $P = 0.04$). Core areas showed a similar trend; there was no overall treatment effect ($F = 1.51$, *d.f.* = 2, $P = 0.24$); however, core areas of home ranges that received supplemental food were smaller than those of controls during the treatment period ($t = 2.71$, *d.f.* = 1, $P < 0.01$). There were no statistical differences in occurrence of any species, such as small mammals or white-tailed deer (*Odocoileus virginianus*), in scats of treatment versus control coyotes. Coyotes within the study site after removals were located closer to feeding stations during treatment than posttreatment ($F = 8.83$, *d.f.* = 1, $P < 0.02$, $n = 897$) periods, yet home-range size with supplemental food was larger than home-range size during the posttreatment period. Our findings suggest that a resource other than food influences coyote spatial patterns.

Key words: canid, field experiment, movement, spatial ecology, supplemental feeding

Spatial stability, defined as the consistent location of home ranges over time, may be related to stable or abundant resources and low turnover rates of individuals (Frey and Conover 2007; White et al. 1996; Young et al. 2006), whereas spatial instability is typically related to changes in resources, such as fluctuating distribution patterns of food (Doncaster and Macdonald 1991). Theories predict that food resources affect both home-range spacing patterns and behavior (Maher and Lott 2000). Changes in spacing related to food abundance and distribution have been observed in canids, including red foxes

(*Vulpes vulpes*—Doncaster and Macdonald 1991), golden jackals (*Canis aureus*—Macdonald 1979), and African wild dogs (*Lycaon pictus*—Creel and Creel 2002). Coyotes (*Canis latrans*) are noted for being highly adaptable, but have stable home ranges between generations (Kitchen et al. 2000; Young et al. 2006). This raises 2 questions: what allows spatial stability, and what environmental factors cause spatial changes in populations of coyotes?

The effects of resource abundance and distribution on spatial patterns of coyotes can be examined through experimental manipulations. The resource dispersion hypothesis predicts that group size will vary with changes in patch richness (e.g., food resources), whereas home-range size depends on the distance between patches (Macdonald 1983). Increases in food abundance can have long-term effects on population densities, movement, individual fitness, social structure, and behavior

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(Carpenter 1987; McLoughlin et al. 2000; Prange et al. 2004). Supplemental feeding resulted in increased recruitment rates in a population of kit foxes (*Vulpes macrotis*), but no information on its influence on spatial patterns was included (Warrick et al. 1999). In fact, we are unaware of any study that has experimentally manipulated space use of canids by altering food availability.

Ranches with carcass dumpsites have allowed for evaluation of how food distribution influences space use of coyotes, suggesting that space-use patterns are influenced by fluctuating patterns of food distribution. For example, the distribution of dumpsites influenced movement patterns of residents and transients and potentially affected long-distance movement of individuals (Danner and Fisher 1977; Hein and Andelt 1996; Kamler et al. 2004). Coyotes also leave areas after carcasses are removed (Todd and Keith 1976).

Some studies have correlated diet and space use with food abundance, suggesting that coyote predation on large mammals is low when small mammals are abundant (Hamlin et al. 1984; Stoddart et al. 2001). In general, rates of trespassing may increase when prey availability is extremely high because resources become too costly to defend (Wiens 1976). However, Bekoff and Wells (1986) noted that rates of trespassing by coyotes into established territories increase during periods of low prey availability. Thus, boundary defense may relax during periods of extremely low or high resources (Camenzind 1978). For example, boundaries of coyote packs overlapped in areas with domestic sheep, even though packs used spatially discrete areas before and after the sheep were present (Shivik et al. 1996). A highly clumped and abundant food resource, especially in a population of coyotes with a high turnover rate, could result in relaxed defense behaviors and spacing patterns. Both a reduction in agonistic behaviors and discrete spatial boundaries have been observed in wolves (*Canis lupus*) when white-tailed deer (*Odocoileus virginianus*) were clumped and abundant (Theberge and Theberge 2004).

Our main objectives were to determine if changes in food availability and distribution would alter the space use and diet of coyotes. We specifically focused on 2 facets of space use: home-range maintenance within an unexploited population, and home-range maintenance by surviving coyotes and establishment of immigrant coyotes after an intensive removal program. We tested the 1st component (experiment 1) with a population of coyotes (population A) that experienced little to no human hunting pressure before, after, and during the 2 study years and a 2nd population (population B) that experienced little to no human hunting pressure before and during year 1 of study. We tested the 2nd component (experiment 2) with population B after it experienced heavy hunting pressure. In both experiments, supplemental food was provided at discrete locations to treatment coyotes so that we could evaluate the impacts of food abundance and distribution on spatial patterns. We hypothesized that increased food abundance would affect diets of coyotes and decrease coyote predation on wildlife and domestic species because coyotes would reduce the amount of time spent throughout their home range and allocate more time near readily available food resources. We predicted that treatment home ranges would be reduced in size, core areas would be shifted to encompass sites where supplemental food was provided, rates of trespassing by coyotes into the ranges of coyotes including food-provisioning sites would increase, and diets of coyotes within treatment home ranges would include fewer natural prey items. For experiment 2, we predicted that coyotes that were not removed would shift home ranges to include supplemental food patches and that immigrant coyotes would be spatially constrained by previous residents while establishing home ranges.

MATERIAL AND METHODS

The study focused on 2 populations of coyotes. Population A was at the 3,157-ha Rob and Bessie Welder Wildlife Refuge (WWR) and adjacent parts of neighboring ranches for a total study area of approximately 3,500 ha, whereas population B was located within a portion of the 22,258-ha McFaddin Enterprises Ranch (MER). Both properties are north of Sinton, Texas. The Aransas River forms the northern border of WWR and flows through MER. The MER study site was equivalent in size (~3,500 ha) and vegetation composition and structure to WWR. Both properties are located in a transition zone between the gulf prairies and marshes and southern Texas plains (Gould 1975). The 2 main mammalian predators were coyotes and bobcats (*Lynx rufus*). Coyotes were not harvested at WWR (Andelt 1985; D. L. Drawe, Welder Wildlife Foundation, Sinton, Texas, pers. comm.). Hunting of coyotes has been minimal on adjacent ranches, allowing population A at WWR to be used for experiment 1 in both years. Before our study, only 1–3 coyotes were removed annually from the MER study site through hunting and lethal trapping. Hunters and ranch managers complied with our requests: they did not hunt or trap coyotes at MER in 2003 or 2004, but hunted and trapped coyotes intensively between experiments 1 and 2. Therefore, population B at MER was used for experiment 1 in 2004 and experiment 2 in 2005. All procedures were approved by the Utah State University animal care committee and followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Adult coyotes were captured using number Victor number 3 Soft Catch padded leghold traps with attached tranquilizer tabs (Woodstream Corporation, Lititz, Pennsylvania—Balser 1965). A radiocollar (Advanced Telemetry Systems, Isanti, Minnesota) was placed on all captured adult coyotes for radiotelemetry via triangulation and visual observations. Three or more bearings were obtained within 20 min for each location of a radiocollared coyote. Compass bearings with an azimuth $<20°$ or $>160°$ from each other were discarded. Point locations were obtained using the maximum-likelihood estimator in program Locate II (Nams 1990). We tested accuracy of triangulation by obtaining triangulation data for a radiocollar that was placed randomly in the field multiple times throughout the study period ($n = 36$). Estimates in Locate II of locations of test collars were <100 m from true locations. Radiotelemetry sessions were conducted at random start times within each 4-week period, and we attempted to obtain 58 locations per

TABLE 1.—Resident status and pack association of individual radiocollared coyotes at McFaddin Enterprises Ranch (MER), Texas.

			2004		2005	
Coyote no.	Sex[a]	Site	Pack[b]	Status[b,c]	Pack[b]	Status[b,c]
43	M	MER	—	—	/	Transient
83	M	MER	—	—	Y	Resident
103	M	MER	—	—	V	**Resident**
143	F	MER	—	—	/	Transient
163	F	MER	—	—	W	**Resident**
172	M	MER	/	**Resident/transient**[d]	/	Transient
232	F	MER	Q	Resident	—	—
252	M	MER	Q	**Resident**	Q	Resident
271	F	MER	T	Resident	T	Resident
293	M	MER	R	Resident	R	**Resident**
312	F	MER	U	**Resident**	—	Shot
351	F	MER	S	**Resident**	—	—
593	M	MER	S	**Resident**	—	Shot

[a] M = male; F = female.
[b] Dash (—) indicates not present or not applicable.
[c] Boldface type indicates coyotes within home ranges randomly selected for treatment.
[d] Resident coyote in treatment home range except during weeks 7–12 of study.

coyote. Locations of coyotes were obtained ≥4 h apart to ensure independence (Swihart and Slade 1985).

Radiocollared coyotes were classified as resident or transient based on spatial patterns from radiotelemetry locations. We defined resident coyotes as those using discrete areas that showed little to no overlap with other resident coyotes that were not pack members, and transients as those with ranges encompassing the entire study site. Transients showed high spatial, but low temporal overlap with resident coyotes. Home-range sizes (90% isopleth curves) and core areas (30% isopleth curves) were calculated using the adaptive kernel home-range model (Worton 1989), with the Home Range Extension for ArcView (Carr and Rodgers 1998). We used the 30% isopleth curve for core areas to evaluate fine-scale changes in high-use areas. Monthly (4-week) home-range estimates were obtained for radiocollared coyotes that had ≥30 locations per month. We used 30 locations as the minimum cutoff to ensure validity of adaptive kernel estimates. We pooled locations from coyotes that were within the same pack.

Experiment 1.—Experiment 1 was initiated in January 2004 with an 8-week pretreatment period, the treatment period began in March and lasted for 16 weeks, and the posttreatment period began in late August and lasted for 8 weeks. The duration of the treatment period was longer to allow evaluation of effects of manipulating food distribution throughout periods of low (mid-March to May) and high (June) occurrences of natural prey in the region (Andelt et al. 1987; Young et al. 2006). The experiment was repeated during the same months in 2005, but dates varied slightly. We obtained monthly home-range estimates, as described above, and we also pooled locations across months to obtain home-range estimates for pretreatment, treatment, and posttreatment periods.

Pretreatment home ranges of resident coyotes were used to randomly assign treatment and control packs in each year. Half of the home ranges observed during the pretreatment period received experimentally placed food at supplemental feeding stations (SFSs), consisting of feral pig (*Sus scrofa*) carcasses and assorted meat scraps (hereafter, treatment home ranges); half did not receive SFSs (control home ranges). Food was added 2 or 3 days each week (50–200 kg SFS^{-1} week^{-1}) to ensure that a constant food supply was available. Coyotes will scavenge from other wildlife and anthropogenic food sources (Fedriani et al. 2001; Kamler et al. 2004), and our SFSs therefore reflected conditions coyotes could naturally experience. Feral pigs were not used at WWR in the 2nd year to allow us to assess the frequency of occurrence of feral pigs in the natural diet of control and treatment coyotes. Once treatment home ranges were assigned, an SFS was randomly selected from all available space that fell within the treatment home range but outside of its core area (30% isopleth curve). This procedure was used for each treatment home range.

All food at each SFS was coated with unique color glitter. Glitter is easy to identify in coyote scat (Burns et al. 1995) and was used to provide evidence of use of SFSs and distances coyotes traveled from SFSs. Scats were collected ≥2 times/ month during the treatment period along all roads and major trails. An equal amount of roads and trails within control and treatment home ranges were traveled for scat collection, for approximately 24 km total. Location and glitter color of each scat was recorded. Because high vehicular traffic displaced and obscured scats on MER roads and trails, only scats collected from WWR were used for distance and dietary analyses. After treatment periods, all remaining food and bones were removed from SFSs. Monitoring continued to evaluate posttreatment period movements.

The experiment was repeated using a crossover design in 2005 at WWR. Thus, in 2005, all 2004 treatment home ranges in population A became controls and some 2004 control home ranges were treatments (Fig. 1). Some home ranges were maintained as controls in both years because there were more home ranges available for SFSs in 2005 than could be logistically managed. Because some changes in pack membership occurred between 2004 and 2005 (Tables 1 and 2), home-

TABLE 2.—Resident status and pack association of individual radiocollared coyotes at Welder Wildlife Refuge (WWR), Texas.

Coyote no.	Sex[a]	Site	2004		2005	
			Pack[b]	Status[b,c]	Pack[b]	Status[b,c]
13	F	WWR	A	Resident	A	Resident
22	M	WWR	—	—	O	Resident
32	M	WWR	—	—	/	Transient
72	M	WWR	J	Resident	J	Resident
93	F	WWR	/	Transient	/	Transient
114	F	WWR	F	**Resident**	—	—
131	F	WWR	B	Resident	—	—
182	M	WWR	—	—	O	Resident
191	F	WWR	—	—	K	**Resident**
202	M	WWR	—	—	L	Resident
212	M	WWR	I	**Resident**	—	—
232	M	WWR	—	—	G	**Resident**
332	M	WWR	H	Resident	H	Resident
372	F	WWR	D	Resident	N	Resident
391	F	WWR	E	Resident	/	Transient
412	M	WWR	F	**Resident**	F	Resident
431	M	WWR	G	Resident	G	**Resident**
453	M	WWR	—	—	G	**Resident**
472	F	WWR	—	—	/	Transient
493	F	WWR	/	Transient	/	Transient
513	F	WWR	/	Transient	/	Transient
532	M	WWR	—	—	P	**Resident**
552	F	WWR	—	—	M	**Resident**
612	M	WWR	C	**Resident**	—	—
632	F	WWR	—	—	/	Transient
652	F	WWR	—	—	/	Transient
672	F	WWR	D	Resident	/	Transient
693	M	WWR	—	—	M	**Resident**

[a] F = female; M = male.
[b] Dash (—) indicates not present or not applicable.
[c] Boldface type indicates coyotes within home ranges randomly selected for treatment.

range positions rather than identification of pack members were used to define treatment sites.

Spatial patterns were analyzed in several ways. First, we obtained an indirect measurement of distances coyotes traveled after visiting SFSs by measuring the distance each glitter scat was located from the corresponding SFS in both years at WWR. We used these distances to determine average distance scats were located from corresponding SFSs. Second, we compared sizes of home ranges and core areas for treatment and control packs among pretreatment, treatment, and post-treatment time periods. This experiment was a modified form of before–after control–impact design (Underwood 1992). Sizes of core areas and home ranges were analyzed using analysis of variance of a mixed model with 3 fixed-effect factors and their interactions: treatment, time period, treatment $\times$ time period, month nested within time period, and treatment $\times$ month nested within time. Using packs as a random-effects factor, total variance was partitioned into variability among packs, variability among repeated measures across time periods, and variability among repeated measures across months within packs. Data were log transformed before analysis to meet assumptions of normality and homogeneity of variance. We used PROC MIXED in SAS for Windows 9.1.2 (SAS Institute Inc. 2004), and assessed significant interactions using contrasts. Third, the distances between SFSs and

all locations of treatment coyotes during pretreatment and treatment periods were compared by using PROC MIXED with a REPEATED statement. Fourth, we compared spatial overlap over time for each control and treatment home range and core area by obtaining Minta's index values (Minta 1992). This comparison specifically focused on individual home ranges over the 3 experimental periods by obtaining mean geometric overlaps (Minta 1992). Mean overlap was calculated as:

$$\text{mean overlap} = \frac{\text{HRoverlapAB} \times 100}{\sqrt{(A \times B)}},$$

where home range (HR) A and B are the matched home-range pairs for pretreatment and treatment or treatment and posttreatment periods for each coyote or pack. Similar calculations were conducted for core-area overlap across time. Fifth, we obtained the proportion of total locations treatment coyotes were found within 150 m of SFSs. A 150-m buffer zone around each SFS was used because it was much greater than any biases from telemetry error and was $\geq 25\%$ of core-area size for all home ranges of residents during the treatment period. Furthermore, this buffer radius prevented us from excluding presence of coyotes at SFSs if coyotes removed food but then moved away before consuming it to avoid potential competitors. Videos from a pilot study and the distribution of bones by the end of each treatment period indicated that coyotes used this strategy

regularly. Last, conservative estimates of trespassing in both years at WWR were determined by measuring percentage of glitter scats collected within versus outside of the treatment home ranges, percentage of times coyotes from control packs were located within treatment home ranges, and percentage of time transients were located within treatment versus control home ranges. All comparisons were made between pretreatment, treatment, and posttreatment periods and between control and treatment packs unless otherwise stated.

All collected scats were weighed, washed in nylon bags, dried, and weighed again before analysis of content. Pure meat, such as that used for SFSs, is expelled in a powder form in scat. The powder washes out of nylon bags, leaving only indigestible material (Johnson and Hansen 1979). Thus, the difference in pre- and postwash weights reflected the amount of pure meat content within scats and were analyzed with PROC GLM procedures in SAS (SAS Institute Inc. 2004). Contents of scats also were coded as presence–absence data. Because relative abundance of small prey items is often overestimated, a prey item was considered present within an individual scat if it made up $\geq$40% of overall volume (Andelt 1985; Bowen 1981). Therefore, each scat could have 0, 1, or 2 items present. Prey items were classified into 3 major categories: mammals, birds, and other (i.e., reptiles, insects, and fruit). Mammalian items were further classified into small ($<$0.3 kg), medium (0.3–10.0 kg), and large ($>$10 kg) size classes, based on capture, handling, and consumption requirements (Andelt 1985; Bowen 1978; Young et al. 2006), and identified to species when possible. Individual scats were treated as independent observations for analysis.

Diets of coyotes were then compared by 2 methods. First, scats that contained glitter (treatment) were compared to those that did not (control) to directly compare consumption of experimentally placed versus natural food. Second, all scats (with and without glitter) collected within treatment home ranges were compared to scats collected outside of treatment home ranges (i.e., control home ranges). For both comparisons, frequency of occurrence was evaluated with logistic regression. EXACT procedures for logistic regressions were used for white-tailed deer and domestic cow (SAS Institute Inc. 2004). All data are presented as mean $\pm$ *SE*.

Experiment 2.—Coyotes were removed by focused hunting at MER to evaluate the influence of prey distribution on spacing patterns of coyotes after large perturbations. During the 2004–2005 hunting season (December 2004–February 2005) hunters shot coyotes regularly and an aerial hunting operation removed additional coyotes (1–3 March 2005). We began providing supplemental food at 3 SFSs on the evening of the final aerial hunting operation (4 March 2005; Fig. 2). SFSs were randomly selected from an area that encompassed all known home ranges from the 2004 study (Fig. 2). No pretreatment period occurred to ensure that treatment periods in experiment 2 coincided with the treatment period in experiment 1. Instead, we provided SFSs for 3 weeks before we trapped and radiocollared coyotes within the study area. We waited 3 weeks to increase the probability of the capture of newly establishing resident coyotes instead of transient

coyotes that also may have investigated the disturbed area postremoval.

Radiotracking methods were identical to those used at WWR in 2004; however, because of logistical constraints, the number of locations obtained per animal was reduced to 40 per 4-week period at MER in 2005. Estimates of home ranges and core areas were obtained for all radiocollared coyotes with $\geq$30 locations during the treatment period (early March–early July) and posttreatment period (July–August). Treatment and posttreatment period values of the Minta index for overlap of core areas and home ranges between 2004 and 2005 were obtained for coyotes that survived the removal process (Minta 1992). These values were used to determine if remaining coyotes altered home ranges when spatial constraints by neighbors were removed.

The 3 home ranges with SFSs were classified as treatment home ranges, whereas the remaining 3 were classified as controls for 2 further comparisons. Minta index values of overlap between treatment and posttreatment periods were compared for home ranges and core areas of each treatment and control coyote (Minta 1992). The distances each treatment coyote was located from SFSs during treatment and posttreatment periods were obtained. Measurements also were obtained for distances of all locations of control coyotes to the nearest SFS for treatment and posttreatment periods and analyzed using PROC MIXED with a REPEATED statement (SAS Institute Inc. 2004).

RESULTS

Experiment 1.—In 2004, there were 8 radiocollared coyotes (7 residents and 1 transient) at MER (Table 1) and 15 radiocollared coyotes (12 residents and 3 transients) at WWR (Table 2). One coyote at MER died of an unknown cause at the end of the pretreatment period. In 2005, there were 24 radiocollared coyotes at WWR (15 residents and 9 transients; Table 2). Four of the WWR radiocollared coyotes from the 2004 study period died or disappeared before the 2005 study. Of these, 2 were killed by other animals (1 by an American alligator [*Alligator mississippiensis*] and 1 by a coyote), 1 was shot by a hunter when it traveled off WWR premises, and 1 apparently dispersed. An animal was defined as a disperser if it was located at a study site for an extended time period, then began moving away from the study site and was continuously located farther from the study site until the signal was lost altogether. Additionally, 3 radiocollared coyotes at WWR died or disappeared during the 2005 study period. Two died of unknown causes and radiocontact was lost with 1 (treatment 191) after more than half of the treatment period had elapsed at WWR. There were sufficient data collected before the disappearance of 191 to include it in estimates and analyses through the treatment period. One of 2 transient radiocollared coyotes apparently dispersed during the posttreatment period. Sufficient locations were obtained for treatment coyotes' home-range estimates during all time periods.

There were 6 treatment home ranges in 2004, 3 at WWR and 3 at MER (Figs. 1 and 2). More than 11,000 kg of meat scraps
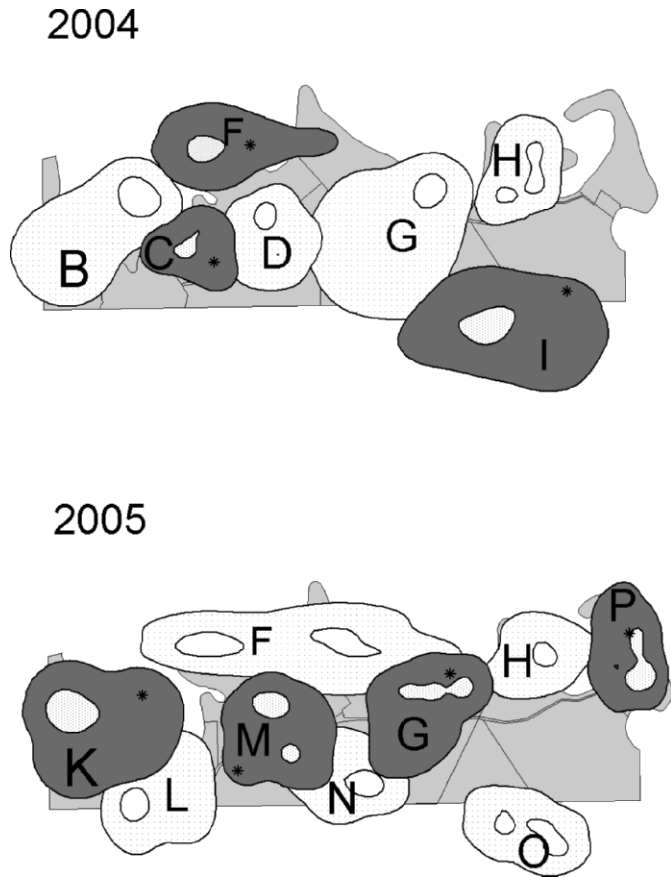
FIG. 1.—Home range and core areas during the treatment period for treatment (dark gray) and control (white with pattern) coyotes in 2004 and 2005 at Welder Wildlife Refuge, Texas (light gray background). Asterisks (*) indicate locations of supplemental feeding stations (SFSs) and the letters correspond to pack membership in Table 2.
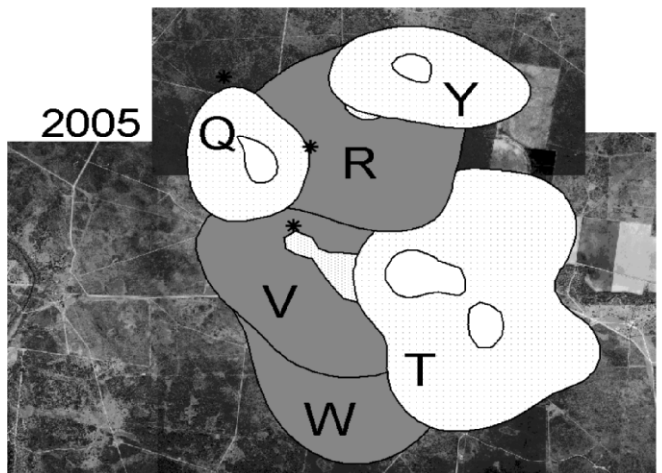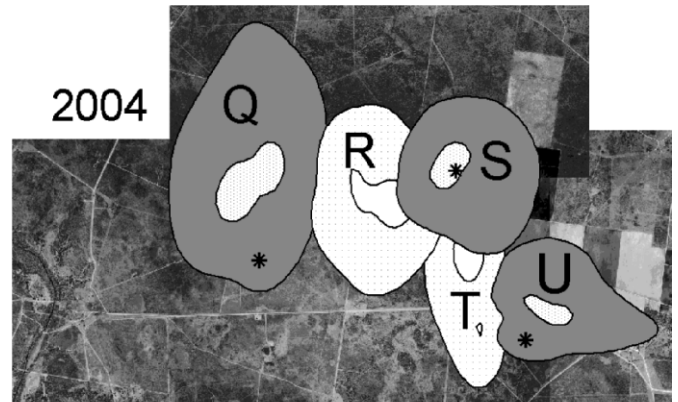

FIG. 2.—Home range and core areas during the treatment period for treatment (dark gray) and control (white with pattern) coyotes in 2004 and 2005 at McFaddin Enterprises Ranch, Texas. Asterisks (*) indicate locations of supplemental feeding stations and the letters correspond to pack membership in Table 1.

and carcasses were evenly distributed to 6 SFSs. There were also 6 control home ranges in 2004, 3 with $\geq$30 locations for home-range estimates during all 3 periods. There were 4 treatment home ranges at WWR in 2005 (Fig. 1), all with $\geq$30 locations during all 3 periods. Approximately 5,000 kg of meat scraps were evenly distributed to 4 SFSs during the treatment period. Six of 7 control home ranges had $\geq$30 locations for home-range estimates during all 3 periods in 2005.

Species using SFSs, as indicated by direct observation or tracks and feces at SFSs, included coyotes, feral pigs, turkey vultures (*Cathartes aura*), black vultures (*Coragyps atratus*), crested caracaras (*Polyborus plancus*), American alligators, and domestic cattle. There were no direct observations of alligators or cows consuming experimentally placed food items. It was evident that coyotes visited SFSs throughout treatment periods in both years because coyotes were found at SFSs during radiotracking sessions, coyote scat and tracks were found at SFSs, and glitter was found in coyote scats throughout WWR and MER.

At WWR, there was no statistical difference in the distance from where scats were located to their corresponding SFS based on year ($t = 1.98$, *d.f.* $= 121$, $P = 0.70$, $n = 129$) or SFS glitter color ($F = 2.68$, *d.f.* $= 3, 125$, $P = 0.51$, $n = 129$), so all

glitter scats were pooled to obtain average distances of scats from their corresponding SFS. On average, scats containing glitter were located within 1.05 ± 0.10 km of the SFS of origin. Locations of coyotes were significantly closer to their respective SFS during the treatment (1.02 ± 0.05 km) than during the pretreatment (1.24 ± 0.06 km) period in both years ($F = 196.62$, *d.f.* $= 1$, $P < 0.0001$, $n = 20$).

Treatment home ranges and core areas were smallest during treatment periods, whereas control home ranges tended to decrease in size throughout the entire study (Fig. 3). In fact, there was no spatial overlap between any neighboring home ranges during the 4-month treatment period at WWR in 2004. However, there was no overall treatment effect on home-range size ($F = 1.66$, *d.f.* $= 5$, $P = 0.15$). There were differences in home-range size between periods ($F = 4.53$, *d.f.* $= 2$, $P < 0.02$) and between months within periods ($F = 2.54$, *d.f.* $= 5$, $P < 0.04$). There was an increase in size of treatment home ranges during the posttreatment period that did not occur in
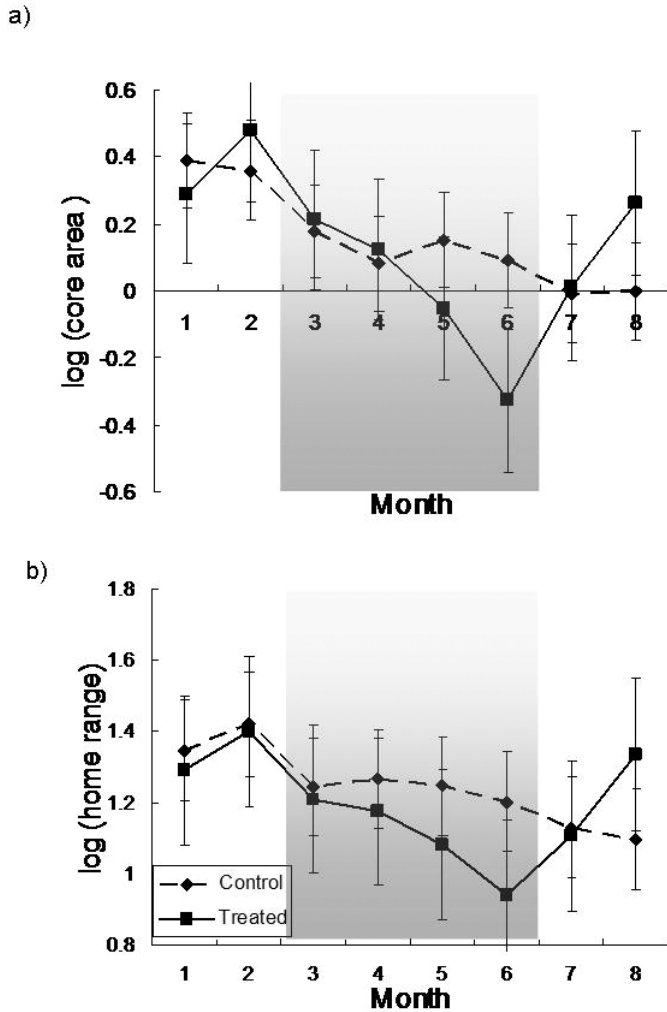
a)

b)

Fig. 3.—Monthly least square mean estimates of a) home ranges and b) core areas for control ($n = 10$) and treatment ($n = 7$) coyote packs at McFaddin Enterprises Ranch in 2004 and Welder Wildlife Refuge in 2004 and 2005. Treatment period is shaded.

control home ranges ($t = 2.09$, $d.f. = 1$, $P = 0.04$). Core areas showed a similar trend; there was no overall treatment effect on size of core areas across periods ($F = 1.51$, $d.f. = 2$, $P = 0.24$). However, there was a significant decrease in the size of core areas of treatment home ranges during the treatment period ($t = 2.71$, $d.f. = 1$, $P < 0.01$), but sizes of control core areas also decreased during the treatment period.

Minta index values of overlap for core areas between pretreatment and treatment periods for control ($38.8\% \pm 8.3\%$, $n = 7$) and treatment ($19.7\% \pm 8.9\%$, $n = 4$) home ranges were not significantly different ($t = 2.31$, $d.f. = 8$, $P = 0.15$). There also was no significant difference ($t = 2.78$, $d.f. = 4$, $P = 0.52$) between treatment and posttreatment periods in Minta index values of overlap for control ($45.1\% \pm 12.0\%$, $n = 6$) and treatment ($30.7\% \pm 16.8\%$, $n = 3$) home ranges.

There was no statistical difference in percentage of times treatment coyotes were located within a 150-m buffer of a SFS between years ($F = 0.08$, $d.f. = 1$, $P = 0.78$, $n = 7$), so years were pooled for further analyses. There was no statistical difference between the 3 periods ($\chi^2 = 5.61$, $d.f. = 5$, $P = 0.35$,
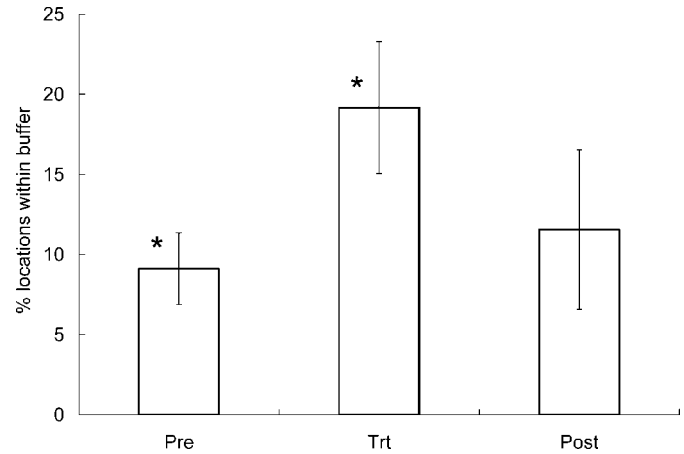

Fig. 4.—Percentage of total radiotelemetry locations of treatment coyotes that were located within 150-m radius (buffer) of their corresponding supplemental feeding stations during pretreatment (Pre), treatment (Trt), and posttreatment (Post) periods at Welder Wildlife Refuge in 2004 and 2005. * $P < 0.05$.

$n = 7$), although post hoc paired *t*-tests revealed a difference between pretreatment and treatment periods at WWR ($t = 2.45$, $d.f. = 6$, $P = 0.03$, $n = 7$; Fig. 4).

Although resident coyotes readily visited SFSs within their home ranges, there was little evidence of use (e.g., trespassing) by radiocollared coyotes from neighboring home ranges or by transient coyotes. Most glitter scats were found within home-range boundaries containing an SFS ($62.80\% \pm 9.29\%$, $n = 129$). Most scats that were not within the treatment home range were found along roads that separated treatment and control home ranges, indicating they too may have been deposited by treatment coyotes. Neighboring resident coyotes at MER and WWR also were located less often in treatment home ranges during the treatment period than during pretreatment or post-treatment periods ($\chi^2 = 15.62$, $d.f. = 5$, $P < 0.01$; Fig. 5). Transients showed a similar trend that approached significance ($\chi^2 = 9.90$, $d.f. = 8$, $P = 0.08$; Fig. 5).

Both analyses of scats yielded similar results, so only results from the comparison of scats collected within treatment home ranges to scats collected outside of treatment home ranges are presented. In total, 630 scats were collected during the treatment period at WWR. Only 534 scats were used for analyses because some bags containing scats were damaged during washing and some contents were lost that could have affected their weight or because they did not contain more than 40% of any 1 prey item. There were no statistical differences in dietary composition within scats based on 3 major prey categories except for differences by month (Table 3). We could identify species sufficiently to evaluate frequency of occurrence for small mammals, white-tailed deer, domestic cow, and feral pig (in 2005 only), but there was no treatment effect for occurrence (Table 3). Only the occurrence of white-tailed deer and small mammals showed an effect by month (Table 3). Meat content found in scats was greater for scats within treatment versus control home ranges ($F = 4.00$, $d.f. = 15$, $P < 0.0001$, $n = 534$).
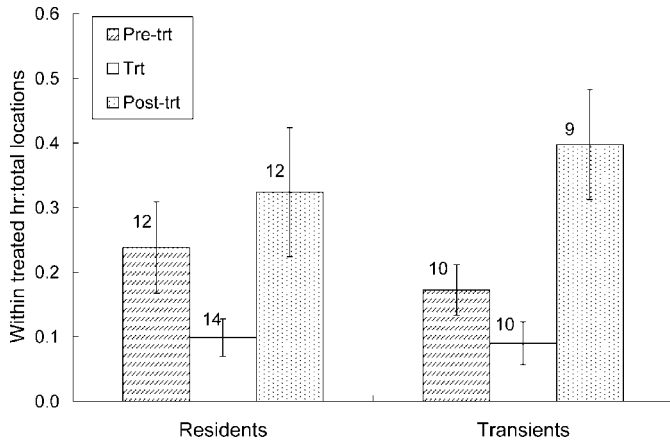
Fig. 5.—Proportion of locations of resident-control and transient coyotes that were trespassing (i.e., located within treatment home ranges) during pretreatment (Pre-trt), treatment (Trt), and posttreatment (Post-trt) periods. Data were collected for resident coyotes at Welder Wildlife Refuge (WWR) and McFaddin Enterprises Ranch in 2004, for all transient coyotes in 2004 and 2005 at WWR, and for resident coyotes at WWR in 2005. Sample sizes for number of packs (residents) or individuals (transients) are indicated above each bar.

TABLE 3.—Dietary analysis of 3 major prey categories (mammal, fruit, and other), white-tailed deer, and small mammals found in coyote scats collected from treatment versus control home ranges during the treatment period at Welder Wildlife Refuge in 2004 and 2005. Chi-square values from logistic regressions are provided ($n = 534$).

	χ^2	*d.f.*	*P*
Diet (mammal, fruit, and other)			
Month	46.89	15	< 0.0001
Year	3.43	5	0.635
Treatment	2.72	5	0.785
Treatment × month	3.76	15	0.998
Treatment × month × year	8.37	15	0.908
White-tailed deer			
Month	110.29	3	< 0.0001
Treatment	0.07	1	0.788
Treatment × month	0.69	3	0.876
Small mammal			
Month	44.75	1	< 0.0001
Treatment	0.0004	1	0.984
Year × month	7.32	1	0.06

Experiment 2.—In 2005, there were 10 radiocollared adult coyotes (8 residents and 2 transients) at MER (Table 1). Three radiocollared coyotes from 2004 died or dispersed, 1 apparently dispersed, and 2 were shot by the aerial hunters (Table 1) before the 2005 study began. Thus, a total of 6 radiocollared coyotes at MER in 2004 were removed in 2005. Another 6 noncollared coyotes were shot at MER by hunters and 12 were shot by the aerial gunner before the experiment began in 2005. In total, 24 coyotes were removed from the study area. During the treatment period, >5,000 kg of assorted meat scraps and feral pigs was evenly distributed among the 3 SFSs.

Seven coyotes were trapped during 21 March–1 July 2005 in addition to 4 radiocollared coyotes that remained on the study site from 2004. One of the 4 surviving coyotes was a transient that was not within the study area when aerial gunning occurred. Two of the trapped coyotes were excluded from analysis because 1 (a lactating female) was found dead within 1 week of capture and the signal was lost (apparent dispersal) on the other. In total, 9 radiocollared coyotes within 6 home ranges were the focus of experiment 2.

The 3 resident radiocollared coyotes that survived after the 2004 study remained residents within the study area in 2005 (Fig. 2). Minta index values of home-range overlap between 2004 and 2005 were 55.1% ± 5.4% during the treatment period and 41.2% ± 12.6% during posttreatment periods. The percent overlap observed between 2004 and 2005 during treatment and posttreatment periods was similar ($t = 4.30$, *d.f.* $= 2$, $P = 0.31$, $n = 3$). Core-area overlap between 2004 and 2005 was 15.4% ± 14.8% for treatment and 10.9% ± 10.9% for posttreatment periods. Two of 3 core areas during treatment and 1 of 3 core areas during posttreatment periods showed overlap between 2004 and 2005.

Home ranges of radiocollared resident coyotes differed in size between treatment (99.9 ± 20.1 ha) and posttreatment

(45.6 ± 11.5 ha; $t = 2.57$, *d.f.* $= 5$, $P = 0.03$, $n = 6$) periods. Although home ranges of residents were smaller after experimentally placed food was removed, the relative positions of home ranges overlapped (Minta index = 59.0% ± 5.4%, $n = 6$). Core areas within all home ranges of residents remained constant in size and relative position during treatment (6.6 ± 1.6 ha) and posttreatment (4.4 ± 1.3 ha; $t = 2.57$, *d.f.* $= 5$, $P = 0.28$, $n = 6$) periods. In fact, only 1 core area within 6 home ranges showed no overlap between periods (Minta index = 42.0% ± 10.6%, $n = 6$). During the treatment period, 3 of 6 home ranges included ≥1 SFS. One of these home ranges included 2 SFSs, 1 within and 1 outside of the core area. Home ranges of the 2 transient coyotes included ≥2 SFSs.

We found no statistical differences in Minta index values of overlap of home ranges ($t = 2.78$, *d.f.* $= 4$, $P = 0.41$, $n = 6$) for treatment (54.0% ± 8.5%) versus control (64.0% ± 7.1) coyotes or of core areas ($t = 4.30$, *d.f.* $= 4$, $P = 0.79$, $n = 6$) for treatment (45.6% ± 22.8%) versus control (38.4% ± 5.4) coyotes. But, a treatment × time interaction for distance between locations of coyotes and their SFS during treatment and posttreatment periods was significant ($F = 8.83$, *d.f.* $= 1$, $P < 0.02$, $n = 897$). These coyotes were found closer to the SFSs during treatment than posttreatment periods.

DISCUSSION

Our primary objective was to determine if changes in food abundance and distribution would alter space use and diet of individual coyotes. None of our predictions regarding changes in space use of resident coyotes or increases in trespassing rates by transients were observed. In fact, the SFS was only included in 1 core area each year during the treatment periods. The remaining control and treatment home ranges for individual coyotes showed changes in locations of core areas between

periods, but in no clear pattern or direction; most core areas maintained some overlap throughout all 3 periods. Two of 3 treatment home ranges at WWR maintained some core-area overlap with their previous locations throughout all 3 time periods in both years. Five of 6 control home ranges in 2004 and 1 of 3 control home ranges in 2005 maintained core-area overlap between all 3 time periods. SFSs did appear to affect movements and spatial distribution of coyotes through time. However, the effects were not dramatic enough to detect statistically with our sample sizes.

Although there were no significant treatment effects on size of home ranges or core areas, other factors were significantly influenced by SFSs. First, treatment coyotes were located closer to SFS during the treatment period, suggesting that coyotes used SFSs regularly. Second, size of treatment home ranges increased during the posttreatment period. Coyotes with SFSs may have spent less time searching for prey and more time engaged in other activities related to use of core areas, such as tending pups. Indeed, the treatment period coincided with pup-rearing season (Andelt 1985), likely explaining the observed decrease in size for treatment and control home ranges. Once SFSs were removed, coyotes may have compensated for loss of a rich prey resource by increasing their home-range size significantly more than did coyotes that did not have SFSs. If more pups survived because of SFSs, then the adult coyotes may have needed to expand the area they searched for food more than control coyotes once the SFS was removed. Mills and Knowlton (1991) also reported that coyotes increased the size of their home ranges when prey was scarce. Increases in home-range size in response to removal of supplemental food has been reported in other studies (Berger 1988), and changes in activity patterns have been observed in response to supplemental feeding of striped skunks (*Mephitis mephitis*—Larivière and Messier 2001).

Third, trespassing rates into home ranges with SFSs decreased during the treatment period, and coyotes from neighboring home ranges and transient coyotes were rarely located at SFSs during telemetry bouts. Spatially clumped food may be easily monopolized and defended (Grant and Guha 1993), and the small size and high stability of home ranges at WWR may have made it difficult for other coyotes to trespass. Contrary to our findings, Roy and Dorrance (1985) found that nonresident coyotes were more likely to be located near a clumped source of livestock carcasses than were residents. However, it is unclear if direct comparisons can be made because coyotes at their study site were transient and experienced intensive exploitation.

Finally, although we found no statistical difference in the types of native prey items consumed by control versus treatment coyotes, we did find an increase in pure meat content in scats of treatment coyotes. This suggests the amount of native prey consumed may be reduced by SFSs. The effects of predators on natural prey may be reduced or exacerbated by alternative prey (Wootton 1994). However, experimentally placed food did not reduce the occurrence of native species such as white-tailed deer in scats. White-tailed deer fawns are preyed upon by coyotes (Hamlin et al. 1984) and are abundant at WWR each summer (Teer et al. 1991). Further studies that can more accurately separate the availability of native prey and consumption by coyotes are needed to evaluate the effects of supplemental feeding on consumption of native prey.

Our results differ from those of other studies that have found that food resources influence spatial patterns (Creel and Creel 2002; Hayward et al. 2004). However, Adams (2001) suggested that species with contiguous home ranges are less likely to respond to changes in food abundance than animals with noncontiguous or highly overlapping home ranges. Established home ranges were contiguous at WWR with little to no overlap between coyotes and our finding of no effect supports Adams' (2001) hypothesis. Stamps and Tanaka (1981) also reported no changes in home-range size of a lizard (*Anolis aeneus*) in response to changes in food levels and discrete spatial patterns continued even when food was superabundant. Home-range boundaries of badgers (*Taxidea taxus*) remained stable when food availability changed (Cheeseman et al. 1987). Shape and size of home ranges of badgers may be influenced by sett locations during colonization, but other factors, such as habitat, also influence long-term spatial dynamics (Doncaster 2001). This may explain the patterns we observed with coyotes. Future studies should evaluate alternative factors that may influence spatial patterns of coyote territories.

Our secondary objective was to determine if food abundance and distribution influenced spatial patterns of coyotes differently when populations fluctuate. Removal efforts during experiment 2 likely created vacancies within the study area that were filled by other coyotes at MER, but few changes to locations of home ranges were observed for coyotes found pre- and postremoval. Instead, coyote home ranges that were present at MER in 2004 showed a high level of overlap with their locations in 2005. Even though neighboring coyotes were removed between 2004 and 2005, surviving coyotes only made slight changes in the boundaries and sizes of home ranges.

Hidalgo-Mihart et al. (2004) found that coyotes with access to a local landfill used smaller areas. Similarly, we had expected to find small home ranges of coyotes establishing a home range with SFSs, but instead found that newly established home ranges were double in size during the treatment compared to the posttreatment period. This may have been a function of transient coyotes settling into a new home range over time. Alternatively, SFSs may have increased energy and time available to explore their environment. Lower foraging and defense costs of abundant and clumped food often results in greater overlap of spatially adjacent home ranges (Adams 2001; Frey and Conover 2007). For example, jackals aggregate at concentrations of food (Hiscocks and Perrin 1987; Macdonald 1979). Although it was unclear if coyotes aggregated, coyotes showed high levels of spatial overlap when food was clumped and abundant. Overlap reduced when SFSs were removed. In fact, during the posttreatment period, SFSs remained within only 1 of 3 home ranges that included an SFS during the treatment period. The position of another home range that did not initially include SFSs shifted to the south to include a former SFS. This shift included the area where

a lactating female was trapped and located before her death, and may reflect a change in neighboring social patterns. Although 1 transient was out of radiocontact during the posttreatment period, the other transient more than quadrupled its home range and, therefore, its posttreatment home range included all SFSs (an increase from 2 during treatment).

Coyotes in our study were more likely to modify space-use patterns under relatively unstable population conditions, but space-use patterns of coyotes under relatively stable conditions were not driven by short-term fluctuations in food distribution. Instead, coyotes may be responding to alternative factors, such as long-term food distribution patterns, habitat features, or denning sites. Thus, studies that manipulate specific environmental factors are still needed to better understand what drives space-use patterns of coyotes under different environmental conditions.

ACKNOWLEDGMENTS

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