

# Overlap in Space Use among Bobcats (*Lynx rufus*), Coyotes (*Canis latrans*) and Gray Foxes (*Urocyon cinereoargenteus*)

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**ABSTRACT.**—Sympatry among bobcats (*Lynx rufus*), coyotes (*Canis latrans*) and gray foxes (*Urocyon cinereoargenteus*) is relatively recent in the southeastern United States given recent expansion of coyote range. Interspecific relationships among canids and felids have been documented in northern latitudes. However, interactions among these three species at southern latitudes are poorly understood. We examined overlap in space use of sympatric bobcats ( $n = 47$ ), coyotes ( $n = 37$ ) and gray foxes ( $n = 27$ ) in central Mississippi during 1993–1997. Home ranges of all three species overlapped extensively. However, gray foxes maintained core use areas that did not overlap substantially with those of bobcats and coyotes. Home range and core area overlap were similar across seasons among all species. Our findings indicate that these three species readily share space, but gray foxes apparently maintain core areas in areas void of concentrated bobcat and coyote use.

## INTRODUCTION

Bobcats, coyotes and gray foxes are sympatric throughout much of North America. In the southeastern United States, sympatry is relatively recent because coyote populations have expanded eastward (Hill *et al.*, 1987). Increasing coyote populations may have displaced red foxes in the Southeast (Lovell *et al.*, 1998) as described for red foxes in northern latitudes (Voigt and Earle, 1983; Sargeant *et al.*, 1987; Harrison *et al.*, 1989).

Gray foxes may not be similarly displaced by coyotes. Sargeant (1982) and Wooding (1984) suggested that sympatry of gray foxes and coyotes occurs because semi-arboreal behaviors in gray foxes provide effective escape mechanisms (Wooding, 1984). Notably, coyotes and gray foxes exhibit substantial overlap in diet and activity (Gipson and Sealander, 1972; Haroldson and Fritzell, 1984) and interference competition occurs (Chamberlain, 1999). Therefore, information detailing spatial relationships between coyotes and gray foxes would provide further insight into mechanisms that facilitate sympatry.

Likewise, bobcats and coyotes are sympatric throughout the United States (McCord and Cardoza, 1982; Voigt and Berg, 1987). Felids and canids generally hunt in different habitats (Kleiman and Eisenberg, 1973), and bobcats and coyotes partition habitats (Chamberlain *et al.*, 2000, 2003) and prey (Chamberlain and Leopold, 1999). Major and Sherburne (1987) reported no evidence of interference competition between coyotes and bobcats and no mutual displacement in Maine. No studies have addressed spatial relationships between sympatric bobcats and coyotes in southern latitudes, and information detailing spatial characteristics of core areas between the species is limited (Witmer and DeCalesta, 1986). Similarly, spatial relationships between bobcats and gray foxes are poorly understood.

We examined interspecific spatial relationships among bobcats, coyotes and gray foxes in central Mississippi during 1993–1997. Our objective was to estimate seasonal overlap of home ranges and core use areas for a sympatric population of adult bobcats, coyotes and gray foxes. We predicted that home ranges would overlap, but that individuals of each species would maintain exclusive core use areas because these spaces contain features critically important to each species (*e.g.*, den sites, escape cover; Ewer, 1968).

#### STUDY AREA

We conducted research on the 14,410-ha Tallahala Wildlife Management Area (TWMA), a 4900-ha area owned by the Timber Company (TC) and surrounding private lands in sections of Jasper, Newton, Scott and Smith counties, Mississippi. TWMA contained 30% mature (>30 y old) bottomland hardwood forests, 37% mature pine (loblolly, *Pinus taeda*; shortleaf, *P. echinata*) forests, 17% mixed pine-hardwood forests and 11% in 1 to 15-y old loblolly pine plantations. A tornado bisected TWMA in 1992, altering approximately 1000 ha of mature pine and hardwood forests; most (90%) of which was replanted to loblolly pine. The TC area, located adjacent to TWMA, was managed primarily for wood fiber production with 90% of the area composed of 1 to 35-y-old loblolly pine plantations, and the remaining 10% in Streamside Management Zones along creeks. Private lands were mostly mixed pine-hardwood and short-rotation pine forests. Topography is gently to moderately rolling, with 0–20% slope. Climate is mild, with a mean annual temperature of 20 C and mean annual precipitation of 152 cm. Hereafter, the TWMA refers to both study areas and the surrounding private lands.

#### METHODS

*Capture and telemetry.*—We captured bobcats, coyotes and gray foxes with Number 3 (bobcats and coyotes only) and 1.5 Victor soft-catch foot-hold traps (Woodstream, Lititz, Pennsylvania) and wire cage traps from 5 January to 5 March 1993–1997. We netted captured bobcats and anesthetized them with Ketamine hydrochloride (Ketaset Veterinary Products, Fort Dodge Laboratories Inc, Fort Dodge, Iowa) at 15 mg/kg of estimated body mass, whereas coyotes and gray foxes were restrained using tape around the rostrum and legs. We fitted each adult bobcat and coyote with a 175–225-g mortality-sensitive radiotransmitter, whereas gray foxes were fitted with 100 g mortality-sensitive radiotransmitters (Advanced Telemetry Systems, Isanti, Minnesota). We did not radiocollar juveniles because of potential for dispersal movements off of TWMA. We placed sedated bobcats in portable pet kennels, monitored their recovery and released them at the capture site the following morning. We released coyotes and gray foxes immediately following processing. We conducted research under Mississippi State University Institutional Animal Care and Use Committee Protocol 93-032.

We located all animals by triangulation (White and Garrott, 1990) using a hand-held 3-element Yagi antenna (Wildlife Materials, Carbondale, Illinois) from fixed telemetry stations ( $n = 480$ ) 2–10 times/week. In most (>85%) instances, distance from observer to each animal was  $\leq 1.0$  km. We monitored animals throughout the diel period and attempted to locate every animal equally. Azimuths for a single radio location were recorded within a 15 min interval to reduce error due to animal movement. Triangulation angles were maintained between  $45^\circ$  and  $135^\circ$  to reduce error (Kitchings and Story, 1979). Telemetry accuracy tests indicated that angular standard deviation was  $5.9^\circ$ . Therefore, a circle circumscribing each animal location 1 km from a telemetry station would have an approximate area of 3.4 ha. To derive this circle, we calculated the average distance from a telemetry station to an estimated

animal location. We calculated the radius of a circle that would be obtained if we were the mean distance from the animal, assuming 1.96 multiplied by our telemetry precision.

*Overlap in space use.*—We converted triangulated locations to a coordinate system using program TELEBASE (Wynn *et al.*, 1990). We divided each year into breeding (1 Feb.–31 May), young-rearing (1 Jun.–30 Sept.) and winter (1 Oct.–31 Jan.) seasons based on reproductive and physiological information for bobcats in Mississippi (Stys and Leopold, 1993) and for coyotes and gray foxes captured during our study (Chamberlain *et al.*, 2000; Chamberlain and Leopold, 2000). We estimated seasonal home range (95%) and core area (50%) contours using an adaptive kernel estimator in program CALHOME (Kie *et al.*, 1994). After examining area-observation curves (Seaman *et al.*, 1999; Chamberlain and Leopold, 2000), we estimated size of home ranges and core areas only for animals with  $\geq 30$  locations/season and monitored  $\geq 75\%$  (3 of 4 mo) of a given season.

We estimated spatial overlap by intersecting seasonal home ranges of neighboring individuals and measuring the area of the overlap region using ARCVIEW (ESRI, 1997). We then superimposed point locations of each animal on the overlap region and counted numbers of locations by each individual within the overlap region to derive a proportion of each individual's locations within the overlap region.

We described the spatial distribution of home ranges and core areas using overlap indices for bobcat and coyote, bobcat and gray fox and coyote and gray fox. During each season within each year, we calculated overlap indices for two neighboring individuals by modifying the simple ratio of Ginsberg and Young (1992) to quantify association:

$$[(n_1 + n_2)/(N_1 + N_2)] \times 100$$

Where  $n_1$  and  $n_2$  are numbers of locations for individuals 1 and 2 within the overlap region and  $N_1$  and  $N_2$  are total numbers of locations recorded for individuals (Gehrt and Fritzell, 1998). We constructed three, 1-way analyses of variance blocked by year to examine differences in indices of space use overlap among pairs of species (*i.e.*, bobcat/coyote, bobcat/gray fox, coyote/gray fox) across season.

## RESULTS

We captured and monitored 47 bobcats, 37 coyotes and 27 gray foxes during 1993–1997. We documented 142 instances of seasonal overlap in space use between 24 bobcats and 15 coyotes. Typically, coyote home ranges overlapped portions of several bobcat home ranges (Fig. 1). Home range ( $F_{2,135} = 0.08$ ,  $P = 0.927$ ) and core area ( $F_{2,135} = 0.60$ ,  $P = 0.551$ ) overlap did not differ across seasons (Table 1). We documented sharing of core areas between bobcats and coyotes and substantial portions ( $>75\%$ ) of bobcat home ranges were contained within coyote core areas (Figs. 2a, b).

We documented 54 instances of overlap in space use between 14 coyotes and 19 gray foxes and coyotes overlapped portions of several gray fox home ranges (Fig. 3). We excluded winter home range and core area overlap indices from comparisons because of low numbers of pairs ( $n = 5$ ) displaying overlap. Low numbers of pairs resulted from relatively fewer animals being monitored during winter. Four gray foxes maintained home ranges entirely within coyote home ranges. Home range ( $F_{1,44} = 1.33$ ,  $P = 0.26$ ) and core area ( $F_{2,44} = 1.32$ ,  $P = 0.26$ ) overlap did not differ between breeding and young-rearing seasons (Table 1). Core area overlap was negligible.

We documented 70 instances of overlap in space use between 19 bobcats and 27 gray foxes. We excluded winter home range and core area overlap indices from comparisons because of low numbers of individuals ( $n = 4$ ) displaying overlap, again because relatively

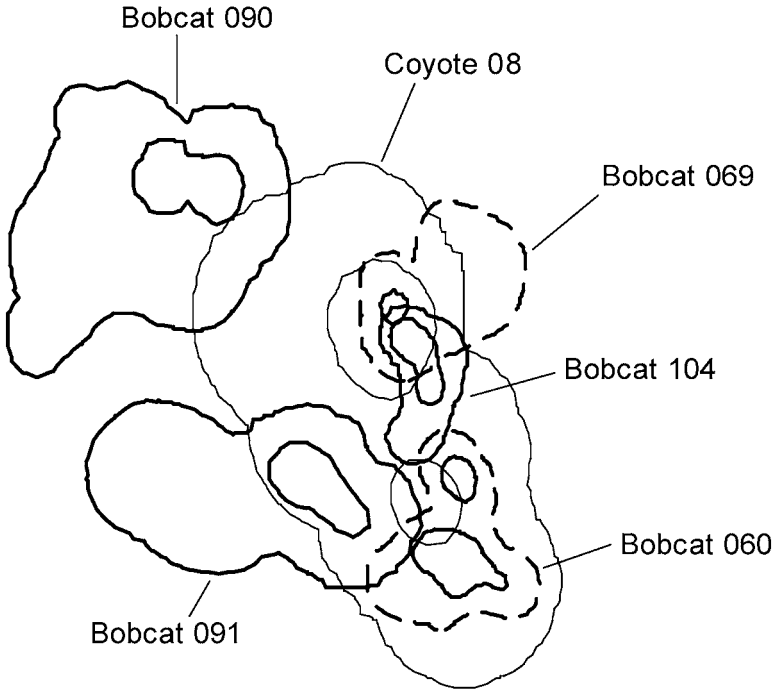


FIG. 1.—Home range (95%) and core area (50%) isopleths for an adult male coyote (08) and 5 adult bobcats (060, 069, 090, 091, 104) illustrating overlap of multiple bobcat home ranges by individual coyotes and core area overlap between the species during breeding 1997

fewer individuals were monitored during winter. Home range ( $F_{1,64} = 0.11$ ,  $P = 0.743$ ) and core area ( $F_{1,64} = 0.23$ ,  $P = 0.634$ ) overlap were similar during breeding and young-rearing (Table 1). Gray foxes shared portions of home ranges with bobcats, but core area overlap was negligible.

#### DISCUSSION

Our method of assessing spatial relationships depended on numbers of individuals monitored within each species and the locations of their respective home ranges on TWMA. Although we trapped the entire study area intensively each year, we certainly did not capture all individuals of each species. However, we consistently monitored all three species in the same portions of TWMA during each year of the study. Hence, we offer that our study was sufficient in methodology and scope to detail interspecific overlap in space use among the three species.

Previous studies of sympatry between bobcats and coyotes in western populations reported similarities in diet, habitat and activity patterns (Litvaitis, 1981; Witmer and DeCalesta, 1986), suggesting potential competitive exclusion. However, Major and Sherburne (1987) found no evidence for interference competition and no instances of avoidance or displacement in spacing patterns. They reported that bobcats and coyotes used similar habitats, occupied overlapping home ranges simultaneously and shared similar diets. Likewise, our findings suggest that bobcats and coyotes do not exclude each other spatially on TWMA. Bobcats and coyotes coexisted within shared areas, and earlier studies found that

TABLE 1.—Mean home range and core area overlap indices (%) with associated standard errors (SE) for adult bobcats, coyotes and gray foxes on the Tallahala Wildlife Management Area, the Timber Company and surrounding private lands, Mississippi, 1993–97

Species combination	Season <sup>1</sup>	n <sup>2</sup>	Home range		Core area	
			% overlap	SE	% overlap	SE
Bobcat/coyote						
	Breeding	74	58	9	5	1
	Young-rearing	48	32	3	5	1
Bobcat/gray fox						
	Breeding	49	25	3	3	1
	Young-rearing	17	23	4	2	1
	Winter	4	26	11	8	6
Coyote/gray fox						
	Breeding	37	23	3	2	1
	Young-rearing	12	30	4	1	>0.5
	Winter	5	40	9	12	8

<sup>1</sup> Breeding = 1 February–31 May, young-rearing = 1 June–30 September, winter = 1 October–31 January

<sup>2</sup> Number of instances of home range overlap

the two species selected similar prey items during some seasons. Specifically, although coyote diets contained a greater diversity of prey items, diets of both species were dominated by deer and lagomorphs outside of spring and brief periods during fall, coinciding with availability of fruits (Chamberlain and Leopold, 1999). Likewise, bobcats and coyotes on TWMA exhibited similar activity patterns (Chamberlain, 1999) while partitioning habitats at the finest spatial scales (Chamberlain and Leopold, 2000; Chamberlain *et al.*, 2000, 2003).

Coyotes apparently do not limit the distribution of gray foxes to the extent observed for red foxes. Similarly, the smaller kit fox (*Vulpes macrotis*) does not avoid coyote-occupied areas and frequently overlaps home ranges with coyotes (White *et al.*, 1994). Gray foxes established home ranges and maintained core areas within the larger home ranges of coyotes and bobcats on TWMA. However, the negligible overlap in core areas suggests that spatial exclusion may exist at that scale, in that gray foxes may avoid areas of concentrated coyote activity. Gray foxes likely maintained core areas in preferred habitats with low coyote use, and habitat partitioning was evident at the core area level among the three species (Chamberlain *et al.*, 2000, 2003; Chamberlain and Leopold, 2000). In contrast, abundance and distribution of coyotes affect abundance and distribution of red foxes through spatial exclusion and interference competition (Johnson and Sargeant, 1977; Sargeant, 1982; Dekker, 1983; Voigt and Earle, 1983; Sargeant *et al.*, 1987). Major and Sherburne (1987) reported that red fox home ranges frequently abutted, but did not overlap coyote home ranges. Theberge and Wedeles (1989) suggested that the ability of these two species to coexist may be a function of habitat partitioning and presence of anthropogenic habitats facilitates red fox persistence in some rural landscapes (Gosselink *et al.*, 2003). Red foxes were present on TWMA prior to 1993 at very low density, but were not detected thereafter (Lovell, 1996) and coyote abundance was likely increasing during the early 1990s on TWMA (Lovell, 1996; Chamberlain, 1999).

Interference competition occurred between coyotes and gray foxes on TWMA, but was considered minimal (two confirmed mortalities of 37 foxes; Chamberlain, 1999) and was

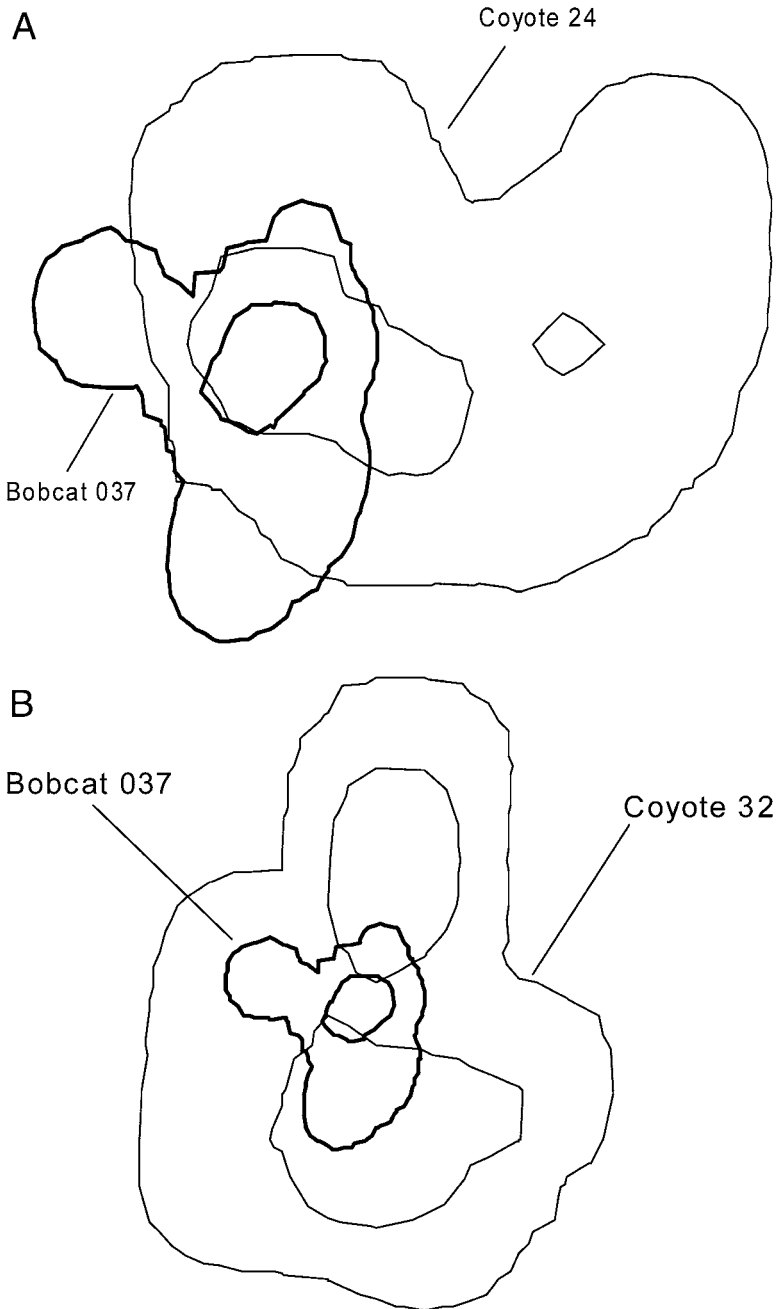


FIG. 2.—(A) Home range (95%) and core area (50%) isopleths for an adult female bobcat (037) and coyote illustrating complete overlap of core areas during breeding 1996; (B). Home range (95%) and core area (50%) isopleths for the same adult female bobcat and an adult female coyote (32) indicating that in concert, coyote core areas frequently overlapped large proportions of bobcat home ranges during 1996

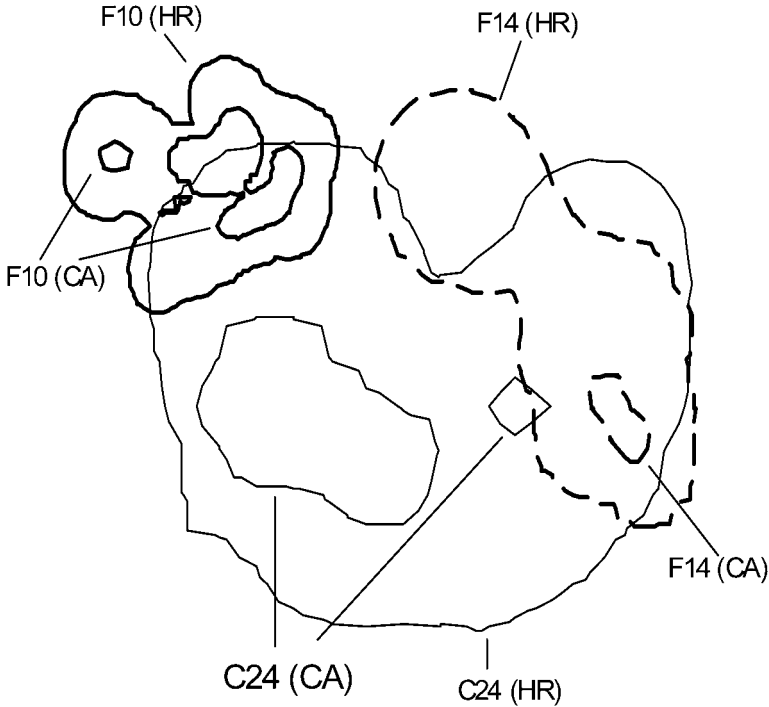


FIG. 3.—Adaptive kernel 95% home range (HR) and 50% core area (CA) isopleths of two male gray foxes (F10 and F14) and one female coyote (C24) illustrating extensive home range overlap, but maintenance of exclusive core areas during breeding 1996

not documented for bobcats and gray foxes. Coyotes and foxes use similar foods (Dibello *et al.*, 1990; Cypher, 1993), resulting in potential for resource competition, whereas bobcat and gray fox diets tend to be less similar (McCord and Cardoza, 1982; Samuel and Nelson, 1982). White *et al.* (1994) indicated that kit foxes exploited certain prey species better than coyotes did and frequently maintained numerous dens likely to facilitate avoidance of coyotes. Conversely, red foxes exhibit greater dietary overlap with coyotes than other fox species (Cypher, 1993) and generally have few dens within their home ranges (Voigt, 1987). Gray foxes on TWMA usually only maintained one den during each season and den locations rarely (documented on two occasions) changed among seasons. Two instances of den abandonment appeared to result from coyote disturbance. However, the arboreal behavior of gray foxes likely provides effective escape from coyotes (Wooding, 1984).

Coyotes have expanded their range throughout the southeastern United States, resulting in recent sympatric relationships with a variety of mesocarnivores. Throughout other portions of their range coyotes displace red foxes spatially (Harrison *et al.*, 1989), but coexist with bobcats through habitat and prey partitioning. Our findings indicate that although interference competition does exist between coyotes and gray foxes, such competition does not lead to spatial exclusion at the home range level. Similarly, bobcats and gray foxes existed within shared areas routinely, with segregation of space use only occurring within core use areas. These findings, in conjunction with earlier findings from our study, suggest that gray foxes in particular maintain sympatry with bobcats, and more recently coyotes,

through partitioning of prey and habitats at certain scales of selection, rather than spatial avoidance observed between coyotes and red foxes.

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