Activity and Distribution of Gray Foxes (*Urocyon cinereoargenteus*) in Southern California

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ACTIVITY AND DISTRIBUTION OF GRAY FOXES (*UROCYON CINEREOARGENTEUS*) IN SOUTHERN CALIFORNIA

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ABSTRACT—To identify activity patterns and distribution of gray foxes (*Urocyon cinereoargenteus*) in chaparral and sage-scrub habitat in southern California, we used radiotelemetry to monitor 18 foxes during May 1997–April 1999. For comparison, we used simultaneously collected telemetry data on sympatric coyotes (*Canis latrans*) and bobcats (*Lynx rufus*). Gray foxes mainly were crepuscular and nocturnal with a daily activity rate of 60% in the summer dry season and 56% in the winter wet season. Gray foxes preferred northern mixed chaparral, used coastal sage scrub and coast live oak woodland more than chamise chaparral, had non-preference for valley oak woodland and non-native grassland, and did not use developed suburban areas. These data, in comparison with behavioral data for other carnivores, support the contention that sympatric carnivores, mainly coyotes but possibly bobcats, may strongly influence the population of gray foxes in southern California, as gray foxes appear to avoid times and habitats where risk of predation is high.

RESUMEN—Para identificar los patrones de actividad y la distribución de zorros grises (*Urocyon cinereoargenteus*) en el chaparral y matorral costero de salvia en el sur de California, utilizamos radiotelemetría para monitorear 18 zorros durante mayo 1997–abril 1999. Para la comparación, utilizamos datos de telemetría colectados simultáneamente de coyotes (*Canis latrans*) y gatos monteses (*Lynx rufus*) simpátricos. Los zorros grises fueron principalmente crepusculares y nocturnos con una tasa de actividad diaria del 60% durante el verano que correspondió a la temporada seca, y del 56 % durante el invierno o temporada de lluvia. Los zorros prefirieron el chaparral norteño mixto, usaron el matorral costero de salvia y el bosque costero de encino más que el chaparral de chamise, no mostraron selección por el bosque de roble de los valles ni por el pastizal no nativo, y no utilizaron áreas suburbanas desarrolladas. Estos datos, en comparación con datos sobre el comportamiento de otros carnívoros, apoyan el argumento de que los carnívoros simpátricos, principalmente los coyotes pero posiblemente los gatos monteses, pueden influenciar fuertemente a la población de zorros grises del sur de California, debido a que los zorros parecen evadir las horas y el hábitat en donde el riesgo de depredación es alto.

Risk of predation is a strong driver of mammalian behavior and can affect distribution and activity patterns of potential prey (Hebblewhite and Merrill, 2009; Sansom et al., 2009; Valeix et al., 2009; Anderson et al., 2010). Intraguild predation (Polis et al., 1989; Polis and Holt, 1992; Palomares and Caro, 1999) helps structure communities of predators and influences behaviors of both competing predators and their prey (Heithaus, 2001; Finke and Denno, 2002; Rosenheim, 2004). For sympatric canids, the threat of such predation appears to have important behavioral effects in a variety of communities (e.g., Gosselink et al., 2003; Switalski, 2003).

Activity patterns of gray foxes (*Urocyon cinereoargenteus*) may vary with temperature, season, activity of prey, or harassment from humans or other predators (Cypher, 2003). Similarly, local use of habitat by gray foxes often relates to foraging opportunities and to protection from intraguild predation (Cypher, 2003; Fuller and Cypher, 2004). During an investigation assessing competition among mesocarnivores in the Santa Monica Mountains of southern California, Fedriani et al. (2000) determined that gray foxes visited baited camera stations most often during the night-crepuscular period, similar to coyotes (*Canis latrans*), but more often than bobcats (*Lynx rufus*). This activity pattern was attributed to diet, with the proportion of diurnal squirrels being higher for bobcats, and mean overlap in diet being lowest for coyotes and gray foxes versus other combinations of species (Fedriani et al., 2000). In addition, limited data from cameras and live-trapping indicated a negative relationship between

abundances of coyotes and gray foxes across habitats, suggesting that gray foxes avoided habitats where there was a high risk of predation by coyotes (Fedriani et al., 2000). This proposition is supported in one portion of the Santa Monica Mountains where 11 of 12 mortalities of radiomonitored gray foxes were due to predation by sympatric coyotes or bobcats (Farias et al., 2005). To more robustly document behavior of gray foxes in the presence of intraguild predators, we used radiotelemetry to investigate patterning of diel activity and use of habitats by gray foxes, coyotes, and bobcats. To reduce chances of attack, we hypothesized that gray foxes would exhibit activity patterns different from coyotes and bobcats, and that they would use habitats in different proportions compared to their sympatric predators.

MATERIALS AND METHODS—We studied a population of gray foxes living within the Simi Hills portion of Santa Monica Mountains National Recreation Area in Ventura and Los Angeles counties, which is adjacent to the metropolitan region of Los Angeles, California. The Simi Hills have large core areas of protected parkland surrounded by undeveloped private and public lands (Riley et al., 2003), and suburban developments that result from continuous fragmentation at the borders of the parkland (National Park Service, in litt.). More than 50,000 visitors/year frequent the park for activities such as hiking, mountain biking, and horse riding (National Park Service, in litt.). Elevation in the Simi Hills is 274–732 m (National Park Service, in litt.). Mild, wet winters (November–April) and hot, dry summers (May–October) characterize the Mediterranean climate of the Santa Monica Mountains National Recreation Area with annual minimum and maximum mean temperatures of 10.5 and 21.3°C, and annual mean precipitation of 376 mm occurring primarily as rains in winter. However, the meteorological phenomena El Niño and La Niña affected southern California during our study, producing dry seasons in 1997 and 1998, and 231% of average rainfall during the wet season in 1998 (National Oceanic and Atmospheric Administration, 1999).

Historically, grazing, fire, and urbanization have influenced distribution and composition of plant communities in the Simi Hills (National Park Service, in litt.). We characterized seven habitats in our study area: 1) northern mixed chaparral (34% of our study area) is a dense association of hard-leaved shrubs dominated by *Ceanothus*; 2) chamise chaparral (6%) is less dense than northern mixed chaparral and is dominated by *Adenostoma fasciculata*; 3) coastal sage scrub (40%) occurs as soft-leaved, grayish-green, aromatic shrubs (*Artemisa*, *Salvia*); 4) coast live oak (*Quercus agrifolia*) woodland (5%) has a dense overstory and can have a dense understory composed of woody species; 5) valley oak (*Quercus lobata*) woodland (<1%) produces less canopy cover than coast live oak and has a grass understory; 6) grassland (3%) is dominated by non-native annual grasses and forbs such as wild oat (*Avena*) and black mustard (*Brassica nigra*), and includes vestiges of native perennial bunchgrasses (*Stipa*, *Elymus*, *Melica*) and native annual grasses (*Festuca*); 7) development (11%) includes residential areas and human-influenced habitats on boundaries of the park.

Coyotes, bobcats, raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*) are other common species of carnivores in the study area, while spotted skunks (*Spilogale putorius*), long-tailed weasels (*Mustela frenata*), American badgers (*Taxidea taxus*), and cougars (*Puma concolor*) are rare locally (National Park Service, in litt.). Lagomorphs comprised the largest component of diets of gray foxes, coyotes, and bobcats in the Santa Monica Mountains (Fedriani et al., 2000), but various species of rodents also are important for each carnivore. In our study area, diets of coyotes and gray foxes were similar (seasonal overlap in foods was 0.52), with main differences being that coyotes consumed more fruits and nuts, and gray foxes ate more insects (Fedriani et al., 2000).

We trapped and radiocollared gray foxes during May–November 1997 and April–October 1998. To avoid injuring foxes, we used 1½ coil-spring, soft-catch, leg-hold traps with padded jaws as used by Riley et al. (2003). We immobilized gray foxes by taping their muzzle and legs, and covering their eyes with a blindfold to reduce stress. We intramuscularly injected aggressive foxes with 5–10 mg/kg of ketamine hydrochloride following methods of Seal and Kreeger (1987). We attached numbered eartags and a 60-g radiocollar with a 20-cm whip antenna and mortality sensor (Lotek Wireless, Inc., Newmarket, Ontario, Canada, and Advanced Telemetry Systems, Isanti, Minnesota) to each fox. Subadults wore loosely fitted radiocollars to allow for growth. We recorded sex of foxes, estimated their age (subadults were <1 year old and adults were >1 year old) by irruption and wear of teeth and by size of body (mass, plus measurements of head, body, tail, hind foot, and ear were recorded as described by Fuller and Cypher, 2004), and then we released them at site of capture site.

We monitored and radiotracked gray foxes during May 1997–April 1999. Activity was treated as a dichotomous variable, i.e., active or inactive. To assess activity, we monitored radiosignals of individuals during telemetry sessions that were 4–10 h in duration. During each session, the radiosignal of each animal was checked for activity once each hour. An animal was considered active if (during a 20-s interval) we could hear regular variation in intensity and stability of the radiosignal, and inactive if the radiosignal had no variation as described by Riley et al. (2003). Every month we attempted to collect 2–4 independent locations/gray fox for each 1-h interval (48–96 locations/gray fox/month).

We used portable receivers (Model LA-12; AVM Instrument Company, Ltd., Colfax, California) and 4-element, hand-held, directional, Yagi antennas to locate gray foxes. We attempted to locate radiocollared foxes at least once during the day and once at night every week by traveling trails in a vehicle and hiking along ridges to get the strongest radiosignal. Locations were triangulated from 2–6 azimuths taken within 30 min by one observer, or two azimuths taken simultaneously (within 1 min) by two observers. Triangulation angles were 35–145°. Mean distance between radiocollared animals and observers during triangulation was 359±269 m. Point locations were taken >8-h apart during daytime, and >3-h apart during nighttime (when foxes were active). We estimated UTM coordinates of each location and its 95% error ellipse using the software package LOCATE II (Nams, 1990). The estimated overall standard deviation (overall error angle) for our dataset was 2.5°; average error polygons were ca. 0.1 ha.

We divided the diel period into 12 sampling intervals of 2 h each and compared activity between dry (May–October) and wet (November–April) seasons. We analyzed activity patterns by

TABLE 1—Percentages ($\pm SE$) of habitats available and used (range in parentheses) by three sympatric carnivores (gray fox, *Urocyon cinereoargenteus*; coyote, *Canis latrans*; and bobcat, *Lynx rufus*) in the Santa Monica Mountains, Ventura and Los Angeles counties, California, during May 1996–July 1999.

Habitat	Habitats available	Habitats used by each species		
		Gray fox	Coyote	Bobcat
Coastal sage scrub	40	29 ± 13 (0–48)	58 ± 38 (0–100)	47 ± 32 (0–100)
Northern mixed chaparral	34	51 ± 16 (30–100)	7 ± 14 (0–50)	4 ± 8 (0–25)
Development	11	0	12 ± 27 (0–100)	9 ± 21 (0–70)
Chamise chaparral	6	9 ± 9 (0–27)	2 ± 5 (0–20)	1 ± 2 (0–7)
Coast live oak	5	10 ± 11 (0–38)	14 ± 33 (0–100)	28 ± 7 (0–100)
Grassland	3	<1 ± <1 (0–6)	9 ± 20 (0–67)	8 ± 12 (0–36)
Valley oak	<1	<1 ± <1 (0–9)	0	4 ± 7 (0–25)

fitting a multiple-logistic-regression model as described by Hosmer and Lemeshow (1989) and Sokal and Rohlf (1994) using SPSS 9.0 statistical software. Activity status (active, inactive) was the outcome variable, and season (dry, wet) and time of day (diurnal, 0800–1559 h; crepuscular, 1600–1959 h and 0400–0759 h; nocturnal, 2000–0359 h) were independent covariates in the logistic-regression model.

Using the Geographic Information System (GIS) database of the Santa Monica Mountains National Recreation Area, we estimated the 100% minimum convex polygon that included the 1,244 locations of gray foxes (capture, telemetry, and mortality) and delineated a 500-m perimeter around this 100% minimum convex polygon using methods described by Hayne (1949) and Dixon and Chapman (1980). We defined this polygon (100% minimum convex polygon + 500-m perimeter) to assess use of habitats and we refer to it as the available-habitat polygon. Using the GIS database and software (ArcView 3.1; Environmental Systems Research Institute, 1998), we generated 1,000 random points (without replacement) within the available-habitat polygon to estimate proportions of habitats that were available. We assessed habitat for every telemetric location and we calculated percentages for availability and use of habitats (Table 1).

We employed compositional analysis (Aebischer and Robertson, 1992; Aebischer et al., 1993) to test the null hypothesis of random habitat used by gray foxes, or to detect if selection for habitats existed. We used log-ratios of available habitats (1,000 random points, y_o) and compositions of habitats that were used (telemetric locations, y). We excluded development areas from this analysis because no gray fox was located in developed areas. We used telemetric locations from 15 gray foxes from which we obtained >31 (range, 32–185) locations; from the other 3 foxes, we obtained <7 locations and excluded them from analysis of composition. We replaced zero proportions (0% use) with 0.001%, which was an order of magnitude less than existing non-zero values in either available or used compositions following the method of Aebischer et al. (1993). Zero proportions were only recorded for valley oak. We calculated the difference $d = y - y_o$ and solved the significance of the matrix of d-values with Wilk's lambda (λ) transformed as -Nlnλ (were N is the number of individuals), which was compared with χ^2. We ranked the preferred habitats and tested statistical significance with the t-distribution.

Simultaneous telemetric studies of coyotes and bobcats in the Santa Monica Mountains National Recreation Area (Riley et al.,

2003) provided the subset of activity data and locations that we used for comparison with our data for gray foxes. Coyotes and bobcats were captured, handled, and monitored similar to gray foxes (Riley et al., 2003). For comparison with gray foxes, we used activity data from the entire population of radiocollared bobcats and coyotes that were monitored during May 1996–April 1999. We obtained locations for coyotes and bobcats that were within the available-habitat polygon during May 1996–April 1999 and we calculated percentages of use for each habitat.

RESULTS—We radiocollared 24 gray foxes (12 adult males, 5 adult females, 3 subadult males, and 4 subadult females), we obtained locations on 18 of them, and we monitored 14 of them for patterns of activity. Our sample included 5,768 transmitter-days for all gray foxes (mean$\pm SD$ = 242$\pm$221, range = 14–688). For analysis of use of habitat, we collected a total of 1,244 locations, including 41 capture and recapture locations, 1,191 telemetric locations, and 12 locations where dead radiocollared gray foxes were recovered. We collected 3,678 checks for activity: 1,641 checks on 8 gray foxes during the dry season and 2,037 checks on 13 gray foxes for the wet season. Activities of 69 coyotes and 45 bobcats determined by radiotelemetry were used for comparisons. We also used 195 telemetric locations of 11 bobcats and 116 of 18 coyotes within our study area for comparisons in use of habitats.

The fitted multiple-logistic-regression model that best described patterns of activity contained both time of day and season, and their interaction was significant ($G =$ 899, $df = 5$, $P < 0.001$; H-$L = 10.6$, $df = 8$, $P = 0.22$). No difference in activity patterns between males and females or between adults and subadults was detected. Gray foxes were, in general, more active during nocturnal and crepuscular times than during the diurnal time interval (odds ratio = 22 and 4, respectively; Fig. 1). Overall, daily levels of activity were 60% in the summer dry season and 56% in the winter wet season. Daily levels of activity were 64 and 60% in summer for bobcats and coyotes, respectively, and 59 and 48% in winter.

Telemetric locations of gray foxes, coyotes, and bobcats differed from availability of habitats in several ways. Gray
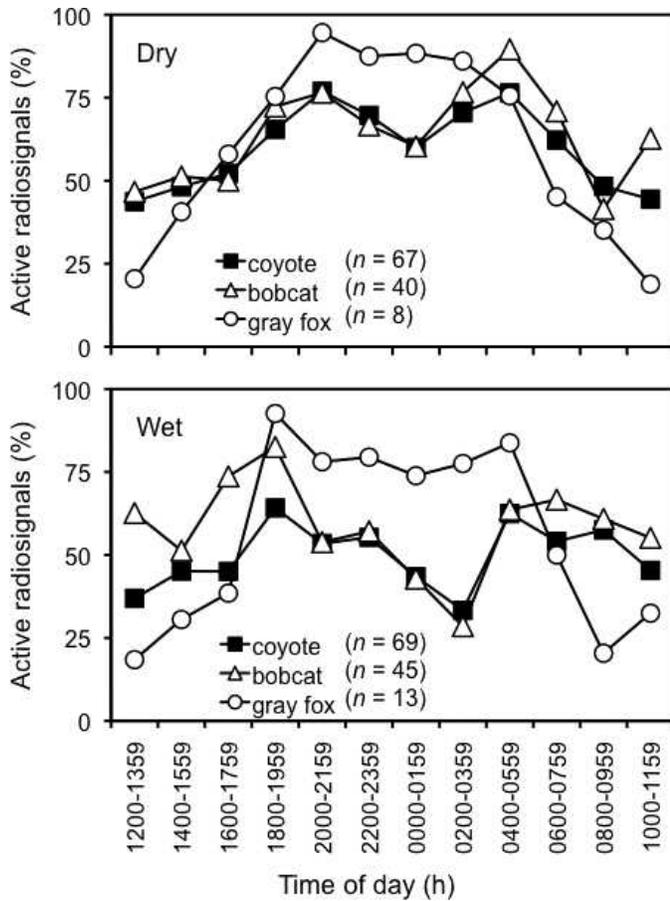
FIG. 1—Activity patterns of radiocollared gray foxes (*Urocyon cinereoargenteus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*) in the Santa Monica Mountains, Ventura and Los Angeles counties, California, in the wet and dry season during May 1997–April 1999. Data for coyotes and bobcats are from Riley et al. (2003).

foxes used all habitats except development, coyotes were located in all habitats except valley oak, and bobcats were in all habitats (Table 1). Gray foxes preferred northern mixed chaparral over other habitats, followed by coastal sage scrub, coast live oak, then chamise chaparral; valley oak and grassland were underused (Table 2; Wilk's $\lambda =$ 0.208, $\chi^2_{[5, 11]} = 23.54$, $P < 0.001$). Coyotes used coastal sage scrub significantly more than the remaining habitats, and significantly less for northern mixed chaparral.

Bobcats used coast live oak significantly more than coastal sage scrub, valley oak, and grassland, and they selected against development, chamise chaparral, and northern mixed chaparral.

DISCUSSION—In previous studies, gray foxes generally were more active at night (77–87% of telemetric checks for activity) than during the day (25–54%; Yearsley and Samuel, 1980; Haroldson and Fritzell, 1984). Activity patterns of gray foxes in our study area were similar; they may reduce activity at daytime and increase activity at nighttime during the dry season (when compared to the wet season) as strategy to avoid heat stress, or to follow activity patterns of prey. However, gray foxes may also temporally avoid larger predators; gray foxes had significantly greater probabilities of being active during nighttime and inactive during daytime than sympatric radiomonitored coyotes and bobcats, probably to reduce predatory pressures (Farias, 2000). The closely related island fox (*Urocyon littoralis*) is relatively active during the day but inhabits islands where no other large mammalian carnivore resides (Moore and Collins, 1995).

Gray foxes may have preferred northern mixed chaparral because their common small-mammal prey were species typical of brushy habitats (e.g., dusky-footed woodrat *Neotoma lepida*; Fedriani et al., 2000). However, it also was the least used habitat by sympatric coyotes and bobcats that were radiomonitored (Table 2). Gray foxes have been reported to live in developed landscapes and open habitats (Fuller, 1978; Fritzell and Haroldson, 1982; Fritzell, 1987; Harrison, 1997), but in our study, gray foxes did not use development and selected against open habitats. Coyotes and bobcats may be limiting occurrence of gray foxes in open habitats (i.e., grassland and valley oak) and developed areas in southern California (Soulé et al., 1988; Crooks and Soulé, 1999; Fedriani et al., 2000). Thus, there may not be enough vegetative cover for escape or protection, leaving gray foxes more vulnerable to agonistic encounters. In central Mississippi, Lovell (1996) also reported spatial segregation among coyotes, bobcats, and gray foxes. Coyotes and bobcats avoided mature stands of pines that supported a lower density of prey, whereas gray foxes preferred mature stands of pines, probably because numbers of predators were lower, and

TABLE 2—Compositional analysis of relative use of habitats by mesocarnivores (gray fox *Urocyon cinereoargenteus*, coyote *Canis latrans*, and bobcat *Lynx rufus*) in the Santa Monica Mountains, Ventura and Los Angeles counties, California, during May 1996–July 1999.

Species	n	Order of compositional preference[a]
Gray fox	18	northern mixed chaparral >> coastal sage scrub > coast live oak >> chamise chaparral >> valley oak > grassland >> development
Coyote	18	coastal sage scrub >> valley oak > grassland > coast live oak >> development > chamise chaparral > northern mixed chaparral
Bobcat	11	coast live oak >> coastal sage scrub > valley oak > grassland >> development > chamise chaparral > northern mixed chaparral

[a] >>Indicates significant difference between habitats.

because trees were available for escape from attacks. Gray foxes seemed absent in regions with large populations of coyotes, but apparently reached their greatest abundance in regions where coyotes were scarce (Fedriani et al., 2000; Riley et al., 2003). Interestingly, most predator-killed gray foxes were killed outside or on the periphery of their ranges (Farias et al., 2005). This phenomenon also has been documented for swift foxes (*Vulpes velox*) by Sovada et al. (1998) and Kitchen et al. (1999) whose observations were that predation on swift foxes usually occurred away from dens and core activity areas. These authors suggested that swift foxes are more vulnerable to predation by coyotes in peripheral areas of their home range.

It is common for sympatric canids to reduce exploitative and interference competition by exhibiting both spatial and temporal segregation (Johnson et al., 1996). White et al. (1995) discovered that kit foxes (*Vulpes macrotis*) and coyotes exhibited habitat partitioning, but White et al. (1994) did not detect evidence of temporal segregation between these canids. Kitchen et al. (1999) reported no evidence of spatial-temporal avoidance of coyotes in movement patterns of swift foxes. Kit and swift foxes use multiple dens as a common escape route to deter attacks by coyotes (White et al., 1994, 1995; Koopman et al., 1998; Sovada et al., 1998; Kitchen et al., 1999), while gray foxes use trees to escape from predators (Wooding, 1984; Cypher, 1993). However, trees were scarce in our study area and gray foxes may find more protection under dense vegetation. Our results suggest that gray foxes in southern California may be more vulnerable to interference competition than kit or swift foxes.

Fedriani et al. (2000) suggested that gray foxes in southern California may be avoiding places and times with high risks of predation to coexist with coyotes and bobcats (Chamberlain and Leopold, 2005). Our results support this notion that spatial and temporal use of habitats by gray foxes in southern California may be regulated mainly by interference competition with other predators. Radiocollared gray foxes probably were mainly nocturnal and crepuscular to reduce predatory pressures during the day, and probably preferred northern mixed chaparral because dense vegetation provided cover for escape and this habitat had fewer predators.

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