

Jose M. Fedriani · Todd K. Fuller
Raymond M. Sauvajot · Eric C. York

Competition and intraguild predation among three sympatric carnivores

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Abstract We examined the relative roles of dominance in agonistic interactions and energetic constraints related to body size in determining local abundances of coyotes (*Canis latrans*, 8–20 kg), gray foxes (*Urocyon cinereoargenteus*, 3–5 kg) and bobcats (*Felis rufus*, 5–15 kg) at three study sites (hereafter referred to as NP, CP, and SP) in the Santa Monica Mountains of California. We hypothesized that the largest and behaviorally dominant species, the coyote, would exploit a wider range of resources (i.e., a higher number of habitat and/or food types) and, consequently, would occur in higher density than the other two carnivores. We evaluated our hypotheses by quantifying their diets, food overlap, habitat-specific abundances, as well as their overall relative abundance at the three study sites. We identified behavioral dominance of coyotes over foxes and bobcats in Santa Monica because 7 of 12 recorded gray fox deaths and 2 of 5 recorded bobcat deaths were due to coyote predation, and no coyotes died as a result of their interactions with bobcats or foxes. Coyotes and bobcats were present in a variety of habitats types (8 out of 9), including both open and brushy habitats, whereas gray foxes were chiefly restricted to brushy habitats. There was a negative relationship between the abundances of coyotes and gray foxes ($P=0.020$) across habitats, suggesting that foxes avoided habitats of high coyote predation risk. Coyote abundance was low in NP, high in CP, and intermediate in SP. Bobcat abundance changed little across study sites, and gray foxes were very abundant in NP, absent in CP, and scarce in SP; this suggests a negative relationship between coyote and fox abundances across

study sites, as well. Bobcats were solely carnivorous, relying on small mammals (lagomorphs and rodents) throughout the year and at all three sites. Coyotes and gray foxes also relied on small mammals year-round at all sites, though they also ate significant amounts of fruit. Though there were strong overall interspecific differences in food habits of carnivores ($P<0.0001$), average seasonal food overlaps were high due to the importance of small mammals in all carnivore diets [bobcat-gray fox: 0.79 ± 0.09 (SD), $n=4$; bobcat-coyote: 0.69 ± 0.16 , $n=6$; coyote-gray fox: 0.52 ± 0.05 , $n=4$]. As hypothesized, coyotes used more food types and more habitat types than did bobcats and gray foxes and, overall, coyotes were the most abundant of the three species and ranged more widely than did gray foxes. We propose that coyotes limit the number and distribution of gray foxes in Santa Monica Mountains, and that those two carnivores exemplified a case in which the relationship between their body size and local abundance is governed by competitive dominance of the largest species rather than by energetic equivalences. However, in the case of the intermediate-sized bobcat no such a pattern emerged, likely due to rarity or inconsistency of agonistic interactions and/or behavioral avoidance of encounters by subordinate species.

Key words *Canis latrans* · *Felis rufus* · Food overlap · Relative abundance · *Urocyon cinereoargenteus*

Introduction

A traditional view of food-web dynamics is that competition operates within a trophic level while predation operates between levels and, consequently, the relative roles of predation and competition have been assessed separately. In many ecological systems, however, one or more species may act as both predator and competitor with other species at the same or similar trophic level. This phenomenon, termed intraguild predation and considered an extreme case of interference competition

J.M. Fedriani · T.K. Fuller
Department of Natural Resources Conservation,
University of Massachusetts, Amherst, MA 01003-4210, USA

R.M. Sauvajot · E.C. York
U.S. National Park Service, 401 West Hillcrest Drive,
Thousand Oaks, CA 91360, USA

J.M. Fedriani
Present address: Estación Biológica de Doñana (CSIC),
Avda. María Luisa s/n, 41013 Sevilla, Spain,
e-mail: fedriani@ebd.csic.es

(Polis et al. 1989), has been studied most often through manipulative experiments in invertebrates (e.g., Johansson 1993; Fincke 1994) and some small vertebrates (e.g., Hughes et al. 1994; Stapp 1997). Large vertebrates, such as mammalian carnivores, are not appropriate for such manipulative approaches due to their high mobility, secretive habits, and low density. Consequently, few attempts to simultaneously evaluate the importance of interspecific competition and intraguild predation among carnivores have been made (Creel and Creel 1996; Sunde et al. 1999). Competition may result in reduced densities of subordinate species (Mac Nally 1983; Korpimäki 1987; Petren and Case 1996) and, ultimately, in their local extinction (Pimm 1991). Although over large geographical areas population densities of animals typically decrease with increasing body size (Griffiths 1992; Cotgreave 1993), this does not often hold within local communities (Nee et al. 1991; Cotgreave 1993; Jones and Barmuta 1998). For instance, greater mobility allowing a broader range of resources, dominance in interspecific aggressive interactions, and better avoidance of predators, are some of the ecological advantages that may enable more individuals of a larger species than a smaller species to be supported within the same local area (Brown and Maurer 1986).

Coyotes (*Canis latrans*, 8–20 kg), bobcats (*Felis rufus*, 5–15 kg), and gray foxes (*Urocyon cinereoargenteus*, 3–5 kg) are sympatric over a large portion of their ranges in North America, where they have been extensively studied (Whitaker and Hamilton 1998). Bobcats are basically carnivorous (Anderson 1987), whereas coyotes and gray foxes are more omnivorous (Trapp and Hallberg 1975; Litvaitis and Harrison 1989; Smith and Danner 1990). Nevertheless, all three species of carnivores prey chiefly on mammals (Litvaitis and Harrison 1989; Smith and Danner 1990; Harrison 1997). In general, the three carnivores behave as generalists in their use of habitats (Whitaker and Hamilton 1998), using both open and brushy habitats (e.g., Litvaitis and Harrison 1989; Harrison 1997; Quinn 1997). Coyotes, however, are more adapted to utilize urbanized areas (Gill and Bonnett 1973; Quinn 1997) and gray foxes may avoid habitats of high predation risk (Nowak and Paradiso 1983; Soule et al. 1988). Finally, the three carnivores are mostly nocturnal and crepuscular (Witmer and DeCalesta 1986; Harrison 1997; Whitaker and Hamilton 1998). In the Mediterranean ecosystem of the Santa Monica Mountains of California these three carnivores are abundant (National Park Service 1994). No published data on their ecology in this system are available, although unpublished information suggests considerable interspecific overlap in resource use (e.g., Kamradt 1995; Sauvajot et al. 1997). Coyotes in Santa Monica kill gray foxes and bobcats (Sauvajot et al. 1997); thus, we expected that a combination of competition for resources and intraguild predation among those carnivores negatively affects populations of subordinate species, and also that the strength of those effects varies with local changes in predator densities (Creel and Creel 1996; Raffaelli and Hall 1996).

In this study, we evaluated the likelihood that current competition among those carnivores is occurring in the Santa Monica Mountains by following the three steps for the assessment of the importance of interspecific competition for guild structure (Mac Nally 1983): (1) the measurement of overlap of resource use, (2) the demonstration of interspecific interactions (by interference or exploitation), and (3) the demonstration of “true” or depressive competition. To address the first two steps, we estimated the relative abundance of the three species in different habitats, quantified their food habits and trophic overlap, and documented aggressive interactions among the three species. Depressive competition (step 3) occurs when interaction between species is responsible for the reduction of population density and/or deleterious effects on fecundity, growth, or survival (Mac Nally 1983; Petren and Case 1996), and its demonstration requires manipulative experiments which, for reasons stated above, were logistically unrealistic in our system. To partly overcome this limitation, we estimated the relative abundances and food overlaps of coyotes, bobcats, and gray foxes in three neighboring and ecologically comparable areas (i.e., of similar habitat composition) which differed in the abundance of the top predator (coyote). We predicted a negative relationship between coyote abundance and the abundances of both gray foxes and bobcats in these areas, and hypothesized that the largest species, the coyote, would exploit a wider range of resources (i.e., higher number of habitat and/or food types) and would occur in higher density than the other two carnivores.

Materials and methods

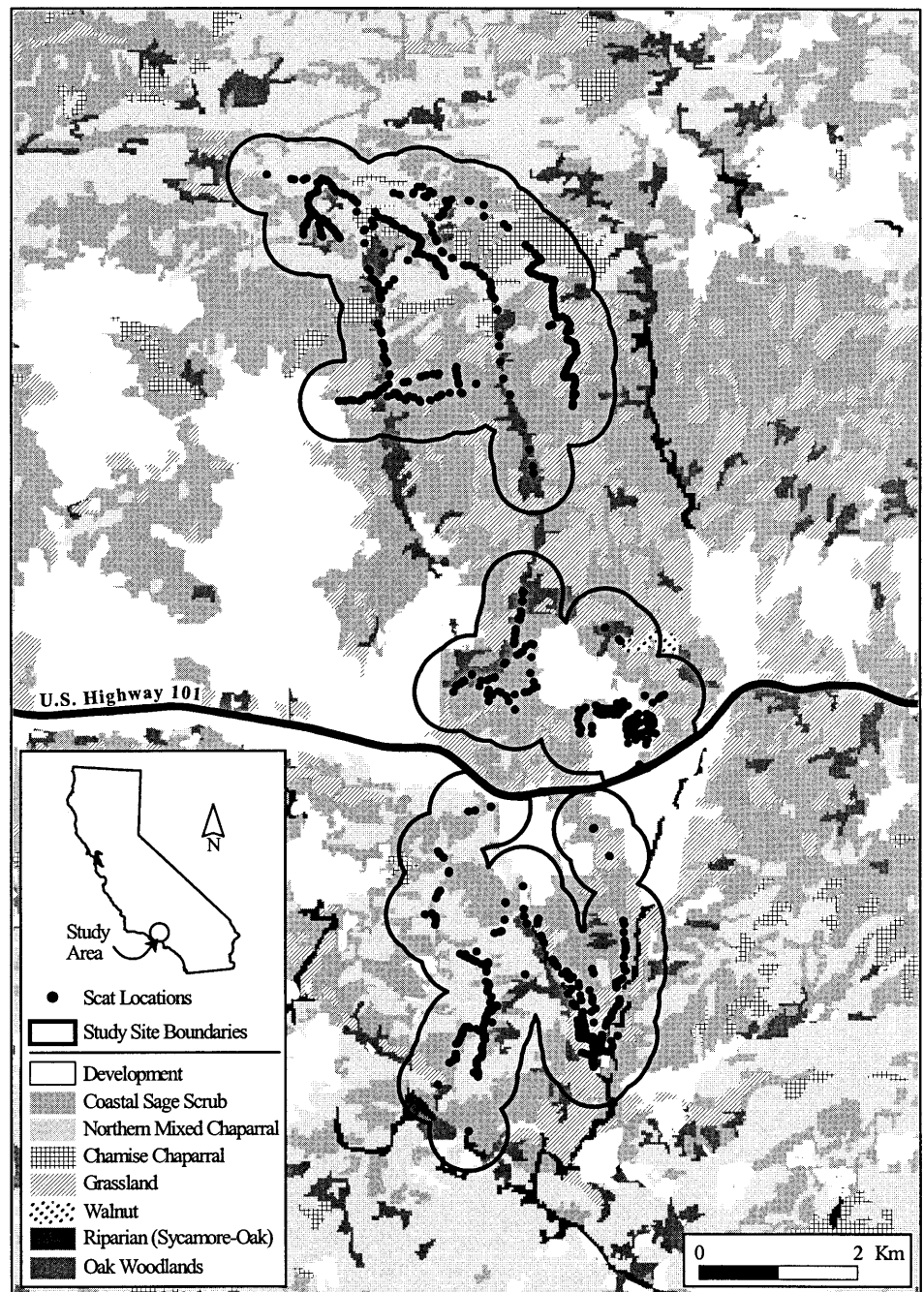
Study area

The study area is located in the Santa Monica Mountains of Los Angeles County, California. The Santa Monica Mountains have an east-west orientation and erosion has carved the range into a series of canyons and ridges which tend to have a north-south orientation. The altitude is generally 300–600 m. The climate is typically Mediterranean with mild rainy winters and hot dry summers; there is a dry season from May to October and a distinct rainy season from November to April (Russell 1926). While over 90% of the land within the Santa Monica Mountains is currently undeveloped, formerly continuous habitat is being rapidly encroached upon and fragmented by urbanization. Two main highways cross the area from east to west: the Pacific Coast Highway follows the coastline but is far from our study site, and the Ventura Freeway (US Highway 101) passes through the middle of our study area.

Many different habitats occur within the Santa Monica Mountains (Holland 1986; Sawyer and Keeler-Wolf 1995). We described the 11 most representative for our study (Fig. 1):

1. Coastal Sage Scrub, a brushy plant community that occupies the western slopes above the beaches; coastal sagebrush (*Artemisia californica*), three species of *Eriogonum* (*E. cinerea*, *E. elongatum*, and *E. fasciculatum*), and several herbs species of the genus *Lotus*, *Lupinus*, and *Mimulus* characterize this association.
2. Northern Mixed Chaparral, with typically 40% of scrub cover is an association of several species of California lilacs (*Ceanothus* spp.), *Arctostaphylos glandulosa* and *Quercus dumosa*.

Fig. 1 Habitat types and location of three study sites (*NP* North Polygon, *CP* Central Polygon, *SP* South Polygon) in the Santa Monica Mountains of Southern California. Scat locations (*solid dots*) were used to define the three polygons; a 500-m perimeter around each scat location was delineated and then all overlapping circles were connected, yielding three non-overlapping polygons. Carnivores on one side of *US Highway 101* did not range to the other. Only one individual (a coyote) was captured in both NP and CP, also suggesting a high degree of independence among these two study sites. Figure legend shows location of our study area within the state of California



3. Chamise Chaparral, with more than 80% relative cover of chamise (*Adenostoma fasciculatum*).
4. Non-native Grassland, with dense to sparse cover of annual grasses, 0.2–0.5 m tall, composed largely of introduced species such as *Avena barbata*, *Bromus mollis*, *B. rigida*, and *B. madri-tensis*, but also with some native grasses such as *Stipa pulchra*.
5. Development, including residential areas where native vegetation is almost absent, and some parks and house yards used by wildlife.
6. Valley Oak, with open woodlands (usually less than 40% tree cover), where *Quercus lobata* usually is the only tree species present, with a grass understory.
7. Coast Live Oak, with a dense overstory dominated by *Quercus agrifolia*, medium developed shrub layer that includes *Malosma laurina*, and *Toxicodendron diversilobum*, and a grass understory.
8. Coastal Sage-Chaparral Transition, with >70% cover of coastal sage scrub and chaparral species.
9. Riparian Areas, located along the banks of permanent streams; commonest species are *Platanus racemosa*, *Populus fremontii*, and *Umbellularia californica*.
10. Rock Outcrops located in some ridges, where vegetation is poorly represented and dominated by herb species.
11. Walnut is similar to and intergrades with Coast Live Oak Woodland but with a canopy locally dominated by *Juglans californica* and an understory of introduced grasses.

Definition of study sites

To detect potential local variation in carnivore diets and relative abundances, we defined three sites where field activities (collec-

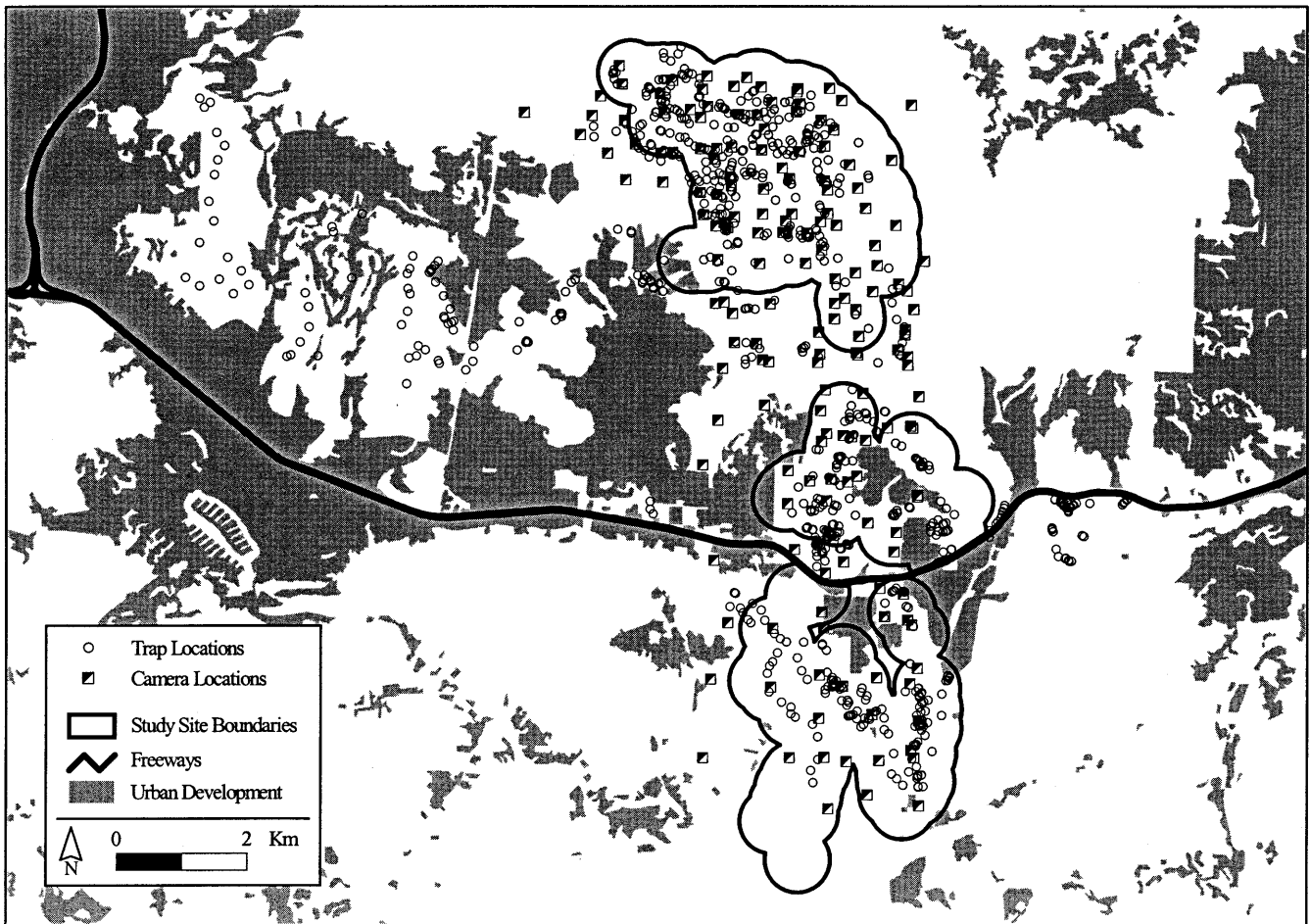


Fig. 2 Foot-hold and camera trap locations inside and outside the three study-site polygons. When estimating habitat-specific carnivore abundances all sampling effort and captures made inside and outside of polygons were considered, whereas for estimating relative carnivore abundance for each study site we only considered efforts and captures made within the corresponding site

tion of feces and trap surveys) were focused. Because collection of feces was spatially more restricted than trap surveys, we conservatively based the definition of study sites on this activity. For each scat we obtained a global positioning system (GPS) reading that was recorded into a geographic information system (GIS) to establish its map location. Then we delineated a 500-m perimeter around each scat location and connected all overlapping circles, yielding three non-overlapping polygons (Fig. 1). Carnivores virtually did not range from one side of U.S. Highway 101 to the other (Sauvajot et al. 1997); therefore, when estimating the habitat composition of each study site we did not include small portions of some polygons located on the opposite side of the highway (Fig. 1).

Carnivore relative abundances

To estimate the relative abundance of carnivores we used separately results of both foot-hold and camera-trap surveys (Carthew and Slater 1991; Linhart and Dasch 1992) carried out from February 1996 to February 1999. The foot-hold trap survey effort (9,734 trap-nights) involved 817 trap locations (Fig. 2). Victor foot-hold traps (Nos. 2 and 3) were checked twice per day (immediately before dusk and after sunrise), and captured animals were marked

with ear-tags and radio-collars, allowing their identification when recaptured. All animals were handled and released at capture sites. The camera-trap survey effort (5,844 trap-nights) involved 308 camera stations (Fig. 2). Each camera station consisted of a 35-mm point-and-shoot camera (Canon Sure Shot Owl) hard-wired to a 20×20 cm pressure-sensitive pad (cf. Danielson et al. 1996). Photos were taken when animals stepped on the pressure-sensitive pad and triggered the camera shutter release (day and time was recorded for most photos). A few camera stations were equipped with infrared detection devices (Trailmaster or cam-Trakker systems) instead of pressure pads. To minimize the number of counted "recaptures" when estimating carnivore abundances, only one photograph per species was considered for each camera station (the one with higher number of individuals), unless it was possible to accurately differentiate individuals photographed at the same camera station (tagged individuals, or adult vs. pup). Since each species may differ in its trappability to both kinds of traps (Sauvajot et al. 1997), indices of relative abundances were estimated separately for foot-hold trap and camera surveys as: number of individuals captured×1000 traps-night/total trapping effort (i.e., total trap-nights). Both kinds of traps were set in areas frequented by carnivores and baited with non-species-specific lures (Turkowski et al. 1979). All sites were baited in the same way and were not purposely biased towards any one species. When estimating habitat-specific carnivore abundances all sampling effort and captures made inside and outside of polygons were considered, yielding overall patterns (i.e., not local); for estimating relative carnivore abundance for each study site we only considered efforts and captures made within the corresponding site. Because of contrasting interspecific patterns of habitat occupancy, the estimation of local carnivore abundances from surveys could be skewed if most effort was made in habitats little represented, or if differing effort was made in different habitats

throughout the three study sites. However, 89–96% of the effort of camera trap surveys, and 80–88% of the effort of foot-hold trap surveys was made in the five main habitat types (Coastal Sage Scrub, Northern Mixed Chaparral, Chamise Chaparral, Non-Native Grassland, and Development).

Diet

Carnivore diets were assessed through fecal analyses. Fresh feces were collected on roads, trails, and ridges during 1-week period each month from November 1997 to October 1998. Total sample size was 761 for coyotes, 660 for bobcats, and 347 for gray foxes. Most samples were well distributed over the year and by areas. Feces of bobcats were easily identified on the basis of odor, color, and shape (Murie 1954). Because feces of canids can be misidentified, we assigned feces of 21 mm or larger in diameter to coyotes (Dennis and Norris 1982). For feces under 21 mm diameter, gray fox feces were differentiated from coyote feces on the basis of their long, tapered ends and strong fox odor. When present, associated tracks were also used to help species identification. Kohn et al. (1999) using DNA techniques to identify species for fresh and old feces in the study area, estimated that 10–15% of feces might be misidentified (M. Kohn, personal communication). Since we only collected fresh feces, which better preserve species-specific characteristics (size, shape, odor), we assumed that our error was smaller.

Feces were analyzed by standard methods (Reynolds and Aebischer 1991), and prey items identified were categorized into five types: lagomorphs, rodents, "other vertebrates", invertebrates, and fruit. The importance in the diet of each prey type was quantified by two methods: (1) percentage of occurrence = number of occurrences of each prey type $\times 100$ / number of occurrences of all prey types, and (2) dry weight of remains of prey types = dry weight of remains of each prey type $\times 100$ / dry weight of total feces. According to patterns of precipitation (Russell 1926), we considered separately diets of dry (May–October) and wet (November–April) seasons. Overall differences in the occurrence of prey categories among diets were detected by chi-square analyses of contingency tables. We then examined the contribution of each cell to the overall chi-square statistic to identify major sources of discrepancy between compared diets. When the percentage of expected values lower than 5 in the contingency tables was higher than 20%, we used the Fisher exact test instead of the chi-square test (Wells and King 1980). Sequential Bonferroni confidence intervals (Rice 1989) were used in multiple comparisons to control the experiment-wise error. Seasonal diet diversity was calculated using Levins' index, standardized following Hespeneheide (1975). The formula of diversity of Levins is:

$$B = (\sum p_i^2)^{-1}$$

where p_i is the proportion of food item i in the total diet. The standardized formula is: $B_s = (B-1)/(n-1)$; where n is the maximum number of food categories identified ($0 \leq B_s \leq 1$). On the other hand, seasonal food overlap was estimated for each pair of species with the index of Pianka (1973):

$$O_{jk} = \sum p_{ij} p_{ik} / (\sum p_{ij}^2 p_{ik}^2)^{1/2}$$

where p_{ij} (or p_{ik}) is the proportion of food item i in the diet of the predator species j (or k) ($0 \leq O \leq 1$). In calculating both metrics we used percentages of dry weight (Fedriani and Travaini 2000) and classified vertebrates and fruit at the species or generic level, and invertebrates at the ordinal level (see Appendix; Greene and Jaksic 1983). Overall, 3,465 different food items were identified and about 80% of them were classified at the species or generic level. This level of taxonomic resolution was consistent for both vertebrate and invertebrate prey, and also for fruit.

Results

Carnivore interferences

A key assumption when evaluating our predictions (see Introduction) was the competitive dominance of coyotes in aggressive interactions with both bobcats and gray foxes. In order to confirm that assumption in our study area, we report both cases and evidences of intraguild predation. This information is derived from the fecal analyses of the three target species and from a parallel radio-tracking project (Sauvajot et al. 1997) carried out from February 1996 to February 1999.

Twelve radio-tagged gray foxes were found dead in 2 years of study; seven were killed by coyotes and two by bobcats (V. Farias, T.K. Fuller, J.M. Fedriani, R.B. Wayne, R.M. Sauvajot, unpublished work). All sexes and ages of gray foxes suffered carnivore predation. Of a total of five radio-tagged bobcats deaths, two (male and female, both adult) were due to coyote predation. In addition, remains of bobcats and gray foxes were found in coyote feces (4 and 2 cases, respectively). Evidence of cannibalism was also detected; one coyote was found dead that was killed by conspecifics, and remains of bobcats in one bobcat scat and remains of gray foxes in one gray fox scat were also found. Evidence of interference among carnivores involving non-targeted species included the death of a radio-tagged adult male coyote probably killed by a mountain lion (*Felis concolor*), an American badger (*Taxidea taxus*) killed by coyote, and the remains of spotted skunk (*Spilogale putorius*) and long-tailed weasel (*Mustela frenata*) in feces of coyotes (1 case) and bobcats (2 cases), respectively.

Most dead animals were consumed to variable extent. No fly maggots were found in feces of carnivores containing remains of other carnivores, which suggests predation or cannibalism but not scavenging.

Study site habitat composition and carnivore abundance

Three non-overlapping polygons called North, Central, and South Polygons (hereafter, NP, CP, SP, respectively) were defined (Fig. 1). Habitat composition of each site was estimated using a GIS data base (e.g., Koeln et al. 1994) and employing the habitat classification system detailed above. Between 88 and 95% of each area consisted of three brushy habitats (Coastal Sage Scrub, Northern Mixed Chaparral, and Chamise Chaparral) and two open habitats (Non-Native Grassland and Development) (Table 1). Consequently, habitat similarity among sites was high (range 0.80–0.96; Table 1). There were, however, some differences among sites. The NP site had more brushy and less open habitat, whereas CP had less brushy and more open habitat. Size of study sites (6.5–14.4 km²) was consistent with the recommendation of Cousins (1996) that the spatial limit of system under investigation should be determined by the size of the home range of their top predators (coyote home range

Table 1 Habitat composition of each study site, carnivore species detected by means of camera or trapping surveys (a *dash* indicates habitat not present or not sampled), and habitat similarity (Pianka 1973) among pairs of study sites in the Santa Monica Mountains

	North Polygon		Central Polygon		South Polygon	
	%	Species	%	Species	%	Species
Brushy habitats (Total)	84.6		47.8		73.6	
Coastal sage scrub	46.2	C, B, GF	43.0	C, B	40.1	C, B, GF
Northern mixed chaparral	22.2	B, GF	0.5	C	27.5	C, B, GF
Chamise chaparral	10.0	B, GF	0.0	–	0.4	–
Coastal sage scrub-chaparral transition	0.0	–	0.0	–	0.9	–
Coast live oak	6.2	B, GF	4.3	C, B	4.7	–
Open habitats (Total)	15.4		52.3		26.4	
Development	2.1	–	24.1	–	10.1	C
Valley oak	1.3	C, B	6.6	C, B	1.4	–
Non-native grassland	12.0	C, GF	20.4	C, B	10.8	C, B
Riparian	0.0	–	0.0	–	3.3	–
Rock outcrops	0.0	–	0.0	–	0.8	–
Walnut	0.0 ^a	–	1.2	C	0.0 ^a	–
Total area (km ²)	14.4		6.5		11.9	
Index of habitat similarity:	0.798					
Central Polygon						
South Polygon	0.958		0.808			

^aScattered trees present

Table 2 Number of individuals captured (*in parentheses*) and indices of relative abundance (number of different individuals captured × 1000 trap-nights/total sampling effort) for coyotes, bobcats, and gray foxes from both trapping (TS) and camera (CS) surveys

	Trap-nights		Coyote		Bobcat		Gray fox	
	TS	CS	TS	CS	TS	CS	TS	CS
North Polygon	4,961	4,156	2.42 (12 ind.)	0.24 (1 ind.)	3.02 (15 ind.)	2.89 (12 ind.)	5.64 (28 ind.)	8.18 (34 ind.)
Central Polygon	1,835	407	19.01 (35 ind.)	– (3 ind.)	4.90 (9 ind.)	– (6 ind.)	0 ^a (0 ind.)	– ^a (0 ind.)
South Polygon	1,655	377	12.70 (21 ind.)	– (1 ind.)	10.30 (17 ind.)	– (2 ind.)	0 ^b (0 ind.)	– ^b (2 ind.)

^aLack of sightings and feces, and data from radio-tracked individuals corroborated that foxes were not present

^bInfrequent sightings and feces also supported the notion of low fox density

size at Santa Monica ranged from 1.1 to 12.0 km²; Sauvajot et al. 1997).

To estimate relative abundances of carnivores at each study site, we only considered 887 trap-sites (foot-hold and camera traps) located within the three polygons (Fig. 2) which totaled 13,391 trap-nights and 198 captures (73 coyotes, 61 bobcats, and 64 gray foxes). Results of foot-hold-trap surveys indicated that coyote abundance was lowest in NP, intermediate in SP, and highest in CP (Table 2). Bobcats were most abundant in SP, whereas in NP and CP they occurred in lower but similar abundances. Foxes were frequently captured in NP (28 individuals), but none were captured in other sites, despite high trapping effort (Table 2). Camera surveys were mainly focused on NP, where 84% of the total effort (4,940 trap-nights) and most captures (46 out of 60) were made. Results from camera survey in NP corroborated the presence of three species in this area, foxes being the most “captured”, followed by bobcats and then

of southwestern California (*C* coyote, *B* bobcat, *GF* gray fox). We did not consider species detected in traps or cameras located outside study sites

for each of the three study sites selected in the Santa Monica Mountains of California. Since camera survey effort was very small in Central and South Polygons, indexes of abundance based on this survey were not calculated for these sites

coyotes (Table 2). The small camera survey effort made in SP and CP (only 377 and 407 trap-nights, respectively) prevented us from considering their results as accurate. Nevertheless, the occurrence of the three carnivores in SP was verified, and the hypothesis that CP lacked gray foxes was strengthened. In summary, the results of foot-hold surveys carried out within the three study sites suggested an inverse relationship between the local relative abundances of gray foxes and coyotes (Table 2), while there was no obvious relationship among other carnivores pairs. Limited data of camera surveys, unpublished radio-tracking data, and our casual field observations coincided with results of foot-hold surveys (Table 2).

To estimate habitat specific carnivore abundance we considered all foot-hold survey efforts inside and outside of study sites (Fig. 2). Foot-hold surveys accounted for a total of 220 independent captures gathered during 9,734 trap-nights. These results revealed that coyotes were

Table 3 Overall indices of relative abundance (number of different individuals captured×1000 trap-nights/total sampling effort) for each carnivore species in each habitat sampled, estimated by means of foot-hold traps, in the Santa Monica Mountains

Habitat type	Trap-nights	Coyote	Bobcat	Gray Fox
Coastal sage scrub	4,960	9.3	7.7	2.6
Northern mixed chaparral	1,986	4.0	2.5	10.1
Chamise chaparral	1,029	0	4.9	7.8
Non-native grassland	670	41.8	3.0	0
Development	310	19.3	6.4	0
Valley oak	730	6.8	5.5	0
Coast live oak	544	3.7	9.2	1.7
Riparian	77	39.0	26.0	0
Walnut	78	115.4	0	0

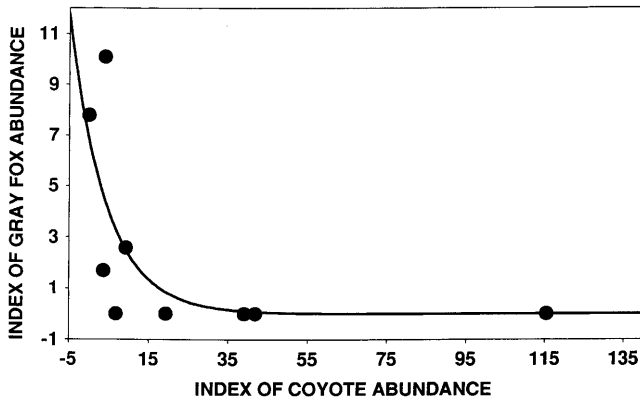


Fig. 3 Negative exponential relationship between indices of gray fox and coyote relative abundance in different habitats at Santa Monica Mountains

present in most (8 of 9) habitats (Table 3). Walnut, Grasslands, Riparian, and Development were, in that order, the habitats with greater coyote abundance, whereas Chamise Chaparral, Coast Live Oak, Northern-Mixed Chaparral, Valley Oak, and Coastal Sage Scrub were, in that order, the habitats with lower relative coyote abundances (Table 3). Bobcats ranged equally widely throughout habitats; their highest abundance was in Riparian habitat, whereas there were little differences among indices for remaining habitats (Table 3). Gray foxes were rather specialized in their pattern of habitat occupation, being captured only in Northern-Mixed Chaparral, Chamise Chaparral, Coastal Sage Scrub, and Coast Live Oak. As predicted, there was a negative relationship between gray fox-coyote habitat relative abundances (Spearman correlation, $r=-0.748$, $n=9$, $P=0.020$, Fig. 3), but no significant relationship was found among habitat relative abundances of other pairs of species (Spearman correlation, $P>0.573$).

Carnivore activity patterns

To roughly evaluate whether interfering carnivores avoided each other by temporal segregation, we grouped daytime vs. nighttime camera surveys “captures” (time was recorded for most photographs); results indicated a nocturnal/crepuscular pattern for gray foxes and coyotes, whereas bobcats seemed to be active throughout the cir-

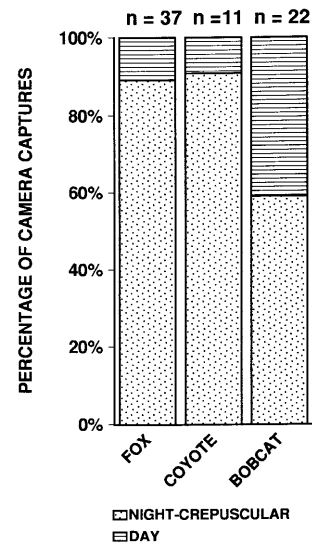
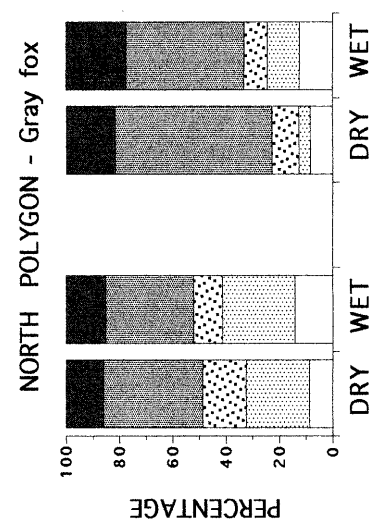
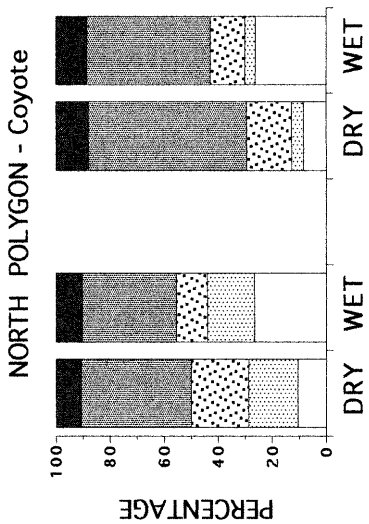
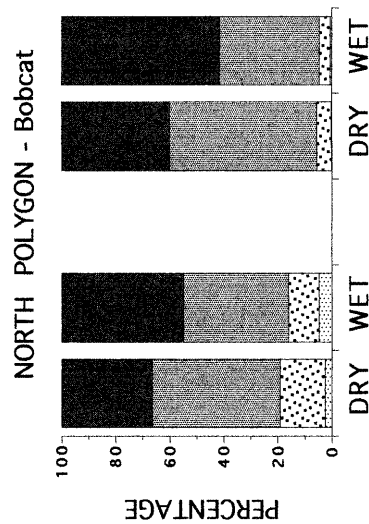
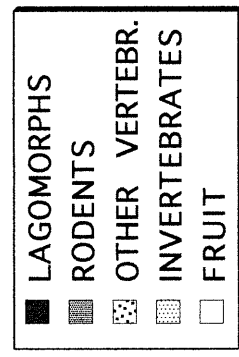
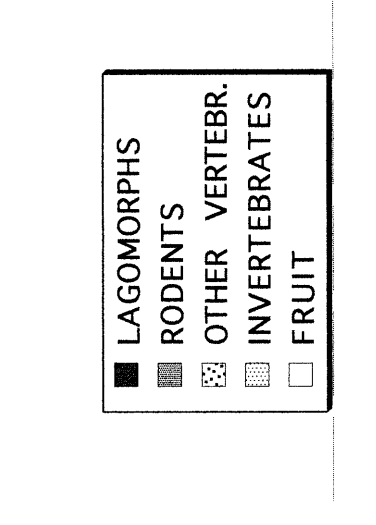
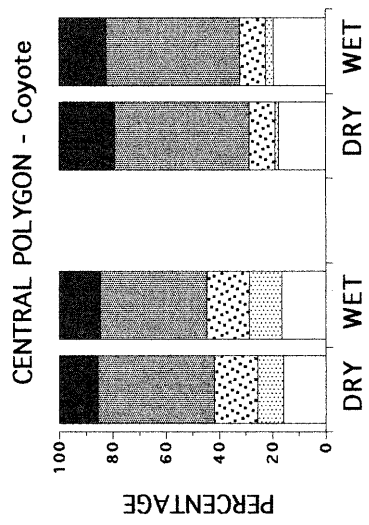
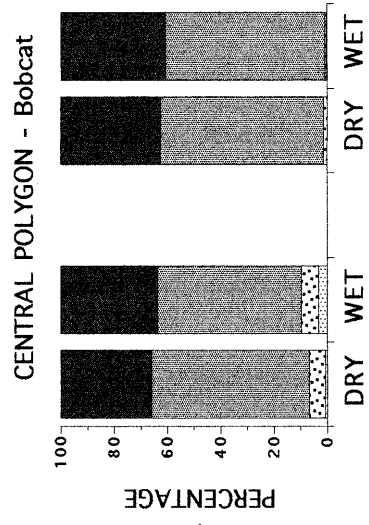
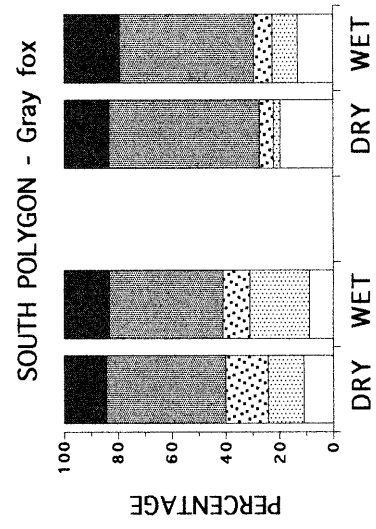
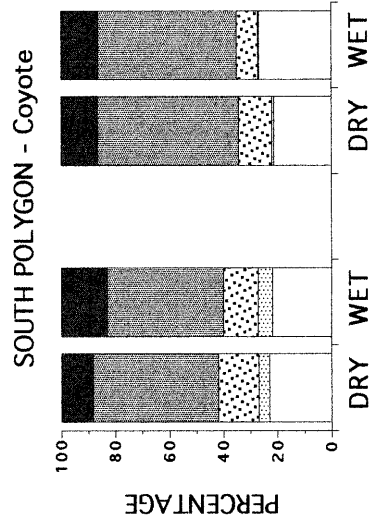
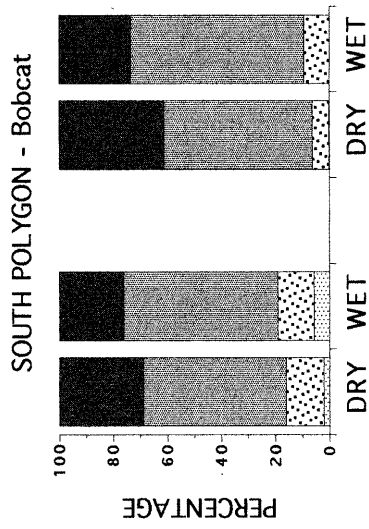


Fig. 4 Percentages of camera survey “captures” during the night/crepuscular period (19:00–08:59 hours) and daytime (09:00–18:59 hours) considering all photographs for which time was recorded

cadian cycle (Fig. 4). In addition, results of foot-hold surveys supported the notion of predominantly nocturnal/crepuscular patterns by carnivores since of a total of 245 foot-hold trap events (captures plus recaptures), all but three were between dusk and sunrise, though these data must be treated with some caution since several traps were purposefully inactivated during extreme daytime temperatures.

Fig. 5 Diets of bobcats, coyotes, and gray foxes during the dry and wet seasons at each study site (NP North Polygon, CP Central Polygon, SP South Polygon). For each species and site, the two first columns represent percentage of occurrence of different prey types and the two second columns represent percentage of dry weight of remains of different prey types (see Methods). Sample sizes (number of scats) for dry and wet seasons, respectively, were: 105 and 100 (NP), 114 and 112 (CP), and 131 and 98 (SP) for bobcat; 141 and 145 (NP), 137 and 113 (CP), and 121 and 104 (SP) for coyote; 156 and 105 (NP), and 31 and 55 (SP) for gray foxes. Plastics and other sythetic materials were not considered



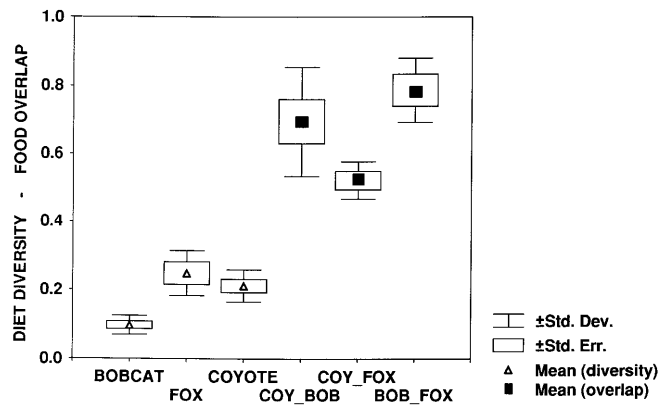


Fig. 6 Diet diversity (as standardized Levins index) for bobcats, gray foxes, and coyotes and food overlap (as Pianka index) for each pair of species in the Santa Monica Mountains of California (*coy_bob* coyote-bobcat, *coy_fox* coyote-fox, *bob_fox* bobcat-fox)

Food spectrum, local diets, and interspecific food overlap

Bobcats were solely carnivorous (Fig. 5), and their seasonal diet diversity was always low (Fig. 6). Seasonally, small mammals (rodents and lagomorphs) made up 91–99% of the dry weight of bobcat feces (Fig. 5). Prey other than lagomorphs and rodents were always of little importance in bobcat diets (Fig. 5). Consequently, there were no seasonal differences in their diets in any area ($P=0.082$). Comparing bobcat diets from different areas, we found significant differences between diets in NP and diets in other areas (Table 4). Those results indicated, for example, a greater consumption of “other vertebrates” during the dry season in NP than in CP (17% and 6% in occurrence, respectively) and a greater consumption of lagomorphs during the wet season in NP than in SP (45% and 26% in occurrence, respectively).

Coyotes were mainly carnivorous (Fig. 5), although they frequently consumed other food types, such as fruit and invertebrates. Consequently, their seasonal diets were diverse (Fig. 6). Their main prey, in all areas and both seasons, were rodents (46–59%, dry weight), though lagomorphs were also important (Fig. 5). “Other vertebrates” were relatively important, seasonally making up from 8–17% (dry weight) of their diet (Fig. 5). Invertebrate remains were frequent (4–18%, occurrence), but made up only 0.3–4% of dry weight. Coyotes also fed intensively on fruit, which occurred in 10–27% of feces and made up 8–27% of dry weight. There was a seasonal difference among coyote diets in the NP area ($\chi^2=28.7$, $df=4$, $P<0.001$), indicating, for example, that “other vertebrates” were found more frequently in feces during the dry season than during the wet season (21% and 11% in occurrence, respectively), whereas fruit was more frequent during the wet season (27% and 10% in occurrence, respectively). We did not identify seasonal differences in coyote diets in CP nor in SP ($P=0.655$). Overall, coyote diets from different sites were different in both seasons, but not when comparing CP and SP (Table 4). During both dry and wet seasons, coyotes in

Table 4 Overall intraspecific differences for each carnivore species between diets at different study sites (NP North Polygon, CP Central Polygon, SP South Polygon) during both seasons detected by chi-square analyses of contingency tables, or by Fisher exact tests (FET) when the percent of expected values lower than 5 in the contingency tables was higher than 20%. Sequential Bonferroni confidence intervals were used in multiple comparisons to control the experiment-wise error (*ns* not significant once the Bonferroni method was applied)

	Dry season			Wet season		
	χ^2	<i>df</i>	<i>P</i>	χ^2	<i>df</i>	<i>P</i>
Bobcat						
NP×CP×SP	12.7	6	0.048	17.2	6	0.008
NP×CP (FET)			0.05	7.5	3	0.058
NP×SP	1.2	3	0.760	13.8	3	0.01
CP×SP (FET)			ns	5.9	3	0.118
Coyote						
NP×CP×SP	40.4	8	0.001	26.5	8	0.001
NP×CP	12.9	4	0.05	13.2	4	0.05
NP×SP	36.3	4	0.001	19.1	4	0.01
CP×SP	9.0	4	0.061	6.9	4	0.141
Gray fox						
NP×SP	2.7	4	0.604	3.6	4	0.460

NP preyed more frequently on invertebrates than in the other two areas (Fig. 5). In NP, consumption of fruit was smaller than in SP during the dry season but greater during the wet season (Fig. 5). Consumption of fruit during the wet season was greater in NP than in CP (Fig. 5).

Gray foxes also were omnivorous (Fig. 5), and their diets were very diverse (Fig. 6). Rodents were the main prey type in all areas and seasons, seasonally making up 44–59% of dry weight (Fig. 5). Lagomorphs were the second most important prey, making up 16–22% of dry weight. “Other vertebrates” were of little importance in fox diets (Fig. 5). Invertebrates appeared frequently (13–27%), although they were not important in terms of dry weight (2–12%). Fruit also was an important food type, making up 8–19% of dry weight. We did not detect seasonal differences in fox diet in any area ($P=0.156$), and we did not detect differences when comparing diets from different areas (Table 4), although sample size for SP was small. When carnivore diets were compared simultaneously there were always strong interspecific differences in the occurrence of prey types among diets of the three species in both seasons (Table 5). Those overall differences indicated that, for example, seasonally, coyotes preyed less frequently on lagomorphs than did bobcats (Fig. 5), and that coyotes preyed more on “other vertebrates” than did bobcats in CP during both seasons (Fig. 5). Coyotes were partially frugivorous while bobcats were not. Bobcats preyed more frequently on lagomorphs and less frequently on invertebrates and fruit than did foxes in NP during both seasons (Fig. 5). In SP, bobcats preyed more often on lagomorphs during the dry season and less often on invertebrates and fruit during both seasons than did foxes (Fig. 5). During the wet season coyotes consumed more fruit in NP and less invertebrates in SP than did foxes (Fig. 5).

Table 5 Overall interspecific differences between diets of carnivores (*C* coyote, *B* bobcat, *GF* gray fox) in different study sites, during dry and wet seasons, detected by chi-square analyses of contingency tables, or by Fisher exact tests (*FET*) when the percent of expected values lower than 5 in the contingency tables was higher than 20%. Sequential Bonferroni confidence intervals were used in multiple comparisons to control the experiment-wise error

	Dry season			Wet season		
	χ^2	<i>df</i>	<i>P</i>	χ^2	<i>df</i>	<i>P</i>
North Polygon						
C×B×GF	88.1	8	0.001	136.9	8	0.001
C×B	72.3	4	0.001	111.6	4	0.001
C×GF	7.0	4	0.134	16.5	4	0.01
B×GF	66.5	4	0.001	73.9	4	0.001
Central Polygon						
C×B	63.0	4	0.001	58.7	4	0.001
South Polygon						
C×B×GF	76.1	8	0.001	62.0	8	0.001
C×B	65.9	4	0.001	32.8	4	0.001
C×GF	8.7	4	0.068	20.6	4	0.001
B×GF	(FET)		0.001	31.8	4	0.001

Interspecific food overlap values were highest for bobcat-gray fox, smallest for coyote-gray fox, and intermediate and more variable for coyote-bobcat (Kruskal-Wallis test, $Z=6.16$, $P=0.046$; Fig. 6). Seasonal food overlap between coyote and fox was smaller than between bobcat and fox (Mann-Whitney *U*-test, $U=5.33$, $P<0.021$; Fig. 6) but we did not find differences in other pairwise comparisons ($P=0.088$). There was a difference among seasonal diet diversity of carnivores ($Z=11.25$, $P=0.004$, Fig. 6); bobcat diet was less diverse than coyote diet ($U=8.31$, $P=0.004$) and gray fox diet ($U=6.54$, $P=0.010$). We did not find any difference between coyote and gray fox diet diversity ($P=0.201$).

Discussion

Overall patterns of food habits of carnivores (i.e., the three species relied on small mammals) and habitat occupancy for coyotes and bobcats (i.e., they were present in wide range of habitats) in the Santa Monica Mountains were similar to those reported elsewhere (see Whitaker and Hamilton 1998 and references therein). There were, however, two major unexpected findings of our research:

1. Gray foxes seem to behave as habitat specialists in brushy habitats; this contrasts with most assessments of their habitat use indicating generalist habits and usage of both open and brushy habitats (Trani 1980; Haroldson and Fritzell 1984; Harrison 1997).
2. Predation by coyotes was an important source of mortality for gray foxes and, apparently, also for bobcats, contrasting with studies that implicate diseases and human-related factors as major causes of death (Nicholson et al. 1985; Fuller and Berendzen 1995). Hereafter, we examine the role of our findings (both expected and unexpected) regarding the coexistence and potential for competition among those three carnivores in the Santa Monica Mountains.

The consistently high importance of small mammals (lagomorphs and rodents) in diets of all three carnivores,

study sites, and seasons yielded high interspecific food overlaps, giving a potential for food competition among carnivores, though there are no adequate data or models on consumer requirements and prey availability, necessary to establish whether competition occurred (Wiens 1993). We can only infer that bobcats were likely to suffer more from the effects of exploitation competition than the other two species, since they overlapped largely with both coyotes and gray foxes and they had the smallest diet diversity (Fig. 6). Although specialization on small mammals could allow bobcats to use these prey more efficiently (Krebs 1978), bobcats were not able to exploit alternative resources which could alleviate food competition when and where availability of small mammals was limited (Pianka 1978; also see later discussion on temporal segregation between carnivores). Interestingly, food overlap among both omnivores (foxes and coyotes) was smaller than among other pairs of carnivores. This can be explained by the fact that foxes, as a consequence of their pattern of habitat use, mostly preyed on small mammals species typical of brushy habitats (e.g., dusky-footed wood rat, *Neotoma lepida*; Quinn 1990) whereas coyotes preyed intensively on small mammals species typical of open habitats (e.g., California meadow vole, *Microtus californicus*; Jameson and Peeters 1988).

On the other hand, lack of seasonal differences in interspecific food overlaps and consistent importance of small mammal prey for all carnivores suggest constant availability of that prey type. This pattern may have been facilitated by presence of a high number of small mammals species preyed on by carnivores in the Santa Monica Mountains ($n=19$; Appendix), and by the fact that temporal and habitat variation of those prey is species-specific (M'Closkey 1972; Meserve 1976; Quinn 1990), thus ensuring that at all sites and seasons some small mammal species were abundant. This proposal is consistent with Wiens (1993) who predicted that for guilds of predators relying on small mammals periods of resource abundance and scarcity are expressed on the scale of years not seasons (Jaksic et al. 1993; Jones and Barmuta 1998).

Although gray foxes were basically restricted to brushy habitats, this did not necessarily suppose a clear segregation since coyotes and bobcats occupied all habitats. Nonetheless, the negative relationship between habitat-specific abundances of coyotes and gray foxes suggests that foxes (the subordinate species) could avoid habitats where coyotes were most abundant in order to elude interference. Interestingly, the negative relationship between abundances of gray foxes and coyotes across habitats was exponential (Fig. 3) suggesting that foxes could be more efficiently depressed in habitats where coyote abundance is high than in habitats where coyote abundance is low (Laurenson 1995; Creel and Creel 1996). Nevertheless, conforming to theoretical source-sink habitat models (Morris 1991; Watkinson and Sutherland 1995), we would also expect that some gray foxes occupy habitats where coyotes are abundant (e.g., grassland) after periods of high gray fox productivity.

Despite the co-occurrence of carnivores in some habitats, interfering carnivores may relax the effects of interspecific competition by temporal segregation (Johnson et al. 1996). Results of camera surveys (Fig. 4) suggest that bobcats were active throughout the circadian cycle, whereas coyotes and foxes were mainly nocturnal/crepuscular, which is consistent with a greater predation by bobcats of diurnal squirrels (see Appendix for species) that comprised between 5–14% of their diets (in dry weight), versus 1–4% and 0% for coyotes and foxes, respectively. This greater consumption of diurnal prey, however, did not apparently lead to major food segregation between bobcat-other carnivores compared with overlap between coyote and fox, likely because bobcats yet shared with other carnivores their main prey (nocturnal/crepuscular small mammals), and these prey are not renewed within the period involved in temporal segregation (MacArthur and Levins 1967; Jaksic 1982)

Predation by coyotes on gray foxes and bobcats also supports the view that carnivores coexisted in space and time, since those carnivores were most likely killed when active. These agonistic interactions seem to alter patterns of habitat occupancy and, consequently, prey use by gray foxes. Nonetheless, if changes in fox population characteristics (i.e., density) did not happen as a consequence of their interactions with coyotes, true or depressive competition (*sensu* Mac Nally 1983) might not have been manifested. For instance, a surfeit or occurrence of alternative resources and inconsistency or rarity of interferences may preclude the appearance of true competition (Mac Nally 1983).

In spite of the fact that manipulative experiments are required to unequivocally demonstrate depressive competition, our evaluations of relative abundances of coyotes and gray foxes at the three sites indicated that, even at this scale, there was a negative relationship between them, suggesting that high coyote abundance can lower fox numbers and, as in CP, is likely to locally exclude them. The absence of gray foxes at CP is decidedly supported by 2 years of gray fox radio-tracking, during which no individuals ($n=24$) used CP (V. Farias, T.K.

Fuller, J.M. Fedriani, R.B. Wayne, R.M. Sauvajot, unpublished work), and also by the absence of sightings or feces of foxes at this site. Prey availability and conflicts with humans are other potential factors limiting carnivore population size and distribution (Hersteinsson and Macdonald 1992; Creel and Creel 1996). Because abundance of small mammals varies among habitats (Quinn 1990), differences in habitat composition among study sites could lead to contrasting prey availabilities. This seems unlikely for NP and SP (they are very similar in habitat composition) but more feasible for CP when compared to the other two sites, although the availability of habitats preferred by foxes (brushy habitats) in CP is also high (Table 1). Preliminary assessments of rabbit abundance (by counting their pellets in fixed plots) indicated that brushy habitats of CP were at least as rich in rabbits as the same kind of habitats at the other two sites (authors, unpublished work), and there is no evidence that rodents were more limited in CP than in other sites (in fact, bobcats and coyotes preyed intensively on rodents in CP). On the other hand, gray foxes often range in natural patches surrounded by residential areas (Soule et al. 1988; Harrison 1993, 1997); thus, it is unlikely that the higher proportion of development in CP accounted for low abundance of gray foxes there. Indeed, Soule et al. (1988) and Crooks and Soule (1999) found statistical evidence that coyotes control gray fox populations in urbanized chaparral canyons of San Diego (California), though they did not report direct evidence of agonistic interactions between them. Coyote density in an area (15 km²) overlapping CP was estimated by genotyping their feces by Kohn et al. (1999), and ranged from 2.4 to 3.0 individuals km⁻² which is a very high value. Assuming similar coyote density at CP (which seems reasonable given spatial overlap and high habitat similarity between study sites), 16–19 individuals were simultaneously using CP (size 6.5 km²). At this high density of coyotes, gray fox-coyote encounters would be frequent and the behavioral decision of individual foxes to avoid CP seems the best alternative for survival (see Lima 1998 for review).

We propose that the sum of population losses due to coyote predation plus the avoidance of areas of high coyote predation risk by foxes limit the size and range of gray fox populations in the Santa Monica Mountains, whereas no evidence of food limitation is indicated. However, it remains to be explained why bobcats did not respond, apparently, to coyote competition in a similar manner to foxes, since some bobcats were also killed by coyotes, and bobcats and coyotes overlapped in food habits even more than did foxes and coyotes. Several non-exclusive hypotheses can be drawn. It is likely that coyote predation on bobcats is not frequent enough to provoke noticeable consequences in bobcat population (only two bobcats were found killed by coyotes), or that bobcats living in areas with high coyote density are large enough to avoid coyotes. Also, we did not find any negative relationship between abundances of bobcats and gray foxes, which would be expected since they overlapped considerably in resource use and agonistic interactions among

them did occur. Inconsistency in behavioral dominance between the two species (Dudley 1976) and the effects of interactions with the larger, widespread coyote could annul or mask expected patterns. Further work is required to address these questions. As hypothesized, coyotes used more food types and more habitat types than did, respectively, bobcats and gray foxes. Although this study shows the potential for the subordinate species (gray fox) to reach a high density in an area (NP) where coyotes were scarce, overall coyotes were the most abundant species and ranged more widely than did foxes. Thus, even though we present the notion that substantial changes in relative abundances of interfering species within a given carnivore guild are likely at a microgeographical scale, gray foxes and coyotes in the Santa Monica Mountains exemplified a case in which the relationship between their body size and local abundance is governed by competitive dominance of the largest species rather than by energetic equivalences (Brown and Maurer 1986; Cotgreave 1993). However, for the intermediate-sized bobcat no such a pattern emerged, likely due to rarity or inconsistency of interactions and/or behavioral avoidance of encounters by subordinate species (Fedriani et al. 1999).

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Appendix

Taxonomic categories of prey of carnivores used to estimate diet diversity and interspecific food overlaps. Vertebrates and fruit were classed to species or generic level whereas invertebrates were classed to ordinal level (Greene and Jaksic 1983).

Opossum, *Didelphis virginiana*; ornate shrew, *Sorex ornatus*; *Myotis* sp.; brush rabbit, *Sylvilagus bachmani*; desert cottontail, *S. audubonii*; *Sylvilagus* sp.; black-tailed hare, *Lepus californicus*; California ground squirrel, *Spermophilus beecheyi*; fox squirrel, *Sciurus niger*; *Sciurus* sp.; Botta's pocket gopher, *Thomomys bottae*; California kangaroo rat, *Dipodomys agilis*; California pocket mouse, *Perognathus californicus*; Western harvest mouse, *Reithrodontomys megalotis*; cactus mouse, *Peromyscus eremicus*; California mouse, *P. californicus*; deer mouse, *P. maniculatus*; brush mouse, *P. boylii*; pinion mouse, *P. truei*; *Peromyscus* sp.; dusky-footed wood rat, *Neotoma fuscipes*; desert wood rat, *N. lepida*; *Neotoma* sp.; California meadow vole, *Microtus californicus*; black rat, *Rattus rattus*; house mouse, *Mus musculus*; coyote, *Canis latrans*; gray fox, *Urocyon cinereoargenteus*; long-tailed weasel, *Mustela frenata*; Western spotted skunk, *Spilogale gracilis*; bobcat, *Felis rufus*; domestic cat, *Felis catus*; mule deer, *Odocoileus hemionus*; California quail, *Callipepla californica*; Western scrub-jay, *Aphelocoma californica*; *Corvus* sp.; Western skink, *Eumeces skiltonianus*; *Crotalus* sp.; Scorpionida; Araneae; Orthoptera; Coleoptera; Lepidoptera; Diplopoda; Polydesmida; California walnut, *Junglans californica*; *Rush lancea*; apricot, *Prunus armeniaca*;

peach, *P. persica*; *Prunus* sp.; coffeeberry, *Rhamnus californica*; Eastwood manzanita, *Arctostaphylos glandulosa*; calabazilla, *Cucurbita foetidissima*; Christmas berry, *Heteromeles arbutifolia*; coastal prickly pear, *Opuntia littoralis*; Southern honeysuckle, *Lonicera subspicata*; *Quercus* sp.; *Rubus* sp.; tomato, *Lycopersicon alkekengi*; grape, *Vitis vinifera*; olive, *Olea europaea*; apple, *Malus domestica*; pear, *Pyrus communis*; fig, *Ficus carica*.

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