Food habits and space use of gray foxes in relation to sympatric coyotes and bobcats

Jennifer C.C. Neale and Benjamin N. Sacks

Abstract: To investigate interspecific relationships between gray foxes (*Urocyon cinereoargenteus*) and sympatric coyotes (*Canis latrans*) and bobcats (*Lynx rufus*), we quantified occurrence of food items in carnivore scats and used relative abundances of scats on transects to assess space use. Dietary-overlap indices between the two canid species were high during summer and fall ($\bar{x} = 0.89$) when fruits were prevalent in scats of both species, and were lower during winter and spring ($\bar{x} = 0.70$) when fruits were less available. Foxes differed most from coyotes in their relatively less frequent ungulate consumption. Fox–bobcat dietary-overlap indices were relatively low in summer and fall ($\bar{x} = 0.37$) and greater in winter and spring ($\bar{x} = 0.74$). Foxes differed most from bobcats in their more frequent consumption of fruits and less frequent consumption of lagomorphs. Abundance of fox scats was positively correlated with abundance of coyote scats during both winter–spring ($r = 0.52$, $p = 0.02$) and summer–fall ($r = 0.75$, $p < 0.001$) and with abundance of bobcat scats during winter–spring ($r = 0.59$, $p < 0.01$) and summer–fall ($r = 0.22$, $p > 0.10$). Thus, despite similarities in diet, we found no evidence that gray foxes avoided these larger predators in space.

Résumé : Pour décrire les interactions interspécifiques entre les Renards argentés (*Urocyon cinereoargenteus*) et les coyotes (*Canis latrans*) et lynx (*Lynx rufus*) sympatriques, nous avons quantifié la fréquence des aliments dans les fèces de ces carnivores et déterminé les abondances relatives des fèces pour évaluer leur utilisation de l'espace. Les indices de chevauchement de niches alimentaires entre les deux canidés sont élevés durant l'été et à l'automne ($\bar{x} = 0,89$) lorsque les fruits prédominent dans les fèces des deux espèces et moins élevés en hiver et au printemps ($\bar{x} = 0,70$) lorsqu'il y a moins de fruits. Les renards diffèrent des coyotes par leur consommation relativement moins fréquente d'ongulés. Les indices de chevauchement alimentaire entre les renards et les lynx sont relativement faibles en été et à l'automne ($\bar{x} = 0,37$), mais plus élevés en hiver et au printemps ($\bar{x} = 0,74$). Les renards diffèrent des lynx surtout par leur consommation plus fréquente de fruits et leur consommation moins fréquente de lagomorphes. L'abondance des fèces de renard est en corrélation positive avec celle des fèces de coyote, aussi bien durant la période hiver–printemps ($r = 0,52$, $p = 0,02$) que durant la période été–automne ($r = 0,75$, $p < 0,001$) et avec l'abondance des fèces de lynx au cours de la période hiver–printemps ($r = 0,59$, $p < 0,01$) et au cours de l'été–automne ($r = 0,22$, $p > 0,10$). Donc, en dépit de la ressemblance des régimes alimentaires, rien n'indique que les Renards argentés évitent ces grands prédateurs.

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Introduction

Gray foxes (*Urocyon cinereoargenteus*) co-occur with both coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) over a large part of their range in North America. Consequently, gray foxes might be expected to experience negative interactions, including exploitation competition and interference, with the two larger predators, especially where dense populations occur in sympatry. The degree of overlap in food habits represents a major interspecific relation that strongly affects the potential for competition.

J.C.C. Neale[1,2] and B.N. Sacks.[3] Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720, U.S.A.

[1]Corresponding author (e-mail: jcneale@ucdavis.edu).
[2]Present address: Graduate Group in Ecology, Department of Environmental Toxicology, One Shields Avenue, University of California, Davis, CA 95616, U.S.A.
[3]Present address: Graduate Group in Ecology, John Muir Institute of the Environment, One Shields Avenue, University of California, Davis, CA 95616, U.S.A.

Ecological relations between gray foxes and sympatric coyotes or bobcats have received little attention (Small 1971; Riley 1999; Fedriani et al. 2000). However, relations between other fox species and coyotes have been well studied and broadly characterized as agonistic, with coyotes dominant over red foxes (*Vulpes vulpes*; Major and Sherburne 1987; Sargeant and Allen 1989), swift foxes (*Vulpes velox*; Kitchen et al. 1999), and kit foxes (*Vulpes macrotis*; Ralls and White 1995). Relations between foxes and bobcats have received less attention, although one study that examined diet and space use showed no evidence of competition between red foxes and bobcats (Major and Sherburne 1987).

Previously, we assessed niche relationships between sympatric high-density populations of coyotes and bobcats in the northern California foothills and observed few negative interactions despite extensive spatial overlap and similarities in use of habitats and foods (Neale and Sacks 2001). We hypothesized that gray foxes in the study area would be more negatively impacted by coyotes than were bobcats, owing to their smaller size as well as the omnivorous diet of both canids. We also investigated whether the intermediate-sized bobcat might also overlap gray foxes in use of foods and (or) interfere with foxes' use of space. To investigate these questions and better understand ecological relations between gray foxes and both coyotes and bobcats, we com-

pared composition, breadth, and interspecific overlap of diets as well as distribution of scats as indicators of space use.

Materials and methods

Study area

The study area was located at the 21-km² Hopland Research and Extension Center (HREC; 39°00′N, 123°05′W) in Mendocino County, California. This site was located in the Coast Range mountains in the Russian River drainage and had a primarily southwest aspect; topography was hilly to semi-rugged, with elevations ranging from 150 to 915 m. Vegetation consisted of a mosaic of four principal types: chaparral (24%), mixed evergreen–deciduous forest (16%), annual grassland (34%), and oak woodland (19%). A detailed description of the vegetation was given in Murphy and Heady (1983). The climate was characterized by cool wet winters and warm dry summers. Potential prey included 2 lagomorph species, 13 rodent species, black-tailed deer (*Odocoileus hemionus columbianus*), and various birds, reptiles, and invertebrates. In addition to wild prey, 900–2500 domestic sheep were maintained at the site.

Scat collection

Scats of foxes, coyotes, and bobcats were collected biweekly from 21 transects (0.5 km in length) established throughout the study area, and opportunistically when found fresh. Transects were established along dirt roads because carnivores frequently used these for travel and defecation. Our deliberate use of roads meant that transect placement was not random with respect to microhabitat. However, transects, which were selected to cover the study area uniformly, also covered a representative variety of vegetation types. On each transect, five points separated by 100 m were classified as to their adjacent vegetation as follows: 29, 22, 39, 11, and 4 points in chaparral, woodland, grassland, forest, and other, respectively, which did not differ significantly from the composition of these vegetation types on the HREC ($\chi^2_{4\,df}$ = 4.96, p = 0.29).

Scats were assigned to predator species primarily on the basis of size (Murie 1954; Danner and Dodd 1982) as well as tracks, odor, and other sign. Fox and coyote scats were similarly shaped and overlapped somewhat in size (Danner and Dodd 1982). Approximately 10% of carnivore scats were of ambiguous origin and were discarded. Inspection of scats collected from known individuals from traps or during radio-tracking sessions helped to confirm classification.

Food habits

All scats of gray foxes (n = 205) and bobcats (n = 226) and a random sample of coyote scats (n = 537 of 1095 collected) were analyzed for prey remains. Scats were oven-dried, placed in nylon bags, and washed in an automatic clothes washer to remove the fecal matrix, then tumble-dried (Neale 1996). Hair, teeth, and bone were identified using reference material from the study area, keys, and photomicrographs (e.g., Mayer 1952; Glass 1973; Moore et al. 1974). Grass, found in scats of all 3 predators, was assumed to be used as an aid to digestion (Makar 1980) or as a purgative for accumulations of tapeworms in the digestive tract (Toweill and Anthony 1984) and was excluded from analyses.

Ideally, food-habits analyses are based on estimation of actual biomass consumed (Kelly and Garton 1997; Neale and Sacks 2001) and (or) energy gain. Because correction factors were not available for foxes, we used frequency of occurrence of food items in scats to make comparisons of relative consumption of prey over time and among consumers. Because the larger scats of coyotes and bobcats contained more items, on average, than fox scats, we calculated and compared the relative frequency of occurrence. The relative frequency of occurrence of each food type in scats was cal-

culated for each predator during summer (July–September) 1994, fall (October–December) 1994, winter (January–March) 1995, spring (April–June) 1995, and summer–fall 1995 (July–December combined, owing to low numbers of fox scats). We also compared annual diets (i.e., based on averaged values for summer 1994, fall 1994, winter 1995, and spring 1995). For simplicity, food items constituting ≤2% of occurrences in every season and for all 3 predators were excluded from analyses.

We calculated measures of dietary breadth (B) and food-niche overlap (α) according to Pianka (1973):

$$[1] \qquad B = \frac{1}{\sum p_i^2}$$

$$[2] \qquad \alpha = \frac{\sum (p_i \times q_i)}{\sqrt{\sum p_i^2 \times \sum q_i^2}}$$

where p_i is the proportion of food item i in the diet of predator p and q_i is the proportion of food item i in the diet of predator q. We identified 14 different foods consumed by the 3 predators, therefore seasonal dietary breadths potentially ranged from 1 (only 1 food item taken) to 14 (all food items taken, in equal proportions). The index of dietary overlap ranged from 0 (complete dissimilarity) to 1 (complete similarity). Dietary-overlap indices should be based on resource categories at least as fine as those perceived by consumers (Krebs 1989), therefore we categorized prey to the species level whenever possible (Greene and Jaksíc 1983).

Nevertheless, it is also important to identify groups of prey that may be selected similarly by sympatric carnivores. Neale and Sacks (2001) found that coyotes and bobcats at this site selected similarly among rodent species but differently among higher taxonomic groupings. To investigate whether similarity in prey groups existed between foxes and coyotes and between foxes and bobcats, we plotted relative frequencies of occurrence of prey species in fox scats versus those in scats of coyotes and of bobcats. Regressions were used to quantify relative use of rodent species (R^2) and rodents as a group relative to other prey (slope).

Spatial overlap

For spatial analyses, only scats collected on transects (n = 179, 475, and 121 scats of fox, coyote, and bobcat, respectively) were used. We examined correlations between numbers of scats (log-transformed; Zar 1984) of foxes and both coyotes and bobcats to investigate interspecific spatial overlap during wet (winter–spring) and dry (summer–fall) periods. We assumed that relative abundance of scats corresponded to relative use of space and that avoidance of coyotes and bobcats by foxes would be indicated by negative correlations between numbers of their scats. We used a standard multiple-regression analysis to test for effects of bobcat- and coyote-scat abundance on fox-scat abundance. The significance of each explanatory variable (i.e., numbers of bobcat and coyote scats) was based on the T statistic of the multiple regression. If numbers of bobcat and coyote scats were intercorrelated, the magnitude of the T statistics (and associated p values) would be underestimated (Tabachnick and Fidell 1989). Therefore, we also report Pearson's product moment correlation coefficients (r).

Results

Food habits

Most prey were present in the diets of all 3 carnivores, but the relative frequencies of food items differed among seasons and among predators (Table 1). Fruit occurred at a high frequency in canid (especially fox) scats relative to its frequency in bobcat scats during summer and fall in both years. Almost all fruits consumed by foxes and coyotes were

Table 1. Seasonal relative frequency of occurrence (percentage of occurrences in scats) of food types in scats of gray foxes (F), coyotes (C), and bobcats (B).

Prey[a]	Summer 1994			Fall 1994			Winter 1995			Spring 1995			Summer–fall 1995		
	F	C	B	F	C	B	F	C	B	F	C	B	F	C	B
	(29)	(113)	(34)	(84)	(123)	(20)	(35)	(80)	(76)	(34)	(103)	(49)	(23)	(118)	(47)
Ungulate	4.7	22.0	11.3	4.8	22.9	17.2	12.7	38.5	14.4	12.5	35.2	9.1	2.6	19.8	5.1
Deer	2.4	10.1	7.9	5.1	12.8	9.7	9.3	21.4	8.4	2.5	18.7	3.9	0.0	11.6	3.2
Sheep	2.4	11.1	3.2	0.0	10.6	6.5	4.6	13.7	3.1	10.3	17.1	2.0	2.8	7.3	1.1
Lagomorph[b]	0.0	5.4	13.2	2.4	4.9	3.4	6.4	8.2	15.2	7.5	8.4	23.9	10.2	3.8	21.5
Rodent	32.6	18.5	51.0	17.8	15.9	58.6	44.7	36.7	47.2	52.6	27.4	40.9	25.6	33.0	43.1
Squirrel[c]	0.0	1.4	7.9	0.0	0.6	6.5	7.0	0.9	3.8	5.1	3.6	2.9	0.0	4.2	8.4
Wood rat	4.9	5.1	14.3	3.5	2.2	22.6	11.6	6.8	16.6	23.1	7.2	17.5	8.3	7.8	8.4
Pocket gopher	2.4	3.7	4.7	1.7	2.2	3.2	2.4	15.4	15.1	10.3	4.2	3.9	0.0	2.6	4.2
Kangaroo rat	0.0	2.3	3.2	0.9	0.0	6.5	0.0	1.7	1.5	0.0	1.5	1.0	0.0	0.5	3.2
Chipmunk	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.9	0.7	2.5	0.5	1.0	0.0	0.5	1.1
Vole	9.8	6.4	19.1	3.5	3.9	9.7	11.6	12.0	9.9	7.7	8.3	12.6	11.1	13.1	14.7
Mice[d]	12.2	3.4	7.9	2.6	5.6	12.9	4.6	4.3	4.6	2.5	4.2	12.6	0.0	7.3	12.6
Bird	6.9	8.8	1.9	8.9	1.6	6.9	8.5	3.7	11.2	2.5	7.8	2.3	2.6	3.3	8.9
Insect	4.7	5.4	5.6	4.8	11.5	3.4	12.7	3.7	1.6	10.0	11.2	3.4	12.8	6.0	8.9
Reptile	4.7	6.8	13.2	2.4	1.6	6.9	0.0	0.9	8.8	15.0	7.3	17.0	2.6	6.6	8.9
Fruit	46.5	33.2	3.8	58.9	41.5	3.4	14.9	8.3	1.6	0.0	2.8	3.4	43.6	27.5	3.8

Note: Numbers in parentheses are numbers of scats.

[a]Composite categories "ungulate" and "rodent" include unidentified large and small mammals, respectively. Component species are listed separately.

[b]*Sylvilagus bachmani* and *Lepus californicus.*

[c]*Sciurus griseus* and *Spermophilus beecheyi.*

[d]*Peromyscus* sp. and *Reithrodontomys megalotis.*

Table 2. Seasonal dietary niche breadth (possible range 1–14) and overlap (possible range 0–1) of gray foxes, coyotes, and bobcats.

	Niche breadth			Niche overlap	
	Fox	Coyote	Bobcat	Fox–coyote	Fox–bobcat
Summer 1994	3.60	6.80	9.25	0.91	0.37
Fall 1994	2.41	4.38	8.98	0.93	0.24
Winter 1995	9.49	8.10	8.97	0.70	0.67
Spring 1995	7.94	9.22	7.59	0.70	0.80
Summer–fall 1995	3.62	7.81	9.51	0.86	0.43

manzanita (*Arctostaphylos* spp.) berries. Rodents were present in diets of all 3 predators but were highest year-round in bobcat scats and spring fox scats (Table 1). Lagomorphs were generally more prevalent in seasonal diets of the two larger predators (especially bobcats) than foxes. Coyotes consumed ungulate prey with much greater frequency than did either bobcats or foxes. During summer and fall, when fox scats were largely composed of manzanita berries, dietary breadth was narrower for gray foxes than for coyotes and bobcats (Table 2). During winter and spring, dietary breadths were similar among the 3 carnivores.

Fox–coyote dietary overlap was generally high and was greatest, and fox–bobcat overlap least, during seasons when the majority of scats of both canids contained fruits (summer and fall; Table 2). Overlap of fox and bobcat diets was greatest during winter and spring, when both predators consumed rodents at high frequencies. Figure 1A demonstrates the shared high frequency of fruits in annual diets of gray foxes and coyotes, the relatively greater frequency of deer and sheep in the coyotes' diet, and the similarity in frequency of rodent species, lagomorphs, and other food items. In contrast, Fig. 1B demonstrates that selection of ungulates and rodents was similar for bobcats and foxes, lagomorphs occurred more frequently in the annual diet of bobcats relative to foxes, and fruits were very rare in the annual diet of bobcats. Rodent species were selected in a similar fashion by bobcats and foxes, as indicated by the close fit of points about the rodent regression line, but as a group were relatively more frequent in bobcat scats, as indicated by the slope of the regression line (Fig. 1B).

Spatial overlap

During winter–spring, the multiple regression of fox scats on coyote and bobcat scats was significant ($F_{[2,18]}$ = 6.19, R^2 = 0.41, p = 0.009). The slopes were nonsignificant for both coyote scats (T = 1.40, p = 0.18) and bobcat scats (T = 2.02, p = 0.06) because of intercorrelation (coyote scats vs. bobcat scats, r = 0.52, p = 0.02). Univariate regressions were significant for both predictors (Figs. 2A, 2B). During summer–fall, the multiple regression of fox scats on coyote scats and bobcat scats was also significant ($F_{[2,18]}$ = 11.25, R^2 = 0.56, p = 0.001). The slope was significant for coyote scats (T = 4.53, p < 0.001) but not bobcats scats (T = 0.00, p = 1.00). Similarly, the univariate regression was significant for coyote scats but not for bobcat scats (Figs. 2C, 2D).

Discussion

Food habits

Use of fruits by foxes during summer and fall constituted

Fig. 1. Annual relative frequency of occurrence (FO; percentage of total occurrences) of foods in scats of gray foxes versus those of coyotes (A) and bobcats (B). Each open circle represents a different rodent (squirrel, wood rat, pocket gopher, kangaroo rat, chipmunk, vole, or mice). Likewise, the three ×'s represent bird, insect, and reptile prey, and the two solid circles represent deer and sheep. Regression lines and statistics refer to rodent species.

$y = 1.16x$
$R^2 = 0.58$

$y = 0.60x$
$R^2 = 0.96$
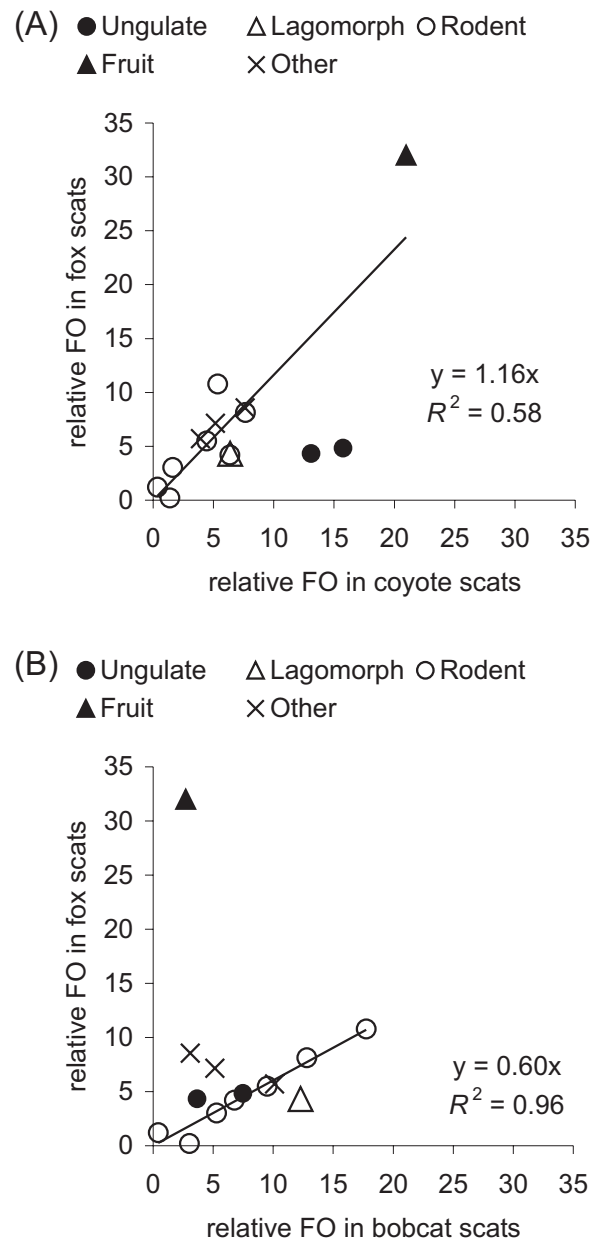
Fig. 2. Abundance of fox scats versus coyote scats (A and C) and bobcat scats (B and D) on 21 transects during winter–spring and summer–fall periods.
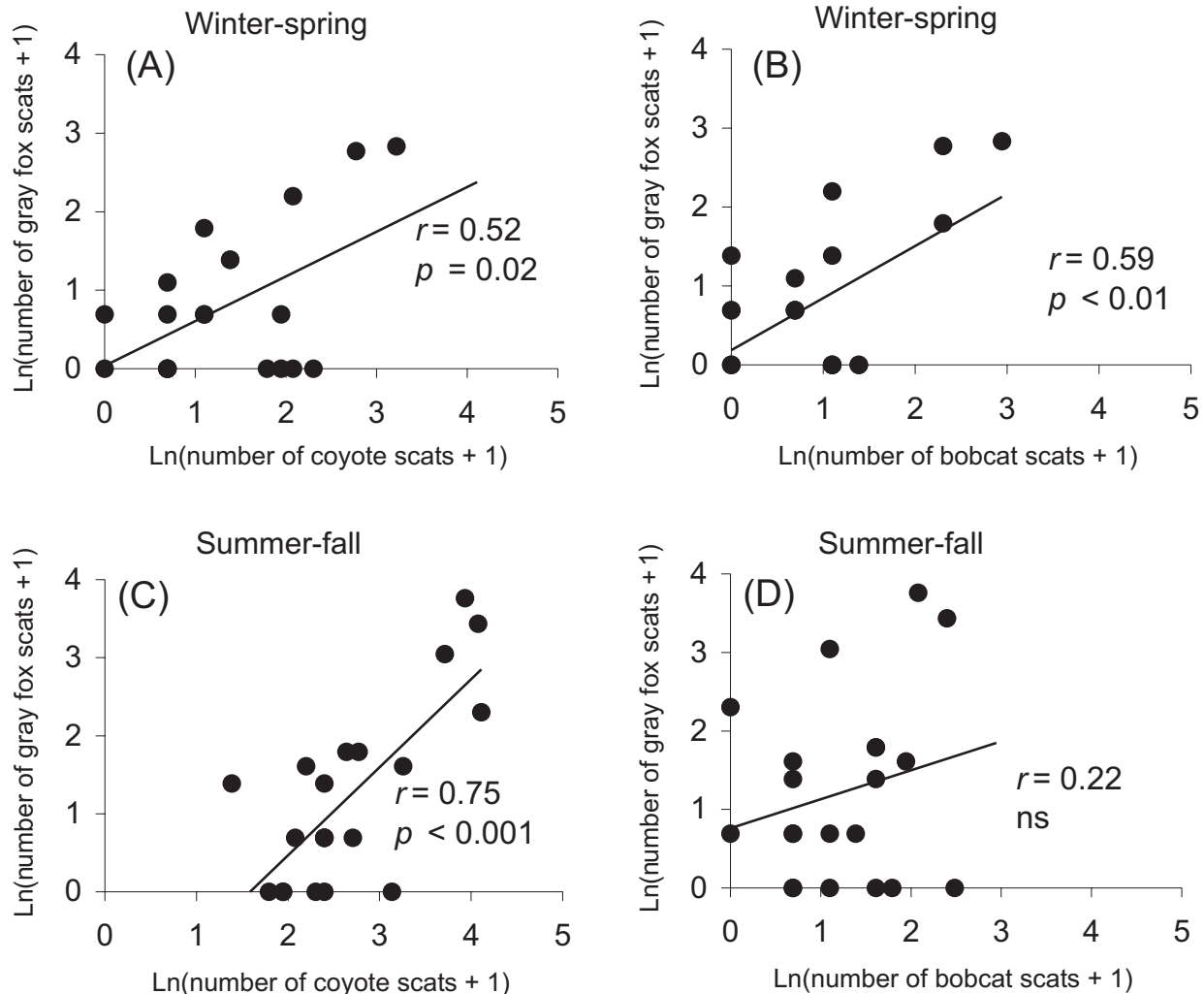
a major commonality with coyotes and a major difference from bobcats, resulting in relatively high fox–coyote and low fox–bobcat dietary-overlap indices during these seasons. Fruits have been reported to be heavily utilized seasonally by gray foxes (Small 1971; Novaro et al. 1995) and coyotes (Andelt et al. 1987) in other regions. During winter and spring in this study, when fruits were largely unavailable, fox–coyote and fox–bobcat dietary-overlap indices were similar.

The apparent importance of fruit consumption in interspecific food relations raises the issue of the limitations of measures of occurrence for food-habits analyses. Because fruit consumption tends to increase scat production, the high frequency of manzanita berries in summer and fall scats of canids reduced the *apparent* consumption of other prey. However, manzanita berries, which were found in 34% of coyote scats (21% of occurrences), were estimated to have contributed <4% of the biomass consumed by this carnivore (Neale and Sacks 2001). The amount of fruit consumed by the smaller gray fox may represent a more substantial energetic contribution to its diet. Indeed, the considerably narrower dietary breadth for foxes than for coyotes (and bobcats) in

summer and fall, when manzanita berries were consumed most frequently by canids, suggests that foxes specialized on this fruit when it was abundant.

The primary difference between the diets of coyotes and foxes in this study was in the use of ungulate prey, which likely reflected differences in body size of the predators. Coyotes were known to both kill and scavenge ungulates in the study area (Neale et al. 1998; Sacks et al. 1999). As with coyotes, the frequency of ungulate consumption by the much smaller foxes peaked in winter–spring, suggesting scavenging on coyote kills or possibly predation on lambs.

In addition to differences in fruit consumption between foxes and bobcats, lagomorphs were prevalent in bobcat scats and much rarer in fox scats. The main similarity in diets of bobcats and foxes was in their consumption of rodents. During winter and spring, when fruits were less available, foxes consumed rodents at high frequencies similar to bobcats, and the fox–bobcat dietary-overlap index peaked during spring, coincident with a peak in occurrence of rodents in fox scats. Further, the relative occurences *among* rodent species were similar between the two predators, suggesting that they selected similarly among rodent species.

Spatial overlap

Analyses of spatial overlap based on locations of predator scats did not support the hypotheses that gray foxes avoided coyotes and bobcats. In fact, correlations were positive. The high correlation coefficient ($r = 0.75$) during summer–fall between abundances of fox and coyote scats probably incorporated a bias due to increased production by canids of scats containing manzanita berries on high-elevation transects that contained most of these fruiting bushes. Nevertheless, during winter–spring, when fruits generally were not available, the abundance of scats on transects remained positively correlated among all 3 carnivores (pairwise $r = 0.52$–0.59).

Because our scat sampling was restricted to roads, it is conceivable that the results were biased. For example, roads could have been selected as travel ways similarly by all 3 carnivores, even if these predators partitioned habitat used for other purposes. Nevertheless, our study site was large enough to encompass 10–20 gray fox home ranges, so that if foxes established home ranges in such a way as to avoid larger carnivores, we should have detected a negative relationship between numbers of fox scats and numbers of bobcat and (or) coyote scats, regardless of microhabitat selection. Thus, at the landscape scale, foxes' space use was apparently more influenced by the distribution of resources than by the distribution of larger carnivores.

Interspecific relations between gray foxes and sympatric coyotes and bobcats

Interspecific relations among sympatric gray foxes and larger predators such as coyotes and bobcats have received very little study and are poorly understood. In previous field studies, the nature of relations between bobcats and gray foxes was unclear but there was no indication of competition between bobcats and gray foxes or avoidance of bobcats by gray foxes (Small 1971; Fedriani et al. 2000). However, negative interactions between coyotes and gray foxes were suggested. Evidence included differential use of habitat types by gray foxes and coyotes, indicating the possibility of avoidance (Small 1971), and significant coyote-caused gray fox mortality and possible spatial avoidance of coyotes by gray foxes (Fedriani et al. 2000). In both cases, high dietary overlap between gray foxes and coyotes was reported.

High overlap in food use between carnivores has frequently been associated with competition. In the present study, fox–coyote dietary overlap was high year-round and fox–bobcat overlap was high during winter and spring (the observed low summer and fall fox–bobcat dietary-overlap indices may have been artifacts of using frequency of occurrence data, as explained above). Our investigation occurred during flush, postdrought conditions in highly suitable habitat, and populations of coyotes and bobcats were dense. (Although the number of coyote scats collected was much greater than for foxes or bobcats, this probably indicated behavioral differences related to the use of roads and trails rather than predator density, given that coyotes and bobcats occurred at similar (high) densities on the study area, based on mark–resight methods (Neale 1996).) We hypothesized that high dietary overlap would indicate the potential for interspecific food competition, which might be mitigated via avoidance of bobcats and especially coyotes by foxes. However, despite similarities in diet between gray foxes and both coyotes and bobcats, space use by foxes did not suggest avoidance of either larger predator.

Likewise, radiotelemetry studies of kit foxes and swift foxes co-occurring with coyotes failed to reveal avoidance of coyotes by foxes even though coyotes were responsible for 65 and 48% of kit fox and swift fox mortalities, respectively (White et al. 1994; Kitchen et al. 1999). One explanation for the apparent lack of avoidance in space is that these smaller foxes maintain numerous dens to facilitate escape from coyotes, which may result in finer scale avoidance than that exhibited by red foxes (White et al. 1994; Kitchen et al. 1999). The tree-climbing ability of gray foxes has been proposed as a similar means of fine-scale avoidance of coyotes (Cypher 1993). However, much of our study area frequented by gray foxes had heavy shrub cover and no trees were available.

Our failure to find evidence of spatial separation between foxes and bobcats and especially between foxes and coyotes suggests that if foxes avoided larger carnivores, they did so in time (although there was no apparent difference in consumption of nocturnal versus diurnal prey) or at scales finer than we examined. Because we did not monitor foxes directly, we did not know the density of foxes nor the extent, if any, of coyote-caused injury or mortality of gray foxes. Alternatively, sympatric gray foxes, coyotes, and bobcats may have exhibited interspecific tolerance, possibly related to abundant resource conditions (Neale and Sacks 2001) as has been observed between red foxes and coyotes (Gese et al. 1996). Coyotes were able to exploit larger prey than were foxes, suggesting that competition might also be more intense where ungulates are not available. Future investigations using radiotelemetry, focal observations, and a range of environmental conditions would clarify relations between gray foxes and sympatric predators.

Acknowledgements

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