Abstract Previous studies carried out in the Doñana National Park reported that red foxes (Vulpes vulpes) were killed by Iberian lynxes (Lynx pardinus), whereas similar-sized Eurasian badgers (Meles meles) were not. Therefore, we predicted that fox would avoid lynx predation risk by niche segregation whereas we did not expect such a segregation between badger and lynx. As an approach for evaluating our predictions, we compared their diet, activity patterns, and habitat use in an area of Doñana where the three carnivores are sympatric. Lynxes preyed almost uniquely on European rabbits (Oryctolagus cuniculus), and though badgers and foxes were omnivorous, rabbits also were a major prey, resulting in high overlaps throughout the year. However, badgers preyed largely on small rabbits, whereas lynxes and foxes preyed mainly on medium-sized rabbits. There were also interspecific differences in activity patterns. Maximum levels of activity among lynxes were during sunrise and dusk (49–67%). Foxes were most active during dusk and night (34–67%), and badgers were mainly nocturnal (53–87%). Though there were seasonal differences in the amount of activity of each species, specific activity patterns changed little throughout the year. There was a strong difference in annual habitat use by the three species ($P < 0.0001$). Lynxes used mainly the Mediterranean scrubland during both the active ($P_{\text{MAX}}$) and the resting ($P_{\text{MIN}}$) periods. During $P_{\text{MIN}}$, foxes used the Mediterranean scrubland intensively (40% of locations on average), but during $P_{\text{MAX}}$, they used the pastureland much more intensively despite this habitat being poorer in their main prey (rabbits). As a consequence, foxes and lynxes exhibited segregation in their habitat use during the active period. Badgers also used the Mediterranean scrubland intensively, especially during $P_{\text{MIN}}$. There were no seasonal differences in habitat use for lynx and fox, but there was for badgers ($P < 0.015$). Within the study area, the three species selected habitat suggesting they were sensitive to factors such as vegetation and prey abundance. However, in general, carnivore habitat use did not correlate with rabbit abundance. We propose that foxes avoided lynxes by using, during activity, habitats not frequented by lynxes, and that a low predation risk associated with the distinctive foraging mode of badgers may facilitate its coexistence with other carnivores.

Key words Mediterranean ecosystem · Lynx pardinus · Meles meles · Niche relations · Vulpes vulpes

Introduction

Ecologists have long considered that niche segregation serves to reduce exploitative competition and thus facilitates coexistence of similar species (Pianka 1978). Increasingly, however, emphasis is placed on the role of intraguild predation (sensu Polis et al. 1989) on niche segregation as a consequence of the antipredator behavior of species under predation risk (Sih et al. 1985). We chose one top and two intermediate sympatric predators (one of them frequently killed by the top predator) to test the hypothesis of greater segregation among the two interfering species in some of the most important dimensions of the ecological niche (habitat, food, and time; Schoener 1974).

In Mediterranean ecosystems, trophic relations among sympatric carnivores have been studied (e.g., Jaksic and Delibes 1987) but multidimensional niche approaches are scare (Palomares and Delibes 1991), although they are essential for a comprehensive understanding of the niche relation among predators (Wiens 1993). In the Mediterranean Doñana National Park (southwest Spain), the Iberian lynx (Lynx pardinus, 9–12 kg), Eurasian badger (Meles meles, 7–8 kg), and the
red fox (*Vulpes vulpes*, 5–7 kg) occur in sympatry. Previous studies identified the importance of the European rabbit (*Oryctolagus cuniculus*) in the diet of these three carnivores (Delibes 1980; Rau et al. 1985; Martin et al. 1995). However, little is known about either activity patterns or habitat use by both foxes and badgers in Doñana, although elsewhere they have been reported as mainly nocturnal and crepuscular (Macdonald 1984) and as habitat generalist species (Ginsberg and Macdonald 1991; Neal and Cheseman 1996). Lynxes in Doñana are crepuscular (Beltran and Delibes 1994) and habitat specialists (e.g., Palomares et al. 1991). Because carnivore habitat use often correlates with prey abundance (e.g., Murray et al. 1994) and habitat-related variations in rabbit abundance occur in Doñana (Beltran 1991; Palomares and Delibes 1997), we expected lynx, fox, and badger habitat use to correlate with rabbit abundance in relation to the importance of rabbits in their diet. However, recent studies on carnivores emphasize the role of interference competition in shaping their niches (Friarte et al. 1990; Hersteinsson and Macdonald 1992; Mills and Biggs 1993). In Doñana, lynxes kill foxes (Palomares et al. 1996; Fedriani 1997); thus, we expected some temporal and/or spatial segregation between those sympatric species (Schoener 1974). No aggressive interactions between lynxes and badgers are known; therefore, we did not expect such a segregation. Little is known about fox-badger relationships in Doñana, but in other areas, cases of both aggressive and peaceful encounters have been reported (Neal and Cheseman 1996). Thus, we had no clear expectations about their potential segregation of resource use in Doñana.

Our specific goals were: (1) to estimate the relative importance of different prey in carnivore diets, their seasonal variations in prey use and the degree of interspecific food overlap, (2) to describe the activity patterns of the three carnivores, to estimate seasonal and interspecific differences, and to assess the degree of interspecific overlap in activity patterns, (3) to assess their habitat use and preference during their resting and active periods, to evaluate their seasonal and interspecific variations, and to estimate the interspecific overlap in habitat use, and (4) to explore whether carnivore habitat use correlated with rabbit abundance. Annual diets of both foxes and badgers have been published (Fedriani 1996; Fedriani et al. 1998), and data on lynx habitat use is currently being reviewed (F. Palomares, M. Delibes, P. Ferreras, J.M. Fedriani, J. Calzada, E. Revilla, unpublished data).

**Materials and methods**

**Study area**

Our field work was conducted from November 1992 through May 1995 in the northern portion of the Doñana National Park (37°9'N, 6°26'W), located on the west bank of the Guadalquivir River mouth in southwestern Spain. The climate is Mediterranean sub-humid, characterized by dry, hot summers and mild, wet winters. Average annual rainfall is 500–600 mm.

Marshes, scrubland and dunes are the three main habitats of Doñana (Valverde 1958), though a finer classification revealing six habitat types is possible within our specific study area. (1) The Mediterranean scrubland is mainly formed by *Pistacia lentiscus* shrubs with variable brush of *Halimium halimifolium* and scattered *Quercus suber* and *Pirus bourgaea* trees. (2) Pastureland is an open area of *Juncca*, *Silene laeta* and *Gaudinia fragilis* but with some *H. halimifolium* bushes and scattered *O. suber* and *Olea europaeae*. (3) Grassland mainly surrounds the Mediterranean scrubland and the pastureland, and includes some patches of variable size dominated by *Asphodelus ramosus* and *Armeria gaditana*. (4) Tree plantations are comprised of *Pinus pinea* and *Eucalyptus* spp. with shrubs of *P. lentiscus* common. (5) Marshes are open areas where trees and shrubs are practically absent. (6) Ash forest (*Fraxinus* sp.) occurs in several patches, the two largest associated with natural streams, and has shrubs of *P. lentiscus* (Fig. 1).

Numbers of individuals of the target carnivore species within the study area were estimated by Fedriani (1997), and ranged from 9 to 12 lynxes, from 9 to 16 badgers, and from 26 to 42 foxes. Other mammalian carnivore species also abundant in our study area were the Egyptian mongoose (*Herpestes ichneumon*) and the common genet (*Genetta genetta*).

**Food habits**

Carnivore diets were assessed through feces analyses. Feces were collected weekly from November 1992 to December 1994, and all samples were well distributed over the year. Total sample sizes were 320 for fox, 279 for badger, and 240 for lynx. The analysis of feces was made by standard methods (Reynolds and Aesbischer 1991), and prey items identified were categorized into six types: lagomorphs, other vertebrates, carrion, invertebrates, fruit, and miscellaneous. The importance in the diet of each prey type was quantified by two methods: (1) frequency of occurrence = number of feces containing each prey type/total number of feces; (2) fresh biomass ingested = dry weight of remains of a particular prey type × its correction factors (CF) × 100/200 (dry weight of remains of each prey type × CF of each prey type). Correction factors were obtained from the literature (Lockie 1959; Aldama 1993; Martin et al. 1995). Rabbits found in feces were classed into three size categories (small, ≤200 g; medium, >200 but ≤800 g; large, >800 g) by comparing their remains (mainly bones and nails) with those from reference specimens of known weight. Because the availability of rabbits varies seasonally in Doñana (Delibes and Calderón 1979; Rogers et al. 1994), we considered the diets of the autumn/winter (November–February), spring (March–June), and summer (July–October) periods separately.

Differences in the importance of particular prey categories among compared diets were detected by χ² analysis of contingency tables, or by Fisher exact test when the percentage of expected values lower than five in the contingency tables was higher than 20% (Wells and King 1980). The sequential Bonferroni confidence intervals (Rice 1989) were used in multiple comparisons to control the experimentwise error. Seasonal food overlap was estimated for each pair of species with Pianka’s (1973) index, using percentages of fresh biomass ingested by carnivores. For food overlap calculations, vertebrates and fruit were classed to species or genus and invertebrates to order (Greene and Jaksic 1983).

**Animal capture, immobilization, and radio-tagging**

Because activity patterns and habitat use of carnivores were studied by radio-tracking, the three species of carnivores were captured using coil-spring traps (Victor no. 2, Woodstream, Pennsylvania) and baited box-traps. Once captured, the animals were immobilized with an intramuscular injection of ketamine hydrochloride (50 mg/ml, Ketolar, Parke-Davis) and xylazine hydrochloride (23.3 mg/ml, Rompun, Bayer). Drug doses, induction, and recovery times are