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DIETARY OVERLAP OF AN ALIEN AND NATIVE CARNIVORE ON SAN CLEMENTE ISLAND, CALIFORNIA

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Predation by feral cats (*Felis catus*) is recognized as a major threat to native fauna worldwide, but the competitive effects of cats on native species have not been extensively studied. Cats occur on San Clemente Island, California, in sympatry with endemic island foxes (*Urocyon littoralis clementae*). We examined diets of cats and island foxes between years, seasons, and habitats to assess the potential for resource competition between the 2 species. Analysis of 602 cat and 958 fox feces revealed a high level of dietary overlap ($O = 0.93$) and relatively narrow niche breadths for both species ($B_{\text{standard Fox}} = 0.37$; $B_{\text{standard Cat}} = 0.49$). Despite the overlap in diet, cats and foxes appear to partition prey resources. Cats consume approximately equal proportions of arthropod (47.9%) and vertebrate (44.2%) prey, the latter primarily rodents (29.2%) and lizards (12.9%). In contrast, foxes appear to rely more on arthropods (57.7%), with plants (20.5%) and vertebrates (21.6%) occurring in lower, but roughly equal frequencies. Season appeared to have little effect on diet; however, diet did vary between habitats and years for both species. Diets of cats on San Clemente Island are consistent with those from other studies. We found no evidence of a dietary shift by foxes that were in sympatry with cats.

Key words: alien species, competition, diet, *Felis catus*, feral cat, island fox, San Clemente Island, *Urocyon littoralis*

Alien species are now recognized as one of the greatest threats to global biodiversity (Vitousek et al. 1997; Wilcove et al. 1998). Among alien species, feral cats (*Felis catus*) are considered one of the most harmful invaders (Lowe et al. 2001). Cats have been introduced worldwide into a great number of continental and insular systems (Courchamp et al. 2003; Nogales et al. 2004). Feral cat predation has had widespread and detrimental effects on native fauna, especially on islands (Courchamp et al. 2003; Gaucel and Pontier 2005; Whittaker 1998). Feral cats consume a wide variety of insular fauna ranging from native arthropods, reptiles, and birds, to alien lagomorphs (Biro et al. 2005; Fitzgerald et al. 1991; Nogales and Medina 1996; Paltridge et al. 1997; Tidemann et al. 1994; Van Aarde 1980). Although the impacts from feral cat predation on native insular faunas have been demonstrated conclusively, the competitive effects from feral cats have not emerged. This is

likely due to several factors, including the rarity of native mammalian predators on oceanic islands (Alcover and McMinn 1994; Lawlor 1986) and the difficulty of detecting interspecific competition in natural systems (Connell 1983).

The fauna of the California Channel Islands, a continental archipelago, although depauperate relative to mainland California, is diverse compared to many oceanic archipelagos. Present are many vertebrate taxa often absent from oceanic islands, including mammalian carnivores. The island fox (*Urocyon littoralis*), a diminutive descendent of the gray fox (*U. cinereoargenteus*), is found on 6 of the 8 California Channel Islands (northern islands: San Miguel, Santa Cruz, and Santa Rosa; southern islands: San Clemente, San Nicolas, and Santa Catalina—Moore and Collins 1995), with each of the 6 islands having an endemic subspecies. Genetic analyses and archeological studies suggest that island foxes were introduced to the southern Channel Islands between 2,200 and 5,200 years ago by Native Americans (Collins 1991a, 1991b; Vellanoweth 1998; Wayne et al. 1991). Recently, many of the subpopulations of the island fox have experienced severe reductions in size (Coonan et al. 2005; Roemer et al. 2004). Factors causing declines in island fox subpopulations are varied. On Santa Catalina Island,

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canine distemper virus caused an estimated 95% decline in the fox population across 87% of the island from 1998 to 2000 (Timm et al. 2000). Hyperpredation by golden eagles (*Aquila chrysaetos*) is the probable cause of catastrophic declines of 3 subspecies of island fox on San Miguel Island, Santa Rosa Island, and Santa Cruz Island (Roemer et al. 2001, 2002), the latter facilitated by the presence of feral pigs (*Sus scrofa*), highlighting the importance of understanding the interactions of island foxes with alien species.

On San Clemente Island, island foxes (*U. l. clementae*) and feral cats have coexisted for more than 100 years (USFWS 1984). In communities of coevolved species, coexistence is facilitated by segregation along 1 or more niche axes (Pianka 1981). The most important niche dimensions in resource partitioning between species are habitat and food (Schoener 1974). Among sympatric carnivores, coexistence often is possible by utilization of different-sized prey, stemming from different predator body sizes (Gittleman 1985; Rosenzweig 1966). On San Clemente Island, foxes (males = 2.0 kg, females = 1.8 kg—Roemer et al. 2004) are, on average, considerably smaller than feral cats (males $\bar{X} = 3.1 \text{ kg} \pm 0.81 \text{ SD}$, $n = 180$; females $\bar{X} = 2.6 \pm 0.76 \text{ kg}$, $n = 98$ —R. B. Phillips, in litt.). Studies on the food habits of island foxes on other islands reveal a catholic diet of fruit, invertebrates, and various vertebrate prey (Collins 1980; Crooks and Van Vuren 1995; Laughrin 1977); however, analyses of feral cat diets globally suggest there is potential for overlap and interspecific competition for food resources (Pearre and Maass 1998). San Clemente Island provides an opportunity to examine potential competitive interactions between alien and native mammalian predators.

Laughrin (1973) speculated that feral cats are the principal competitors of island foxes on San Clemente Island. To date, negative impacts from feral cats on island foxes on San Clemente Island have not been documented, but are suspected (USFWS 1984). However, negative interactions in the past may have caused a decline in the fox population, and may presently be limiting their population size. With the current precarious status of many of the subpopulations of island foxes (listed as endangered on San Miguel, Santa Rosa, Santa Cruz, and Santa Catalina Islands and declining on San Clemente—Roemer and Wayne 2003; USFWS 2004), it is critical to understand their competitive interactions with feral cats. We examined the diet of sympatric feral cats and island foxes on San Clemente Island. We compared diets over multiple years, and in varying habitats and seasons, measuring the dietary breadth and level of overlap to assess the potential for resource competition between cats and foxes.

MATERIALS AND METHODS

Study area.—Our study area covered most of San Clemente Island, California (32°55'N, 118°30'W), the southernmost of the 8 Channel Islands and 4th largest. The island is located 102 km west-northwest of San Diego. It is approximately 33 km long, and 2.4–7.4 km wide, covering 146 km² (Olmstead 1958). A central plateau runs the length of the island, with the west and east sides marked by marine terraces and a steep

escarpment, respectively, both dissected by deep canyons. The maximum elevation is 599 m. The predominant habitats are grassland and maritime desert scrub, with woodland covering a smaller area (Philbrick and Haller 1977; Raven 1963). Grassland (Grass) is characterized by perennial and annual grasses, including purple needlegrass (*Nassella pulchra*), rip-gut brome (*Bromus diandrus*), and wild oats (*Avena fatua*), and several annual forbs. Maritime desert scrub (Scrub) is dominated by California boxthorn (*Lycium californicum*), and, to a lesser extent, golden snake cactus (*Bergerocactus emoryi*) and coastal prickly pear (*Opuntia littoralis*). Woodlands located in the canyon bottoms are characterized by lemonade berry (*Rhus integrifolia*), island cherry (*Prunus ilicifolia lyonii*), and island oaks (*Quercus tomentella*). Climate is maritime with mild winters (mean 14°C) and cool summers (mean 18°C—Jorgensen and Ferguson 1984). Annual precipitation averages from 13 to 20 cm across the island, mainly as winter (November–April) rains.

In addition to cats and foxes, the terrestrial vertebrate fauna of San Clemente Island includes endemic deer mice (*Peromyscus maniculatus clementis*), introduced black rats (*Rattus rattus*) and house mice (*Mus musculus*), island night lizards (*Xantusia riversiana*), and side-blotched lizards (*Uta stansburiana*). At least 248 bird species have been recorded on the island, with 31 breeding on the island (Jorgensen and Ferguson 1984).

Food habits.—Data on the diet of cats and foxes were obtained from 2 concurrent projects: a 2-year study on the effects of cats and foxes on the small mammal and lizard communities of San Clemente Island (Phillips 1999) and a 3-year predator-removal project to protect the San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*—Phillips and Schmidt 1996). We examined the diet of cats and foxes primarily by identifying prey items from the scats of cats and foxes, supplemented with cat colon contents when possible. For the purposes of data analysis we pooled scats and colon contents, and present both as feces. Scats were collected from the traps of live-captured animals and along trails. The contents of colons were collected from euthanized cats and road-killed foxes. Traps were baited with a meat mixture and dry cat food.

From 1992 through 1994, we regularly collected scats and colon contents. Although collections occurred throughout the year, all 12 months were not equally represented; however, sample sizes between the 2 seasons, wet (November–April) and dry (May–October), were similar. Scats from cats and foxes were distinguished on the basis of size, shape, odor, location, the presence of footprints, and manner of deposition (i.e., tendency for foxes to defecate in a prominent location versus cats' tendency to cover scats). Identifying characteristics were determined from scats of known origin; scats of uncertain origin always were excluded from analyses. We checked our ability to correctly distinguish between scats of cats and foxes in the field by comparing contents of cat scats (raw occurrences—see data analysis below) with the contents from cat colons using a chi-square test of independence ($\chi^2 = 4.79$, $df = 4$, $P = 0.309$). Too few fox colons were collected to perform a similar analysis. In addition to species of predator, we categorized feces based on year, season, and habitat.

Habitat groupings were Grass, Scrub, and Mixed, the latter comprising canyon bottoms and slopes, plus areas within 400 m of adjacent canyon rims.

All feces were frozen before analysis. We oven-dried the fecal material at 60°C for 24 h (Kelly 1991). To extract identifiable prey remains, we enclosed feces in a fine-weave nylon mesh bag and washed in an automatic washer (Johnson and Aldred 1982). We classified prey into 5 major categories: rodent, lizard, bird, arthropod, and plant (excluding nonnutritive materials such as grass and twigs—Fichter et al. 1955), using undigested materials (e.g., hair, feathers, bones, scales, teeth, exoskeletons, and seeds). We included remains of eggshells in the bird category. When possible, using voucher specimens or published keys (Glass 1951; Powell and Hogue 1979), we identified prey items to more detailed taxonomic levels. Rodents and lizards generally could be identified to species. We did not attempt to identify birds below class. Arthropods normally were identifiable to order and often family. Seeds and fruits were compared with those found on the island and normally were identifiable to species. To determine the minimum number of individuals for each animal prey category, we counted unique structures (e.g., maxillaries, feet, bird beaks, and cephalic capsules). For fruits, we used 2 methods to determine quantity eaten: counting intact skins or counting the number of seeds in feces. For common fruits we calculated the average number of seeds per fruit and determined number of fruits eaten based on quantity of seeds present. For example, feces with less than or equal to the mean number of seeds per fruit were scored with 1 fruit, whereas those with greater than, but not more than double the mean were scored as 2 fruits.

We represented the importance of a particular prey category by calculating the relative frequency of occurrence (number of times each prey item occurs/total number of occurrences of all prey items $\times 100$ —Kelly 1991) and the mean number of individuals per feces. We used frequency of occurrence for calculation of niche breadth and overlap (Reynolds and Aebischer 1991). We evaluated breadth using the standardized Levins index (B_{standard} —Colwell and Futuyma 1971). The Levins index formula is:

$$B = \left(\sum_{i=1}^n p_i^2 \right)^{-1},$$

where n is the number of prey categories and p is the proportion of records in each prey category (i). The standardized form of the formula is:

$$B_{\text{standard}} = (B - 1)/(B_{\text{max}} - 1),$$

where B is the Levins index of niche breadth and B_{max} is the total number of prey categories. B_{standard} values can range between 0 (minimum diet breadth) and 1 (maximum diet breadth). Dietary overlap was calculated using the Pianka index (O —Pianka 1973):

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

where p is the proportion of prey category i for species j and k . Values of O vary from 0 (no diet overlap) to 1 (complete diet

overlap). Diet breadth and overlap were assessed using the major prey categories. We conducted chi-square tests on the raw occurrence for the major prey categories to examine the effect of habitat, season, and year on cat and fox diets, and to compare the diets of cats and foxes overall. Significance of chi-square tests was based on a probability level of $P \leq 0.05$. Our research followed guidelines for capture, handling, and care of mammals as approved by the American Society of Mammalogists (Animal Care and Use Committee 1998) and was authorized by the Utah State University Institutional Animal Care and Use Committee, Approval No. 574.

RESULTS

Diet composition.—We collected and analyzed 602 feces from cats from 1992 to 1994. We identified 17 taxa of plants and animals in the diet (Table 1). Overall, cat diets were about equally divided between arthropods (47.9%) and vertebrates (44.2%). Within vertebrates, rodents were the principal dietary component (29.2%; Fig. 1), with house mice and deer mice predominant, occurring in 13.2% and 9.7% of feces, respectively. House mice also were eaten in greater quantity, with 2.1 individuals per feces on average compared with 1.4 individuals for deer mice. Black rats occurred in 4% of feces, with 1.0 individual per feces. Lizards frequently were found in cat feces (12.9%) and averaged 1.3 individuals per feces. Of the 2 species, island night lizards (4.4%) were eaten slightly more frequently than side-blotched lizards (3.0%), and 1.6 versus 1.2 individuals were eaten on average, respectively. Birds were the least important vertebrate prey, found in only 2.1% of feces and 1.0 individual per feces. We identified 8 categories of arthropod prey in the diet of cats (Table 1). Of these, Coleoptera (11.6%), Orthoptera (9.5%), and Formicidae (12.2%) occurred most frequently. Only the Formicidae and Coleoptera were eaten in large quantities, averaging 14.0 and 20.1 individuals per feces, respectively. Armadillidiidae (0.9%) and non-ant Hymenoptera (0.8%), although not eaten frequently, were numerous when taken, 6.8 and 14.0 individuals per feces, respectively. Dermaptera occurred in 4.7% of feces and averaged 4.9 individuals per feces. We found plants in cat feces at a frequency of 7.8%, but they occurred in trace amounts. There was no evidence of cat predation on foxes.

From 1993 to 1994, we collected and analyzed 958 feces from foxes, and identified 18 distinct plant and animal taxa in their diet (Table 1). Overall, arthropods (57.7%) were the most frequently occurring prey category in fox diets (Fig. 1). Vertebrates (21.6%) and plants (20.5%) were consumed in approximately equal proportions. Coleoptera (14.0%) and Orthoptera (12.3%) were the invertebrate prey most frequently consumed, followed by Dermaptera (7.7%) and Formicidae (6.8%). When eaten, Coleoptera were numerous, averaging 36.9 individuals per feces, whereas fewer individuals of Orthoptera (4.6) were consumed. Dermaptera and Formicidae were eaten in moderate abundance, 7.7 and 6.7 individuals per feces, respectively. As with cats, Armadillidiidae were not consumed frequently (3.7%), but an average of 19.9 individuals was found per feces. Of vertebrate prey, foxes ate rodents

TABLE 1.—Frequency of occurrence (%) of prey items and mean number (\bar{X}) of prey items per feces for feral cats and island foxes from 1992 to 1994 on San Clemente Island, California. Values in parentheses are total number of feces and n is number of feces containing a particular prey item.^a

| Taxa | 1992 | | | 1993 | | | | | | 1994 | | | | | |
|--------------------------|----------|------|-----------|-----------|------|-----------------|-----------|------|-----------|-----------|------|-----------|-----------|------|-----------|
| | Cat (71) | | | Cat (315) | | | Fox (476) | | | Cat (216) | | | Fox (482) | | |
| | n | % | \bar{X} | n | % | \bar{X} | n | % | \bar{X} | n | % | \bar{X} | n | % | \bar{X} |
| Rodents | | | | | | | | | | | | | | | |
| House mice | 29 | 8.6 | 2 | 188 | 13.1 | 2.1 | 160 | 7 | 1.4 | 140 | 15.1 | 2.1 | 146 | 6.8 | 1.5 |
| Deer mice | 44 | 13.1 | 1.5 | 158 | 11 | 1.4 | 111 | 4.9 | 1.2 | 60 | 6.5 | 1.3 | 33 | 1.5 | 1.1 |
| Black rats | 3 | 0.9 | 1 | 59 | 4.1 | 1 | 35 | 1.5 | 1 | 45 | 4.8 | 1 | 8 | 0.4 | 1 |
| Unknown rodents | 10 | 3 | 1 | 26 | 1.8 | 1.3 | 114 | 5 | 1.1 | 26 | 2.8 | 1.2 | 58 | 2.7 | 1 |
| Rodent subtotal | 86 | 25.6 | 1.6 | 431 | 30.1 | 1.6 | 420 | 18.4 | 1.2 | 271 | 29.2 | 1.7 | 245 | 11.5 | 1.3 |
| Lizards | | | | | | | | | | | | | | | |
| Side-blotched lizards | 13 | 3.9 | 1.5 | 49 | 3.4 | 1.2 | 10 | 0.4 | 1.2 | 19 | 2 | 1.1 | 40 | 1.9 | 1.1 |
| Island night lizards | 15 | 4.5 | 1.3 | 75 | 5.2 | 1.7 | 28 | 1.2 | 1.5 | 28 | 3 | 1.4 | 16 | 0.7 | 1 |
| Unknown lizards | 21 | 6.3 | 1 | 71 | 5 | 1 | 51 | 2.2 | 1 | 57 | 6.1 | 1 | 51 | 2.4 | 1 |
| Lizard subtotal | 49 | 14.6 | 1.2 | 195 | 13.6 | 1.3 | 89 | 3.9 | 1.2 | 104 | 11.2 | 1.1 | 107 | 5 | 1 |
| Birds | | | | | | | | | | | | | | | |
| Birds | 7 | 2.1 | 1 | 29 | 2 | 1 | 41 | 1.8 | 1 | 19 | 2 | 1 | 35 | 1.6 | 1 |
| Eggshells | | | | 1 | 0.1 | NA ^a | 4 | 0.2 | NA | | | | 8 | 0.4 | NA |
| Bird subtotal | 7 | 2.1 | 1 | 30 | 2.1 | 1 | 45 | 2 | 1 | 19 | 2 | 1 | 43 | 2 | 1 |
| Arthropods | | | | | | | | | | | | | | | |
| Decapoda, crab | | | | 1 | 0.1 | 1 | 31 | 1.4 | 1 | | | | 7 | 0.3 | 1 |
| Hymenoptera | 48 | 14.3 | 18 | 176 | 12.3 | 11.8 | 201 | 8.8 | 4.7 | 109 | 11.7 | 15.6 | 140 | 6.5 | 8.3 |
| Formicidae | 48 | 14.3 | 18 | 175 | 12.2 | 11.8 | 167 | 7.3 | 5.3 | 106 | 11.4 | 15.9 | 133 | 6.2 | 8.5 |
| Coleoptera | 62 | 18.5 | 19.9 | 131 | 9.1 | 14.9 | 179 | 7.8 | 10.6 | 121 | 13 | 25.7 | 437 | 20.4 | 47.7 |
| Orthoptera | 19 | 5.7 | 2.7 | 161 | 11.2 | 3.9 | 320 | 14 | 4.8 | 77 | 8.3 | 3 | 222 | 10.4 | 4.4 |
| Dermoptera | 33 | 9.8 | 5.1 | 36 | 2.5 | 2.9 | 101 | 4.4 | 3.2 | 58 | 6.3 | 6.1 | 235 | 11 | 9.7 |
| Isopoda, Armadillidiidae | 2 | 0.6 | 1 | 10 | 0.7 | 3 | 34 | 1.5 | 20.2 | 13 | 1.4 | 10.6 | 130 | 6.1 | 19.9 |
| Araneae | 3 | 0.9 | 1 | 28 | 2 | 1 | 149 | 6.5 | 1.4 | 8 | 0.9 | 1.1 | 23 | 1.1 | 1.4 |
| Unknown invertebrates | 14 | 4.2 | 1.1 | 90 | 6.3 | 2.3 | 130 | 5.7 | 1.7 | 73 | 7.9 | 3.3 | 181 | 8.5 | 25.1 |
| Arthropod subtotal | 182 | 54.2 | 12.9 | 638 | 44.6 | 7.9 | 1,156 | 50.6 | 5.1 | 471 | 50.1 | 12.3 | 1,377 | 64.4 | 22.2 |
| Plants | | | | | | | | | | | | | | | |
| Coastal prickly pear | 5 | 1.5 | 1 | 23 | 1.6 | 1 | 325 | 14.2 | 2.1 | 16 | 1.7 | 1 | 198 | 9.3 | 1.6 |
| Island nightshade | 5 | 1.5 | 1 | 56 | 3.9 | 1.1 | 96 | 4.2 | 47.6 | 33 | 3.6 | 1 | 137 | 6.4 | 1.6 |
| Sea fig | | | | 3 | 0.2 | 1 | 2 | 0.1 | 1 | 1 | 0.1 | 1 | 2 | 0.1 | 1 |
| Unknown plant, general | 2 | 0.6 | 1 | 56 | 3.9 | 1.4 | 116 | 5.1 | 1.1 | 11 | 1.2 | 1.4 | 25 | 1.2 | 1.2 |
| Unknown plant, species 1 | | | | | | | 33 | 1.4 | 1 | | | | | | |
| Plant subtotal | 12 | 3.6 | 1 | 138 | 9.6 | 1.2 | 572 | 25.1 | 9.5 | 61 | 6.6 | 1.1 | 362 | 16.9 | 1.6 |
| Other | | | | | | | | | | | | | | | |
| Human garbage | | | | | | | 1 | 0.0 | 1 | 2 | 0.2 | 1 | 5 | 0.2 | 1 |

^a NA = not available.

(15.2%) most frequently. Again, house mice (7.0%) were found more frequently than deer mice (3.3%), and black rats occurred in only 1.0% of feces. Foxes varied little in the average number of individual rodents consumed per feces, with 1.5, 1.2, and 1.0 house mice, deer mice, and black rats, respectively. Lizards (4.5%) were eaten one-third as frequently as rodents, with little difference between side-blotched lizards (1.1%) and island night lizards (1.0%), and, when taken, averaged 1.1 and 1.3 individuals per feces, respectively. Birds were relatively unimportant in the diet of foxes, occurring at a frequency of only 2.0% and averaging 1.0 individual per feces. Foxes frequently consumed prickly pear fruits (11.9%) and averaged 1.9 fruits per feces. The fruits of island nightshade (*Solanum clokeyi*—5.3%) were taken about half

as often as those of prickly pear, but averaged 20.6 fruits per feces. Sea fig (*Carpobrotus edulis*) fruits were a minor component in the diet of foxes, with a frequency of occurrence of 0.1% and 1.0 fruit per feces. We found no evidence of fox predation on cats.

Diet analysis and comparison.—There was no difference in the diet of cats between dry ($n = 283$) and wet ($n = 319$) seasons ($\chi^2 = 2.29$, $d.f. = 4$, $P = 0.683$). However, cats did consume prey in different proportions between years ($\chi^2 = 28.57$, $d.f. = 8$, $P < 0.001$; Table 1). This was primarily due to a reduction of arthropods in the diet in 1993, compared to 1992 and 1994. Cats consumed differing proportions of prey in different habitats ($\chi^2 = 119.97$, $d.f. = 8$, $P < 0.001$; Fig. 2a), with fewer rodents eaten in the Mixed habitat compared to

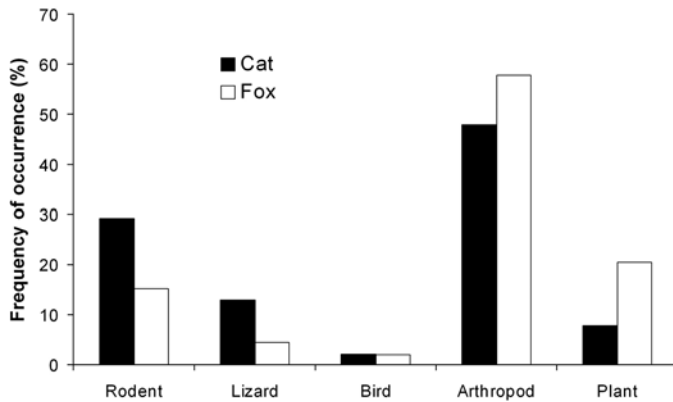


FIG. 1.—Frequency of occurrence of the primary prey categories in feces of feral cats and island foxes on San Clemente Island, California, from 1992 to 1994.

Grass and Scrub habitats. This was due largely to a reduction of house mice in the diet, which occurred at a frequency of 16.75% and 16.5% in the Grass and Scrub habitats, respectively, but only 5.9% in the Mixed. Conversely, the frequency of occurrence of deer mice in the cat diet remained constant across the 3 habitats, 9.9%, 9.7%, and 9.8%, respectively. Black rats also declined in the Mixed habitat, where they comprised 1.3% of the diet, compared to 5.7% in Grass and 4.7% in Scrub. The decline in rodent consumption by cats in Mixed habitat was accompanied by an increase in arthropod consumption (Fig. 2a). The overall increase was largely due to cats eating more Dermaptera, Coleoptera, and Formicidae.

The diet of foxes was similar between dry ($n = 568$) and wet ($n = 390$) seasons ($\chi^2 = 5.71$, $df. = 4$, $P = 0.222$). However, fox diet did vary between years ($\chi^2 = 98.86$, $df. = 4$, $P < 0.001$; Table 1). The proportion of rodents and plants consumed from 1993 to 1994 declined, whereas the proportion of arthropods increased. Fox diet also differed between the 3 habitats ($\chi^2 = 74.9$, $df. = 8$, $P < 0.001$; Fig. 2b). Foxes included more rodents in their diet in Grass habitat compared to Scrub, and ate fewer rodents in the Mixed habitat compared to Scrub. Foxes ate similar proportions of lizards in Grass and Mixed habitats, but in Scrub lizards were less important in the diet. Birds, although not consumed in great quantities overall, were eaten more frequently by foxes in Scrub and Mixed habitats. Foxes ate more arthropods in Mixed habitats compared to Grass and Scrub habitats, which contrasted with the consumption of plants where foxes included fewer plants in the diet in the Mixed habitat compared to the other 2 habitats.

Overall, the diet of cats and foxes differed considerably ($\chi^2 = 517.94$, $df. = 4$, $P < 0.001$), being similar only in their consumption of birds (Fig. 1). Rodents and lizards were both eaten at a higher frequency by cats than by foxes. In contrast, foxes relied more heavily on arthropods and plants. Despite the differences in the diets of cats and foxes, the niche overlap index revealed a high level of dietary overlap ($O = 0.93$). Diet breadth of cats was moderate ($B_{\text{standard}} = 0.49$), with that of foxes slightly lower ($B_{\text{standard}} = 0.37$).

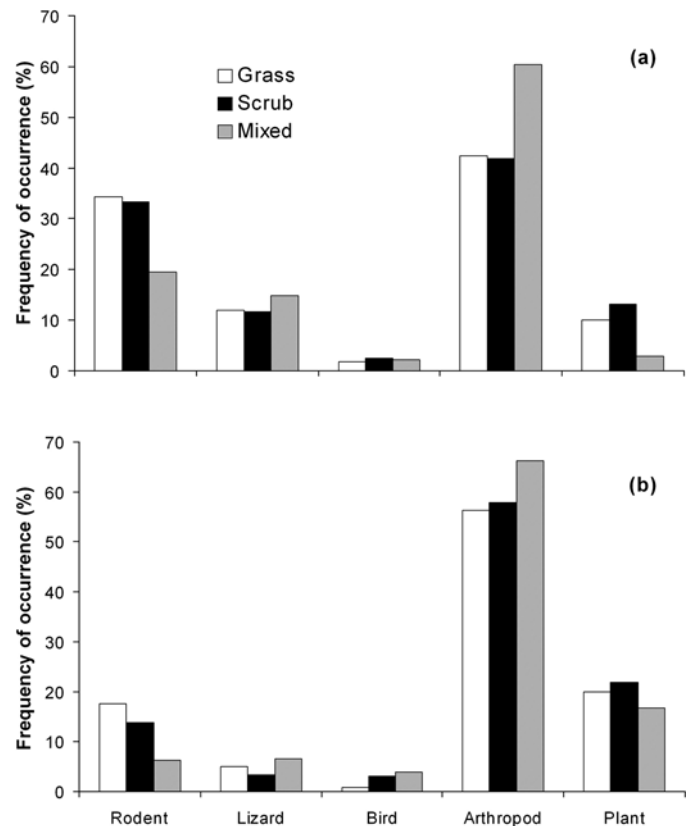


FIG. 2.—Frequency of occurrence of the primary prey categories in feces of a) feral cats and b) island foxes in 3 habitat types on San Clemente Island, California, from 1992 to 1994.

DISCUSSION

Feral cats and island foxes have diverse diets relative to the potential prey categories on San Clemente Island. Our analysis revealed that both cats and foxes are consuming all available classes of vertebrate prey, and virtually the same categories of arthropod prey. However, the latter relationship is likely as much a result of the low resolution of our analysis as it is the dietary preferences of the predators. That is, we only identified arthropod prey to order or family. Although plants occurred at a moderate frequency in the diet of cats, we only found trace amounts, suggesting they are not an important component. It is likely the plants (i.e., seeds) found in the feces of cats are incidental to the consumption of granivores (Sovada et al. 2001). Overall, cats had a slightly higher dietary breadth than foxes, due primarily to reliance of foxes on 1 prey category, arthropods. Cats more evenly distributed their consumption between vertebrate and arthropod prey. More importantly, diets of cats and foxes overlapped almost completely.

Ecological theory predicts that food is a more difficult resource to divide between competing species than is either space or behavior (Tilman and Lehman 2002). Competition between species normally results in a shift in foraging behavior or habitat preference before a change in diet breadth (Hespenheide 1975). On San Clemente Island, cats and foxes each occupy all available habitats (Laughrin 1977; Phillips and

Schmidt 1996). Diel activity patterns of foxes on San Clemente Island are consistent with those on other islands: primarily nocturnal and crepuscular, but often becoming diurnal during periods of cooler temperatures (Fausett 1982; Laughrin 1977). Conversely, cats on San Clemente Island are primarily nocturnal throughout the year (R. B. Phillips, in litt.). Differences in body size of sympatric carnivores often allow species to partition prey by size, and thereby coexist (Gittleman 1985; Rosenzweig 1966). In Florida, bobcats (*Lynx rufus*) and recently colonizing coyotes (*Canis latrans*) are sympatric, and overlap in diet (Thornton et al. 2004). Coexistence between bobcats and the one-third larger coyotes is facilitated by each predator relying on different-sized prey. Although foxes on San Clemente Island are about two-thirds the size of cats, the only evidence of body size contributing to dietary partitioning is with black rats. Black rats are 10 and 7 times larger, respectively, than house and deer mice on San Clemente Island (R. B. Phillips, in litt.), and cats take considerably more black rats than foxes (4.0% versus 1.0%, respectively). The absence of large-sized prey from San Clemente Island, such as European rabbits (*Oryctolagus cuniculus*), appears to prevent cats and foxes from partitioning food resources by size.

Despite the extensive dietary overlap and the narrow range of prey sizes, cats and foxes on San Clemente Island appear to coexist by dividing their most common prey between taxa: compared to foxes, cats rely more heavily on vertebrate prey, primarily rodents, followed by lizards. This is consistent with diets of feral cats elsewhere (Nogales and Medina 1996; Paltridge et al. 1997; Pearre and Maass 1998), suggesting that cats on San Clemente Island have not shifted their dietary preferences in the presence of foxes. Although, sample sizes were limited, a study of feral cats on Santa Catalina Island, where island foxes also occur (Lonquich 1979), revealed a similar dietary pattern. Vertebrate prey was most important in the diet of cats on Santa Catalina Island, followed by invertebrates. Of vertebrates, rodents ranked highest, occurring at a frequency of 41%, with reptiles and birds at 23% and 22%, respectively.

In contrast to cats, the predominant prey item of foxes on San Clemente Island was arthropods, with plants and vertebrates of equal, but secondary importance. Comparison of the diets of island foxes on several Channel Islands reveals considerable variation, and illustrates the possible dietary interactions of foxes with sympatric carnivores. For example, on San Miguel Island, where foxes are the only mammalian predator, plants were the most frequent and abundant food item, with sea fig (*Carpobrotus aequilaterus*) found in 96% of fox scats (Collins 1980). In our study, foxes consumed plants at a frequency of 20.5% and sea fig at only 0.1%. Foxes on San Miguel Island frequently ate insects, but this category was dominated by 1 species, Jerusalem crickets (*Stenopelmatus fuscus*—Collins 1980), which are absent from San Clemente Island. Jerusalem crickets are large (50 mm) and available in all seasons, providing a rich and reliable food source for foxes on San Miguel Island. Black rats and deer mice were the only small mammals present on San Miguel Island, although neither was significant in the diet of foxes: black rats were not eaten

and deer mice were only important during winter. On Santa Cruz Island, where feral cats are absent, foxes occur with another carnivore, the smaller (males = 620 g, females = 500 g—Crooks 1994) island spotted skunk (*Spilogale gracilis amphialus*). Dietary overlap between foxes and skunks on Santa Cruz Island is similar to that of fox and cat overlap on San Clemente Island. Cats and skunks rely more heavily on vertebrate and invertebrate prey, whereas foxes on both islands are more omnivorous (Crooks and Van Vuren 1995). Whether in sympatry with the smaller skunk, sharing a long period of coevolution, or with the larger recently introduced feral cat, or as the sole mammalian predator on an island, foxes maintain an omnivorous diet, primarily of arthropods and plants.

Thus, our results suggest that cats on San Clemente Island have not caused a dietary shift in foxes. Nevertheless, we do not know if cats have impacted the fox population in the past, or that cats do not have the potential to do so in the future. Wiens (1977) emphasized that competitive effects may be transient. Niche overlap can be high when resources are abundant (Cody and Diamond 1975; Schoener 1982), with negative effects manifesting as resources become scarce. We noticed considerable year-to-year variation in the diets of cats and foxes in this study, and a previous study indicated that the population of house mice on San Clemente Island exhibited dramatic seasonal and annual fluctuations (Phillips 1999). The latter study also illustrated complex temporal and spatial relationships between cat and fox predation and the house mice population. Further, availability of vertebrate prey may be seasonally important to foxes and critical to survival of young, because it appears adult foxes provision dependent young with mice and birds (Garcelon et al. 1999).

Competition between species is often asymmetric, with 1 species the stronger competitor (Connell 1983). On San Clemente Island, it is unclear whether cats or foxes are the stronger competitor; however, several factors suggest cats may have a competitive advantage over foxes. A generalist species, with a broad niche, may outcompete a specialist when their niches overlap (MacArthur and Levins 1964). Our results revealed considerable overlap in cat and fox diets and indicated that cats had greater dietary breadth than foxes. Species density also can affect competitive interactions, with a more abundant competitive subordinate suppressing a rarer competitive dominant (Brown and Munger 1985; Crowell and Pimm 1976). In the mid-1990s, cat and fox populations were roughly equal, with cats numbering approximately 700 individuals and foxes fluctuating between 600 and 800 (Phillips and Schmidt 1996; Roemer et al. 1994). Approximately 10 years later, the fox population had declined by almost 50% (Roemer et al. 2004). Thus, a diminished fox population may convey an advantage to a normally competitive equal or subordinate feral cat.

Although competitive impacts of cats on foxes were not evident during our study, we expect that interspecific interactions may change under different climatic conditions (e.g., El Niño—La Niña), with the advantage likely going to feral cats with their greater dietary breadth. Additionally, anthropogenic factors—decades of impact from feral ungulates and their recent eradication (Courchamp et al. 2003)—may

have unsuspected positive or negative effects on the plant and animal communities of the island (Parkes et al. 2006; Zavaleta et al. 2001). To more fully understand the competitive interactions between cats and foxes will require examining their dynamics over a longer period and during varying environmental conditions. Given the current status of “vulnerable” of island fox populations on not only San Clemente Island, but on most of the Channel Islands (Coonan et al. 2005; Roemer and Wayne 2003; Roemer et al. 2004), it is critical to examine and understand factors potentially detrimental to their survival.

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