

DIETS OF SYMPATRIC POPULATIONS OF AMERICAN MARTENS (*MARTES AMERICANA*) AND FISHERS (*MARTES PENNANTI*) IN CALIFORNIA

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American martens (*Martes americana*) and fishers (*M. pennanti*) occur together in mixed-conifer forests of the southern Sierra Nevada. We studied their diets in the area of sympatry by examining their feces and comparing diet diversity and overlap. Diets of both species were more diverse than previously reported in North America. Although the diet of fishers appeared to include more remains of birds, lizards, hypogeous fungi, and insects than that of martens, the rank contribution of prey items to the diets did not differ and the Pianka index of dietary overlap was high. The great diversity of diets of fishers and martens may be due to the absence or rarity of large prey (e.g., snowshoe hares [*Lepus americanus*] and porcupines [*Erethizon dorsatum*]) or to a greater diversity of available prey types in the southern Sierra Nevada compared to other study sites for *Martes* in North America. The high degree of overlap in diets is surprising given the body size differences between martens and fishers, previously described differences in their diets, and similar use of other niche dimensions. The similarity is probably due, in part, to the relatively large pool of diverse and available resources that are exploited by both species by using similar modes of foraging. In addition, our sample of martens was drawn from the lowest margin of their elevational range in the southern Sierra; a more comprehensive survey of the diets of martens at higher elevations may yield different results.

Key words: diet, feces, fisher, food habits, foraging, marten, *Martes americana*, *Martes pennanti*, Sierra Nevada

The American marten (*Martes americana*) is a forest-dwelling mustelid that occurs throughout boreal North America, reaching its southernmost extent in the Sierra Nevada of California and the southern Rocky Mountains of New Mexico (Gibilisco 1994). Diets of the American marten (hereafter, marten) have been previously described at various locations throughout its range (Buskirk and Ruggiero 1994; Martin 1994; Powell et al. 2003), including California (Martin 1987; Zielinski et al. 1983). Small mammals, particularly voles (*Clethrionomys*, *Microtus*, and *Phenacomys*), were the dominant prey, but seasonal food ranged from lagomorphs to fruits (Buskirk and Ruggiero 1994; Martin 1994). Most previous research on the diet of the American marten has been conducted within the central regions of its historical range. Populations at the periphery of the geographic range often encounter environmental conditions that differ from those in the center of the range, including availability of potential prey and foraging conditions (Hoffman and Blows 1994). Thus, it is

of interest to determine whether the diet of martens at the extreme southern margin of the range differs from the diet reported elsewhere.

The congeneric fisher (*M. pennanti*) also occurs at the southern margin of its range in the southern Sierra Nevada (Gibilisco 1994), and previous work revealed that its diet at this location was substantially different than that described farther north (Zielinski et al. 1999). Several authors have noted inverse relationships between marten and fisher fur harvests in a region (de Vos 1952; Douglas and Strickland 1987; Hardy 1907; Krohn et al. 1995). Strickland and Douglas (1987) proposed that this disparity in captures was due to differences in habitat use or to interactions between fishers and martens. Some have proposed that martens and fishers may compete directly for food or space (Clem 1977; de Vos 1952; Grinnell et al. 1937; Raine 1987). In the upper midwestern United States, martens and fishers are sympatric at a regional level, but individual martens and fishers use different habitats at smaller scales (Raine 1983; Thomasma 1996). In the western United States, martens and fishers have parapatric distributions, with martens typically occurring at higher elevations in conifer forests and fishers occurring at slightly lower elevations in mixed conifer-hardwood forests (Gibilisco 1994; Kucera et al. 1995; Zielinski et al. 1995, 1997). The lower margin of the elevational range at

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which martens occur in the southern Sierra Nevada appears to be less characteristic of marten habitat elsewhere in the western United States. Here, martens occur below the true fir (*Abies*) zone and have been detected in a number of nonconiferous vegetation types, resulting in a substantial area of sympatry with fishers (W. J. Zielinski, in litt.).

Diet is a niche dimension for which resource use by 2 species can differ. In North America, fisher diets generally are more diverse than those of martens and tend to include larger prey items (Martin 1994). Fisher diets regularly include prey species that are less common in marten diets, such as snowshoe hares (*Lepus americanus*), porcupines (*Erethizon dorsatum*), and gray squirrels (*Sciurus*—Martin 1994). Interestingly, fishers in the southern Sierra Nevada occur in an area where snowshoe hares are absent, other leporids were not significant food items, and porcupines are uncommon. Consequently, the fisher diet in the southern Sierra Nevada is characterized by its taxonomic diversity and the importance of relatively small prey species (Zielinski et al. 1999). Thus, in addition to spatial overlap in distributions of martens and fishers in the southern Sierra, the absence of larger prey that fishers typically include in their diet leads to the expectation that diets of the 2 species may be similar. The only other studies to report the diet of these 2 species in sympatry were that of Clem (1977), which was based on the stomach contents of trapped animals, and Raine (1987), who interpreted only the winter diet.

We report the diet of martens in the southern Sierra Nevada at a location where they are sympatric with a population of fishers whose diet already has been described (Zielinski et al. 1999). We compare the new data from martens with previously published data from fishers with the expectations that the diet of each species would be more diverse than their northern and less-peripheral populations, and that spatial overlap and absence of larger prey items would result in diets that are more similar than previously described for martens and fishers.

MATERIALS AND METHODS

Study area.—Our 250-km² study area was located in Tulare County, California, on the Middle Fork of the Tule River on land administered primarily by the Tule River Ranger District of the Sequoia National Forest, Mountain Home Demonstration State Forest (California Department of Forestry and Fire Protection), and the Tule River Indian Reservation. Elevations range from 700 to >3,000 m at the crest of the Sierra Nevada. The closest reporting weather station for temperature and precipitation was at Grant Grove in Sequoia-Kings Canyon National Park (approximately 2,000 m; 40 km away); information was available for the period 1971–2000 (National Oceanic and Atmospheric Administration, www.ncdc.noaa.gov/oa/climate/online/coop.precip.html, accessed 8 March 2004). Mean minimum and maximum temperatures over this period for winter (1 November–30 April) were -1.7°C and 7.0°C , respectively, and for summer (1 May–31 October) were 7.9°C and 18.8°C , respectively. Mean annual precipitation was 106.8 cm. Mean snow depth on 1 April (1971–2000) at Mountain Home Demonstration State Forest headquarters (approximately 2,000 m) was 36.3 cm (California Department of Water Resources, <http://cdec.water.ca.gov/snow/>, accessed 8 March 2004).

Plant communities ranged from mixed chaparral (e.g., *Adenostema*, *Cercocarpus*, *Arctostaphylos*, and *Ceanothus*) in the xeric, lower

elevations to true fir (*Abies concolor* and *A. magnifica*) forests and wet meadows at higher elevations. With increasing elevation and moisture, the chaparral community was replaced by montane hardwood forest, and then ponderosa pine (*Pinus ponderosa*) and mixed-conifer forest. The latter was characterized by a dense canopy, an overstory composed of several conifer species, and an often dense understory of black oak (*Quercus kelloggii*) and shade-tolerant conifers. Timber harvest has been primarily by individual selection of the largest-diameter trees, particularly pines. Clear-cutting is not a common practice in the southern portion of the Sierra Nevada (McKelvey and Johnston 1992).

Fecal collection.—We examined the diet of martens and fishers by identifying food items from feces collected as part of a 3-year study that focused on the habitat ecology of fishers and martens in the southern Sierra Nevada of California. Feces came from 4 sources: livetraps where martens and fishers were confined, captured animals that were immobilized for radiocollaring, track-plate detection stations (Zielinski 1995), and rest sites used by radiocollared individuals. Most feces from rest sites were collected within a few days of a radiocollared animal having used the site. Feces were stored frozen before analysis. Processed chicken parts were used as bait in traps, so remains of prey in feces were not confused with remains of trap bait.

Fecal analysis.—Methods for preparing marten feces for analysis were identical to those used in a previous study of diet of fishers (Zielinski et al. 1999). We measured volume of each fecal sample by the water it displaced in a graduated cylinder. We then collected and set aside a small portion from each sample for subsequent analysis for fungal material, due to previous documentation of hypogeous fungi (false truffles) in the stomach of fishers (Grenfell and Fasensfest 1979). These samples were stored in ethyl alcohol and 34 were examined by a technician capable of detecting and identifying fungal spores to genus. Three subsamples were collected from each sample. Each was stirred thoroughly, a drop of Melzers reagent was added, and 0.08 ml was placed on a slide for examination at 400 \times . Twenty-five randomly selected fields of view were selected for analysis from each of the 3 subsamples (75 views/sample total). The area of the view occupied by fungal spores was assigned 1 of 5 classes (0–5%, 6–25%, 26–50%, 51–75%, and 76–95%). Mean area index was calculated for the 25 fields of view, resulting in an index of fungal occurrence for each sample. Spores were identified by using a combination of reference slides and a key (Castellano et al. 1989).

We removed hair, bone, claws, feathers, and other hard parts from the fecal sample for identification. Two techniques have been used to extract remains from feces: use of an automatic washer (Johnson and Aldred 1982) and drier, and lipid extraction (Horwitz 1980). The washing technique (which removed 21.6% of feces from the hard parts) was found to be more efficient than lipid extraction (which removed 2.8% of feces—Gamberg and Atkinson 1988). We modified the washer–drier technique by enclosing fecal samples in a fine-weave nylon mesh bag, soaking samples overnight in soapy tap water, and agitating them by hand for 10 min. Residual fecal matrix was removed by placing the sample on a 500- μm sieve under a stream of tap water.

After a fecal sample was washed, all distinguishable macroscopic components were identified to the finest taxonomic level possible based on available literature and comparison with a voucher collection of hair, scales (for reptiles), and skeletons. A single observer identified remains in all feces (Spaulding et al. 2000). All vertebrate remains were assumed to be from species reported to occur in the study area (Ingles 1965; Jameson and Peters 1988; Stebbins 1966). After preliminary identification of skeletal remains by using published keys (Glass 1951; Ingles 1965; Lawlor 1979), we compared all skeletal material to reference skeletons from the American Museum of Natural History (New York). Because skeletal remains were fragmentary, and

identifications made to genus or species based on hard parts only were usually made from teeth, claws, or both, considerable effort was made to identify individual guard hairs. We identified guard hairs by using keys to cuticle scale and medulla patterns (Adorjan and Kolenosky 1969; Mayer 1952; Moore et al. 1974). A voucher collection of hair from various body locations of each species of mammal that occurred in the study area was created by collecting hair from prepared mammal skins and scales from reptiles preserved in alcohol. We made no attempt to identify birds more specifically than to class. Plant material composed of seeds or fruit was compared with a collection of seeds gathered in the study area and by use of a key (Schopmeyer 1974). All other plant material was identified simply as "plant material." We did not distinguish the life stages (i.e., larva, pupa, or adult) of insect remains.

We represented the contribution of a particular food item in the diet by reporting the percentage of feces in which the item was found. This technique is similar to reports of "percent of scats" or "percent occurrence" (Kelly 1991; Martin 1994; Powell et al. 1997). Although it is preferable to estimate the original biomass of prey represented by fecal remains (e.g., Cumberland et al. 2001), this requires the ability to estimate the volumetric proportion of each food item in the feces and data from feeding trials to develop correction factors for the relative digestibility of items (Kelly 1991; Reynolds and Aebischer 1991; Zielinski 1986). We found it extremely difficult to estimate relative proportion by volume of each item in a fecal sample because remains varied in their detectability and identifiability, ranging from impossible-to-identify underfur hairs of mammals to distinctive seeds and mammal teeth; and because uncertainty that unidentifiable remains represented the same categories of foods as identifiable remains (Reynolds and Aebischer 1991). Due to unknown digestibilities of different foods that are eaten, our use of percentage of feces as our index of marten diet precludes us from quantitative comparisons of the relative importance of food items. This method overestimates the importance of small prey and underestimates the importance of large prey in the diet (Floyd et al. 1978; Lockie 1959; Zielinski 1986). However, percentage of feces is a basic measure of how common a food item is in the diet (Kelly 1991) and is comparable with techniques used in most other studies of the diet of martens and fishers.

Most fecal samples (approximately 75% for both species) were collected during the snow-free period of the year. We did not deem the sample of marten feces sufficient to warrant analysis by season, although such an analysis was conducted on the fisher sample that we used for comparison (Zielinski et al. 1999).

Species comparisons.—Dietary differences were evaluated by using a 2-tailed Mann-Whitney *U*-test. We compared diets at a low taxonomic resolution involving 5 categories (i.e., mammals, birds, reptiles, insects, and plants) and then compared diets at a higher taxonomic resolution involving 20 categories (i.e., Insectivora, Lagomorpha, Sciuridae, Geomyidae, Cricetidae, Artiodactyla, Aves, Iguanidae, Anguillidae, Squamata [Serpentes], Hymenoptera, Orthoptera, Coleoptera, unknown insect, Ericaceae, Grossulariaceae, Rosaceae, Rhamnaceae, Fagaceae, and Pinaceae). We also compared diets by calculating trophic niche breadths and dietary overlap. Breadth was evaluated by using the standardized Levins index (B_{standard} —Colwell and Futuyma 1971) and overlap was evaluated by using the Pianka index (O —Pianka 1973), similar to that conducted by Serafini and Lovari (1993). The Levins index formula is

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

where n is the number of food categories and p is the proportion of records in each food category (i). A food category was any taxon that

TABLE 1.—Distribution of marten ($n = 150$) feces by season and location of collection. All feces were collected from 1994 to 1996 in the Sequoia National Forest, Tulare County, California.

| | Marten | |
|-----------------------------------|----------|------|
| | <i>n</i> | % |
| Season | | |
| Spring (20 March–20 June) | 42 | 28.0 |
| Summer (21 June–21 September) | 53 | 35.3 |
| Autumn (22 September–20 December) | 43 | 28.7 |
| Winter (21 December–19 March) | 12 | 8.0 |
| Location type | | |
| From trap at capture | 66 | 44.0 |
| During immobilization | 16 | 10.7 |
| Track plate | 26 | 17.3 |
| Rest site | 42 | 28.0 |

could be distinguished in the feces of either species. For some categories, this taxon was the species level (e.g., *Tamiasciurus douglasii* and *Rubus parviflorus*) and higher taxonomic levels (e.g., Cichindellidae, *Sorex*, and *Ribes*) were used for others. The standardized form of the formula is $B_{\text{standard}} = (B - 1)/(B_{\text{max}} - 1)$, which results in breadths that range from 0 to 1. The Pianka index is

$$O_{jk} = \sum_{i=1}^n p_{ij} p_{ik} / \sqrt{\left(\sum_{i=1}^n p_{ij}^2 \sum_{i=1}^n p_{ik}^2 \right)}$$

where p_{ij} (or p_{ik}) is the proportion of food category i recorded in diet of the species j (or k). All analysis is based on the total annual collection of feces for each species.

Martin (1994) compared the diversity of diets of martens and fishers by using the Shannon diversity index (H'). We also calculated H' for the diet of each species to compare the diversity of diets of martens and fishers in the southern Sierra with Martin's results. For this purpose only, we followed Martin's method of representing the following categories as single items: birds, insects, and plants.

RESULTS

We analyzed 150 marten feces contributed by 32 individual martens (25 males and 7 females). Thirty-seven of the feces were from females, 87 were from males, and 26 were from unknown sex. Most feces were collected from trapped animals during summer (Table 1). Thirty-four distinguishable taxa of animals and plants were identified in the marten feces, and no single family of animal or plant was represented by more than 24% of the feces (Sciuridae was the most common family).

Of the major taxonomic groups, the remains from mammals were most common, followed by insects and plants (primarily fruits; Fig. 1; Table 2). The most frequently encountered mammal remains were from rodents, of which most were ground-dwelling (*Spermophilus beecheyi* and *Tamias*) and tree-dwelling (*Tamiasciurus douglasii* and *Sciurus griseus*) sciurids and cricetids. Birds were relatively common prey but could not be identified to species.

Especially noteworthy in the marten diet was the preponderance of insect and plant remains. Bees and wasps (Vespididae and Eumenidae) composed the majority of insect remains and most were collected from summer and autumn

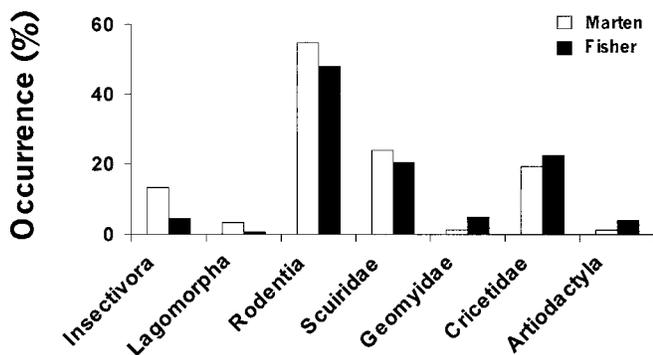
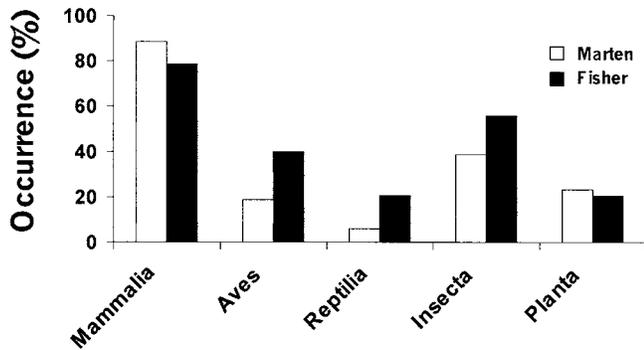


FIG. 1.—Comparison of diets of the marten and fisher in the southern Sierra Nevada, California, on the basis of percentage of feces in which the item occurred. Primary food groups (a) are distinguished from groups within Mammalia (b). Fisher data are from Zielinski et al. (1999).

feces. Cricket and grasshopper (Orthoptera) remains occurred in almost 10% of the samples. Most plant remains were seeds of common fruit-bearing shrubs, such as *Ribes* and *Pinus*. Almost one-half of the samples selected for fungal analysis contained spores of hypogeous fungi, representing 5 taxa, and about one-third of the 75 views/sample contained fungal spores (Table 3). *Melanogaster* was the most common genus, occurring in 41.2% of the samples where spores were found (Table 3).

Comparison of marten and fisher diets.—Comparisons of the marten data reported here with the fisher data reported previously (Zielinski et al. 1999) indicated that both species included foods in their diet from each of the major taxonomic classes (Fig. 1). No difference was found in the rank order of importance of the 5 major (Mann–Whitney $U = 13$, $P > 0.05$) or the 20 minor (Mann–Whitney $U = 242$, $P > 0.05$) food categories. Furthermore, neither Levin’s trophic niche breadth (marten: $B_{\text{standard}} = 0.36$; fisher: $B_{\text{standard}} = 0.39$) nor Pianka’s index of dietary overlap ($O = 0.875$) indicated differences in the composition of the diet or the importance of any of the

TABLE 2.—Distribution of food types as determined from marten feces shown as number of items and percentage of totals. Feces were collected from 1994 to 1996 in the Sequoia National Forest, Tulare County, California.

| Taxa | Total marten ($n = 150$) | |
|--|----------------------------|------|
| | <i>n</i> | % |
| Mammalia | | |
| Insectivora | | |
| Talpidae, <i>Scapanus latimanus</i> | 10 | 6.7 |
| Soricidae, <i>Sorex</i> | 10 | 6.7 |
| Lagomorpha | | |
| Leporidae, <i>Lepus</i> or <i>Sylvilagus</i> | 5 | 3.3 |
| Rodentia | | |
| Scuriidae | | |
| <i>Spermophilus beecheyi</i> | 10 | 6.7 |
| <i>Sciurus griseus</i> | 3 | 2.0 |
| <i>Tamiasciurus douglasii</i> | 8 | 5.3 |
| <i>Tamias</i> | 12 | 8.0 |
| Geomyidae, <i>Thomomys bottae</i> | 2 | 1.3 |
| Cricetidae | 29 | 19.3 |
| <i>Peromyscus</i> | 15 | 10.0 |
| <i>Microtus</i> | 10 | 6.7 |
| Other | 4 | 2.6 |
| Carnivora, Mustelidae, <i>Martes</i> | 37 | 24.7 |
| Artiodactyla, Cervidae, <i>Odocoileus hemionus</i> | 2 | 1.3 |
| Aves | 28 | 18.7 |
| Reptilia | | |
| Squamata, Iguanidae, <i>Sceloporus</i> | 2 | 1.3 |
| Squamata, Anguillidae, <i>Elgaria</i> | 7 | 4.7 |
| Insecta | | |
| Orthoptera | 14 | 9.3 |
| Coleoptera | 9 | 6.0 |
| Buprestidae | 2 | 1.3 |
| Elateridae | 1 | 0.7 |
| Hymenoptera | 34 | 22.7 |
| Vespidae or Eumenidae | 31 | 20.7 |
| Formicidae | 2 | 1.3 |
| Planta | | |
| Ericaceae, <i>Arctostaphylos</i> | 4 | 2.7 |
| Grossulariaceae, <i>Ribes</i> | 10 | 6.7 |
| Caprifoliaceae, <i>Sambucus</i> | 1 | 0.6 |
| Rosaceae, <i>Rubus parviflorus</i> | 1 | 0.6 |
| Rosaceae, <i>Prunus emarginata</i> | 1 | 0.6 |
| Rhamnaceae, <i>Rhamnus</i> | 3 | 2.0 |
| Fagaceae, <i>Quercus</i> | 1 | 0.6 |
| Pinaceae, <i>Pinus</i> | 11 | 7.3 |
| Woody debris | 35 | 23.3 |
| Rock | 3 | 2.0 |
| Eggshell | 8 | 5.3 |
| Termite frass | 3 | 7.1 |

identifiable remains. H' of the marten diet was 2.84, compared to 3.16 for the sample of the fisher diet.

The above comparisons use relatively crude metrics and closer examination reveals some potentially noteworthy contrasts. In particular, reptile and bird remains were more prevalent in the fisher diet (20.4% and 39.8%, respectively) than in the marten diet (6.0% and 18.7%, respectively). The higher incidence of lizards and birds in the fisher diet probably

accounts for the lower percentage of the fisher diet that was composed of mammals (78.6%) when compared to that of martens (88.7%). Furthermore, fisher diets had a higher occurrence of insects than did marten diets (55.7% versus 38.7%), whereas martens had a higher occurrence of fruit (21.1% compared to 9.0%). Fishers also had a substantially higher proportion of fecal samples with truffle spores (91.7% compared to 44.1%), a difference that was statistically significant ($Z = 3.90$, $P < 0.05$). Finally, fisher diets included the remains of other carnivores (1 occurrence each of *Mustela* and *Spilogale gracilis*), whereas remains of other carnivores were not discovered in marten feces. All hair of *Martes* found in feces was assumed to have originated from grooming. Overall, no indication was found that fishers, despite their size advantage over martens, consumed substantially larger prey species.

DISCUSSION

Fishers and martens have diverse and similar diets where they occur sympatrically in the southern Sierra Nevada. Our results confirm the predictions that the diets would be similar and more diverse than diets reported in the northern portions of the geographic ranges of these species. In a review of the diversity of diets of fishers and martens in North America, Martin (1994) reported values of the H' that varied from 0.4 to 1.14 for martens and from 0.5 to 1.1 for fishers. Our values are more than twice the maximum for each species. In 13 previous studies, the total number of identifiable food items ranged from 5 to 18 (Martin 1994), whereas fishers in our study had remains of 23 identifiable items. Some of the difference may be due to a disparity among studies in the level of taxonomic resolution to which individual items were identified, or to differences in sample sizes, but we believe these differences do not explain the diversity in diets we report. Our results also were consistent with Martin's (1994) observation that diet diversities for martens were greatest in the Pacific states (no previous studies of the diet of fishers in the Pacific states were available for comparison). No previous values of niche breadth have been published for North American *Martes*, but our niche breadth values for American martens (0.36) and fishers (0.39) were similar to those reported for Eurasian martens ($\bar{X} = 0.47$ for pine marten [*M. martes*]; $\bar{X} = 0.42$ for stone marten [*M. foina*]—Clevenger 1994).

The great range of prey in the diet of each species may be explained by the low occurrence of relatively large prey (e.g., lagomorphs and porcupines [*E. dorsatum*]) in the diet of either species in the southern Sierra Nevada. Our study area is outside the geographic range of snowshoe hares (*L. americanus*), other lagomorphs are uncommon in the diets, and porcupines have not been reported recently in the study area. A negative relationship between diet diversity and the incidence of large prey in the diet has been reported previously for both species (Martin 1994; but see Clevenger [1994] for contrary results for Eurasian *Martes*).

An alternative, and compelling, explanation for the variety of foods in the diet of both species is the variety of food items available in the southern Sierra Nevada. The Sierra Nevada hosts a great diversity of plant and animal communities

TABLE 3.—Hypogeous fungal spores found in marten and fisher feces collected from 1994 to 1996 in the Sequoia National Forest, Tulare County, California. Index of fungal occurrence refers to the proportion of 75 microscopic fields of view (3 fecal subsamples \times 25 views each) in which the species was identified. Fisher data are from Zielinski et al. (1999).

| | Marten | Fisher |
|----------------------------|--------|--------|
| Number of samples | 34 | 24 |
| Samples with spores (%) | 44.1 | 91.7 |
| Index of fungal occurrence | 36.4 | 79.1 |
| Number of fungal taxa | 5 | >7 |
| Genera represented (%) | | |
| <i>Melanogaster</i> | 41.2 | 79.2 |
| <i>Rhizopogon</i> | 2.9 | 25.0 |
| <i>Gautieria</i> | 8.9 | 4.2 |

(Ricketts et al. 1999), probably more than many of the boreal locations where fishers and martens have been previously studied. In our view, this is a more appealing explanation for the diet diversity than the theoretical prediction that diverse diets should occur where the absolute abundance of food is low (Schoener 1974). However, we also attribute some of the diversity of the marten diet, in particular, to the relatively low proportion (6.7%) of microtine rodents in their diet. Microtines are a favorite prey group elsewhere in the Pacific states (Bull 2000; Zielinski et al. 1983) and North America (Martin 1994) and the low incidence of this favored prey item may have made it necessary for martens to diversify their diet.

Not only were marten and fisher diets extremely diverse, the diets of the 2 species were not substantially different. Although we predicted this result, it is at variance with previous descriptions of the diets (Martin 1994) and appears to be at odds with the prediction that competition among species within the Mustelidae should be greatest within *Martes* and *Mustela* (Powell and Zielinski 1983). Sympatry among related mustelids previously has been explained in terms of body-size differences to reduce competition for food (Erlinge 1986; King and Moors 1979; McNab 1971; Rosenzweig 1966). Indeed, fisher mass exceeds that of martens by a factor of 3 (Powell et al. 2003), suggesting that the species are capable of exploiting different prey. The fisher's larger size does not appear to be an advantage in capturing species that were more common in the fisher diet (i.e., birds, reptiles, and insects). The similarity of the diets of martens and fishers in the southern Sierra Nevada resembles that reported for the 2 Eurasian martens (Clevenger 1994), which are more similar in size. However, size, may be a less successful predictor of niche differentiation in carnivores than differences in dentition (Dayan and Simberloff 1998).

Several factors could account for the similarity in diets reported here. First, martens and fishers are closely related and exhibit similar modes of foraging. They have similar body forms and their cursorial and arboreal hunting abilities (Clark et al. 1987; Powell 1993) make many of the same foods available to them. Although fishers are renowned for their unique ability to kill and eat porcupines (Powell 1993), porcupines could not be a basis for dietary separation because of their rarity in the

study area. In our study area, both species not only were capable of detecting and killing or securing the same suite of species, but they also had access to the same food items. With the exception of studies by Clem (1977) and Raine (1987), previous diet comparisons (e.g., Martin 1994) were derived from analysis of results from separate studies on individual species.

It is important to note that because we only examined the annual diet, it is possible that food selection by sympatric martens and fishers may diverge during a particular season. Diets of martens and fishers elsewhere do not appear to differ within the snow-free season, but winter diets are often different from summer diets (e.g., Bull 2000; Clem 1977; Francis and Stephenson 1972; Lensink et al. 1955; Weckwerth and Hawley 1962; Zielinski et al. 1983). It also is possible that martens and fishers differ in the species of birds that they prey on. We demonstrated a greater prevalence of birds in the diet of fishers, but we could not assess differences in use of bird species by martens and fishers.

It is possible for a potentially unlimited number of species to stably coexist in heterogeneous habitats as long as they have competitive trade-offs (Tilman and Lehman 2002). Theory predicts that as species compete, space and behavior are more easily divided than are food resources. Competing organisms typically respond 1st by expanding habitat preferences or foraging behavior, rather than by changing dietary breadth (Hespenheide 1975). It is possible that fishers and martens in our study area differ in respect to microhabitat use, activity time, or some other niche axis (Park 1940; Schoener 1974), allowing abundant and diverse foods to be exploited by both species without negative effects on either species.

Even without differences in how each species exploits time or structural resources available to them in the southern Sierra Nevada, a high degree of niche overlap does not necessarily mean that competition is taking place (Wiens 1977). Overlap can be high when resources are abundant (Cody and Diamond 1975; Schoener 1982). There are also examples, such as kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*), where competitors show strong overlap in habitat selection and diet, even at a fine spatiotemporal scale, although the dominant competitor often kills the subordinate (White et al. 1994; White and Garrott 1997).

The similarity of diets also must be evaluated in a context larger than our study area. Although the area included the full range of elevations over which fishers occur in the southern Sierra, the study area only included the lower range of elevations where martens occur. Martens in this study were radiocollared and most were residents occupying home ranges (W. J. Zielinski, in litt.). However, martens that reside in more typical high-elevation forests (>2,000 m in the southern Sierra Nevada—Zielinski et al. 1997) use different vegetation types and may find foods available that differ from those eaten by fishers. The marten and fisher distributions are largely allopatric or parapatric across their ranges in western North America (Gibilisco 1994; P. F. Schempf and M. White, in litt.; Zielinski et al. 1997). Therefore, few regions exist that are like our study area where martens and fisher occur together. It may be that their allopatric or parapatric distributions are the result

of some historical avoidance of competition, much like that of Iberian lynx (*Lynx pardinus*) with Egyptian mongoose (*Herpestes ichneumon*) and common genets (*Genetta genetta*—Palomares et al. 1995) and wolves with coyotes (Fuller and Keith 1981).

Marten and fisher distributions may have been determined at the coarse scale by an interaction between interference competition, with fishers holding an apparent advantage on the basis of size, and adaptation to travel in deep snow, which favors martens (Krohn et al. 1995, 1997). These factors would lead to a spatial separation of fisher and marten populations over time where each would encounter, and adapt to, a different pool of available prey. Therefore, comparative studies would reveal divergent diets. Rosenzweig (1966) believed that fishers and martens coexisted on the basis of food differences. Examination of our data suggests that significant food differences do not occur in the southern Sierra Nevada, although spatial overlap of the 2 species is relatively small when viewed at a continental scale. The question of niche differentiation probably requires a much greater scale of inquiry than the data here provide.

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