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Pine marten (*Martes martes* Linné, 1758) comparative feeding ecology in an island and mainland population of Spain

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Abstract

Investigated the feeding ecology of pine martens (*Martes martes*) in an insular (Minorca, Balearic Islands) and mainland (Cantabrian Mountains) Spanish population by analysis of food habits, food niche breadth, prey size index and prey weight distribution. Mammals, birds, fruits and insects were the main four dietary components in both populations. In Minorca all four were important during the year, whereas small mammals and fleshy fruits were dominant in the Cantabrian diet. The insular pine martens were characterized by having a wide food niche breadth and exploited all foods nearly equally compared to the Cantabrian martens and those from two other mainland populations. Pine marten prey size index and mean prey size also were greater in Minorca. Insular gigantism in Minorcan pine martens may be attributed to increased food abundance and reduced interspecific competition.

Introduction

Marten populations are subject to periodic food shortages, patchily distributed resources, and have been selected for a generalist feeding pattern (Erlinge 1986; Thompson and Colgan 1987). Their diets vary according to availability of different food types, their temporal variation, and degree of competition. Studies of European pine marten (*Martes martes*) diets have revealed that mammals were the most important food, whereas plant material (primarily fleshy fruits), birds, and insects were less common (Lockie 1961; Nyholm 1970; Pulliainen 1981; Moreno et al. 1988; Marchesi and Mermod 1989; Clevenger 1992).

In Spain, insular pine marten populations are found in Minorca and Majorca (Balearic Islands). Due to their geographic isolation, these environments are characterized as being depauperate in fauna compared to mainland areas (Lack 1942; Sondaar 1977; Reed 1982). Mammal prey species diversity is low and so are the number of competing small carnivores; the latter include spotted genet (*Genetta genetta*) and weasel (*Mustela nivalis*) on Majorca, whereas just the weasel is present on Minorca. Feral cats (*Felis silvestris* f. catus) are uncommon on both islands. Due to the lack of competitors and limited prey base, island pine marten would be expected to exhibit dietary differences compared to mainland populations. Distinct cranial morphology of Minorcan pine martens compared with Majorcan and those from the Iberian Peninsula (Alcover et al. 1986) suggests that the first exhibits insular gigantism and furthermore may have a unique trophic niche. In this study I describe the feeding ecology of pine marten from an insular (Minorca) and mainland Spanish population (Cantabrian Mountains), and discuss how varying levels of food resource abundance and interspecific competition may account for their divergence in body size.

Material and methods

Study area

The Balearic Island archipelago is located in the western Mediterranean approximately 150–250 km from the Iberian Peninsula and is composed of three main islands, Majorca, Minorca, and Ibiza. Minorca is the second largest island in the archipelago, covering 689 km^2 and is approximately 45 km long and 15 km wide. The highest point raises 358 m above sea level. Climate for the entire archipelago is typically Mediterranean with moderate temperatures whose monthly averages are between 10 °C and 26 °C. Annual precipitation ranges between 425 and 550 mm. Fieldwork was conducted in the northwestern part of the island in the area of La Vall.

The Balearic flora is composed principally of two large vegetal associations: *Quercetum ilicitum* and *Oleo Ceratonion* (Cardona 1979). On Minorca, the dominant forest type is Aleppo pine (*Pinus halepensis*) and holm oak (*Quercus ilex*). Woodlands make up 28 % of the island area with Aleppo pine predominating (83 % of woodland area) (Ministerio de Agricultura 1986). Mediterranean shrublands (*Olea europaea, Pistacia, Erica, Cistus, Phillyrea* spp.) form 9 % of Minorca and cultivated land constitutes more than half of the island.

The Cantabrian Mountains are situated on an east-west axis parallel and adjacent to the Bay of Biscay in northern Spain. They extend for 300 km and occupy an area of approximately 18,000 km^2. The physiography is rugged and elevations range from 600 m to 2500 m. The climate is continental; mean temperatures for the coldest and warmest months range from 0.5 °C (January) to 18 °C (August). Snow is present from January to March and mean precipitation averages 1400 mm. Pine marten faeces were collected in the Riaño, Fuentes Carrionas, Degaña and Somiedo National Hunting Reserves.

The Cantabrian flora is composed of Eurosiberian and Mediterranean vegetation communities. Fragmented stands of mixed deciduous forest occur primarily at middle and low elevations. The forest is composed primarily of durmast oak (*Quercus petraea*), pyrenean oak (*Q. pyrenaica*), and beech (*Fagus sylvatica*) with dispersed stands of birch (*Betula celtiberica*), rowan (*Sorbus aucuparia*), whitebeam (*S. aria*) and hawthorn (*Crataegus monogyna*). Regenerating shrublands (*Genista, Cytisus, Erica, Calluna* spp.) and open pasture cover 70 % of the vegetated area.

Methods

Faeces were collected periodically along foot trails in Minorca between February 1990 and March 1991, and in the Cantabrian Mountains from February to December 1990. Those that might have been confused with other small carnivores were discarded. Deposition dates were estimated to < 2 months and recorded for each respective time period. I sampled six bi-monthly periods in Minorca and three seasonal periods in the Cantabrian Mountains, Spring (15 February–31 May), Summer (1 June–15 September), and Autumn (16 September–30 November). For comparative purposes, Minorcan data also were presented by season as the food category totals for the following bi-monthly periods were averaged: Spring (March–April and May–June), Summer (May–June and July–August), Autumn (September–October and November–December), Winter (January–February).

Procedures for faeces analysis followed the standard techniques of washing, separating and identifying of different food items (Korschgen 1980; Reynolds and Aebischer 1991). Mammalian and avian prey remains were identified by microscopic and macroscopic analysis of hair, teeth, bones and feathers (Day 1966) and compared to a reference collection at the University of León. The identified food items were placed in one of seven food categories: mammals, birds, reptiles, amphibians, insects, plant material and other material (beeswax, human debris, etc.). An ocular estimate of percentage volume of each food item was made, and pooling data from all samples, the mean percentage volume and frequency of occurrence of each category of food item was calculated. Because analysis of remains by percent volume of faeces was found to be most correlated with the actual weight of prey eaten (Zielinski 1986), this method of analysis was used to describe the pine martens diet. Bi-monthly and seasonal differences in diet were assessed by X2 testing for homogeneity of variances for the major food categories (Sokal and Rohlf 1981).

I calculated the following trophic measures for the pine marten diet in Minorca and the Cantabrian Mountains as described in this study, in addition to data collected from the Spanish Pyrenees (Ruiz-Olmo and Lopez-Martin 1992) and a combined Cantabrian/Pyrenean data set (Cuesta et al. 1992).

The standardized feeding niche breadth was calculated for the respective number of food categories ("other material" not included) according to the niche breadth formula of Levins (1968), where pi is the proportion of food item i in the total diet:

$$\text{Feeding niche breadth} \quad B = (\Sigma Pi^2)^{-1}$$

The standardized niche breadth was calculated according to Hespenheide (1975), where n = the number of food categories identified. Bs increases as the diet becomes more generalized, and reaches 1.0 when all foods are exploited equally.

$$\text{Standardized niche breadth} \quad Bs = (B-1)/(n-1)$$

Niche breadths from Minorca were computed for the same 3-season period as the Cantabrian sample. To test whether niche breadth may be a function of sample size, faeces also were randomly selected from the island sample to equal that of the mainland data.

The indices for the mean prey size exploited by both pine marten populations were calculated according to the formula and approximate prey weights used by Erlinge (1987), where fi denotes the frequency of occurrence of prey item i, and wi is the body weight of prey item i. All mammal prey of European pine marten (domestic goat and "unknown mammal" not included) were used with their respective weights, and all avian prey (total contribution) in the diet were assigned a standard weight of 40 g. In this calculation, no distinction was made among male-female and adult-juvenile mammal prey.

$$\text{Mean prey size index} = \Sigma fi \times wi$$

Average prey size was determined by multiplying the weight of each prey item by its number of appearances in the sample. A prey size index and mean prey size also were calculated for the Minorcan data for the three seasons using entire and equalized samples to determine whether they may be affected by sample size.

A distribution of prey body weights (g) was made by creating five categories (0–15; 16–50; 51–100; 101–300; >300) and computing the percent volume of each prey item among mammals and birds in the diet.

Results

Food habits

A wide array of food items were used by pine martens in both populations. In Minorca, a total of 22 identifiable food items were found in 1180 faeces analyzed, whereas the Cantabrian sample consisted of 28 food items from 193 faeces.

In Minorca, mammals and plant material were the most important foods (Fig. 1a). Mammals were consumed most during spring and winter (43 % and 39 % volume, respectively) while plant material was the predominant food type in autumn (64 %). During summer the pine marten diet was nearly equally divided among four of the five food categories with the avian component being greatest. The incidence of insects was highest among all food categories (44 % frequency of occurrence), but only constituted 19 % of the diet volume. Reptiles appeared in low quantities throughout the year.

Prey items varied in size from beetles (Coleoptera) to hedgehogs (*Erinaceus algirus*), rabbits (*Oryctolagus cuniculus*), and Herring gulls (*Larus argentatus*) (Tab. 1). Of special interest were the remains of an unidentified bat (Chiroptera) in one spring faeces and Mediterranean tortoise (*Testudo hermanni*) in 11 faeces throughout the year; the latter were juveniles in 10 of the 11 cases. The four principal components of the pine marten diet during the year were mammals, birds, insects, and plant material.

Mammals were taken all year round, however they were the dominant prey during

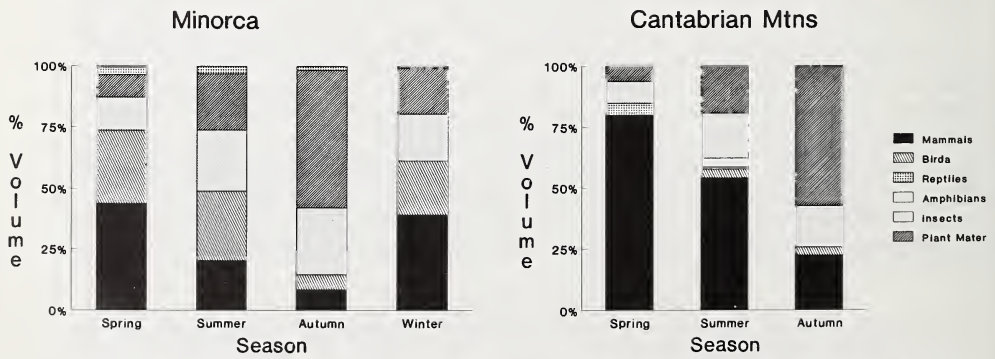

Fig. 1. Major food categories of pine marten diet arranged by seasonal averages in Minorca (N = 1180) and Cantabrian Mountains (N = 193)

Table 1. **Food items in faeces of Pine marten expressed as percent volume on the island of Minorca, Spain, March 1990–February 1991**
(Frequency of occurrence in parentheses)

	March–April (N = 293)	May–June (N = 174)	July–August (N = 307)	Sept–October (N = 98)	Nov–December (N = 116)	Jan–February (N = 192)	Total (N = 1180)
Mammals	58.4 (68.6)	27.4 (35.0)	13.5 (19.8)	8.2 (14.3)	11.9 (18.9)	46.7 (56.7)	31.8 (39.6)
Oryctolagus cuniculus	8.7 (10.9)	3.3 (3.4)	1.7 (2.2)	1.5 (2.0)	0.0 (0.0)	5.5 (6.2)	4.1 (5.0)
Rattus sp.	18.7 (20.8)	10.2 (12.0)	5.5 (7.8)	1.0 (1.0)	0.3 (4.3)	15.7 (17.7)	10.6 (12.3)
Eliomys quercinus	14.6 (16.7)	2.0 (2.8)	1.6 (1.9)	2.3 (3.0)	2.4 (2.6)	4.8 (5.7)	5.6 (6.5)
Apodemus sylvaticus	13.8 (16.4)	7.1 (9.7)	3.2 (4.5)	1.9 (4.1)	4.7 (8.6)	13.1 (18.2)	8.1 (10.8)
Mus sp.	2.2 (2.7)	0.8 (1.1)	0.6 (1.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.8 (1.1)
Crocidura suaveolens	0.0 (0.0)	0.5 (0.5)	0.1 (0.3)	0.9 (1.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.2)
Erinaceus algirus	0.0 (0.0)	0.0 (0.0)	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)	0.5 (0.5)	0.1 (0.1)
Chiroptera	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)
Unknown mammal	0.1 (0.7)	3.3 (5.1)	0.4 (1.3)	0.4 (3.0)	1.8 (3.4)	6.9 (8.3)	1.9 (3.2)
Birds	18.2 (30.7)	39.6 (52.8)	17.3 (30.6)	5.0 (8.1)	8.9 (15.5)	23.6 (38.5)	20.1 (31.7)
Feathers	17.5 (27.6)	36.2 (47.7)	15.6 (25.5)	4.7 (7.1)	8.9 (15.5)	23.0 (37.0)	18.9 (28.5)
Egg fragments	0.7 (2.4)	3.0 (5.1)	1.7 (5.5)	0.3 (1.0)	0.0 (0.0)	0.5 (1.5)	1.2 (3.1)
Reptiles	0.9 (4.7)	6.0 (10.9)	0.3 (0.6)	2.5 (7.1)	1.3 (1.7)	0.1 (0.5)	1.5 (3.8)
Lacertidae	0.9 (4.7)	3.7 (8.0)	0.3 (0.6)	0.5 (1.0)	1.3 (1.7)	0.0 (0.0)	1.1 (2.7)
Testudo hermanni	0.0 (0.0)	2.3 (2.8)	0.0 (0.0)	2.0 (6.1)	0.0 (0.0)	0.1 (0.5)	0.5 (1.0)
Insects	9.2 (30.3)	17.5 (44.8)	32.2 (67.7)	23.0 (46.0)	8.7 (22.4)	19.2 (41.1)	19.2 (44.1)
Coleoptera	7.0 (25.6)	5.4 (21.8)	8.4 (8.8)	20.6 (38.7)	8.5 (20.7)	17.2 (34.3)	8.6 (22.7)
Orthoptera	0.3 (2.0)	9.3 (16.6)	28.6 (56.6)	2.3 (7.1)	0.1 (0.8)	1.9 (5.2)	9.5 (19.2)
Other invertebrates	1.8 (3.6)	2.5 (5.6)	0.9 (1.2)	0.0 (0.0)	0.1 (0.8)	0.1 (1.5)	1.1 (2.3)
Plant material	8.6 (15.0)	9.3 (16.6)	36.5 (65.7)	60.1 (80.6)	68.9 (81.9)	10.3 (14.5)	26.7 (40.4)
Ceratonia siliqua	2.8 (5.1)	7.7 (3.4)	2.8 (5.5)	33.8 (39.8)	49.3 (57.7)	7.3 (9.3)	10.7 (13.7)
Rubus ulmifolius	0.0 (0.0)	0.1 (0.5)	19.4 (35.5)	1.0 (1.0)	0.0 (0.0)	0.0 (0.0)	5.2 (22.6)
Ficus carica	0.0 (0.0)	2.7 (6.3)	7.9 (13.0)	2.4 (3.0)	0.0 (0.0)	0.0 (0.0)	2.7 (4.5)
Vitis vinifera	0.0 (0.0)	0.0 (0.0)	3.0 (6.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.8 (1.6)
Arbutus unedo	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	16.4 (19.8)	0.4 (0.5)	3.0 (4.2)
Rhamnus alaternus	0.0 (0.0)	0.5 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.7 (2.0)
Juniperus phoenicea	0.8 (1.0)	0.0 (0.0)	0.3 (0.3)	4.2 (5.1)	1.7 (1.7)	0.0 (0.0)	0.7 (0.9)
Myrtus communis	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.0 (0.0)	1.3 (1.7)	0.0 (0.0)	0.2 (0.2)
Gramineas	2.9 (5.8)	0.0 (0.0)	0.0 (0.0)	1.5 (2.0)	0.1 (0.8)	0.0 (0.0)	1.8 (1.7)
Other plant material	2.1 (3.0)	3.8 (5.6)	2.8 (5.8)	0.9 (2.0)	0.0 (0.0)	1.0 (3.6)	2.2 (3.8)
Other material	0.9 (1.3)	0.0 (0.0)	0.0 (0.0)	1.0 (1.0)	0.1 (0.8)	0.0 (0.0)	0.3 (0.5)

winter and early spring (January–February, March–April) comprising 52 % of the diet volume. All of the island mammal fauna appeared in the diet; the most frequently taken were rats (*Rattus* sp.) and wood mice (*Apodemus sylvaticus*). Plant material (primarily fleshy fruits) was the main food component during July–August (36 % of diet), September–October (60 %), and November–December (69 %); blackberries (*Rubus ulmifolius*) and figs (*Ficus carica*) were the preferred fruits during the first period and carob fruit (*Ceratonia siliqua*) in the second. The highest incidence occurred in early winter (November–December) where nearly half of the diet was composed of carob fruit; strawberry tree (*Arbutus unedo*) fruit also appeared frequently.

Birds were the most important food in early summer (May–June) comprising 39 % of the diet and also well represented in winter and early spring. Of 50 May–June faeces having feathers, 18 species were identified; 44 faeces (88 %) belonged to breeding species (N = 14; 72 %) while only 6 (12 %) were migratory (N = 4; 28 %) (Tab. 2). The remains of the breeding species were mostly nestlings. Eggshell fragments rarely appeared in the faeces analyzed, however during these two months they doubled in occurrence.

Table 2. **Breeding and migrant birds (X) found in Minorcan pine marten faeces during May–June, 1990**

Species	N	Breeding	Migrant
Larus argentatus	19	X	
Acanthis cannabina	1	X	
Carduelis carduelis	1	X	
Chloris chloris	2	X	
Columba livia	3	X	
Emberiza calandra	1	X	
Erithacus rubecula	1		X
Oenanthe oenanthe	1		X
Passer domesticus	1	X	
Phylloscopus trochilus	1		X
Phylloscopus sp.	3		X
Saxicola torquata	1	X	
Sylvia atricapilla	1	X	
Sylvia borin	1		X
Sylvia cantillans	1	X	
Sylvia melanocephala	8	X	
Sylvia sarda	3	X	
Turdus philomelos	1		X
Total	50	44 (88 %)	6 (12 %)

Insect consumption during the year was relatively uniform, peaking during summer (July–August) as grasshoppers (Orthoptera) composed 89 % of the total; otherwise beetles (Coleoptera) were the most consumed insects. Reptiles (Lacertidae and Mediterranean tortoise) were taken intermittently, primarily during early summer.

The bi-monthly diets in Minorca were extremely variable during the year. Highly significant differences ($P < 0.0001$, $df = 4$) were found between all periods except January–February and March–April, and September–October and November–December ($P > 0.01$, $df = 4$).

Three food categories dominated the Cantabrian pine marten diet during the three seasons, mammals, plant material and insects (Fig. 1b). Mammals were the most important component in the diet (56 %), followed by plant material (24 %) and insects (14 %). The remaining food categories (reptiles, birds and amphibians) were scarcely represented in the diet, and may be a result of the smaller sample size and period.

Prey items also were disparate in size and ranged from beetles and grasshoppers to red squirrels (*Sciurus vulgaris*) and hares (*Lepus* sp.) (Tab. 3). Trace remains of domestic goat appeared in the diet and most likely were taken as carrion. During spring and summer mammals were the dominant food component as they formed 79 % and 54 % of the diet volume, respectively. Of these, wood mice were taken most, followed by field mice (*Microtus agrestis*) and bank voles (*Clethrionomys glareolus*). In autumn, plant material was most important and occupied 57 % of the diet, primarily due to the nearly exclusive consumption (97 % of plant material) of rowan berries. Other fruits eaten by pine martens, although rarely, included: hawthorn, blackberries, alpine buckthorn (*Rhamnus alpinus*).

Table 3. **Food items in faeces of Pine marten expressed as percent volume in the Cantabrian Mountains, Spain, 1990–1991**

(Frequency of occurrence in parentheses)

	Spring (N = 86)	Summer (N = 52)	Autumn (N = 55)	Total (N = 193)
Mammals	79.5 (97.6)	54.2 (80.7)	22.5 (34.5)	56.4 (75.1)
Apodemus sylvaticus	33.3 (44.1)	23.5 (36.5)	9.9 (16.3)	24.0 (34.2)
Apodemus flavicollis	1.1 (1.1)	0.0 (0.0)	0.0 (0.0)	0.5 (0.5)
Microtus agrestis	24.4 (27.9)	12.1 (13.4)	5.4 (9.0)	15.7 (18.6)
Clethrionomys glareolus	6.8 (7.0)	6.0 (11.5)	5.9 (5.4)	5.8 (7.7)
Eliomys quercinus	4.3 (5.8)	7.6 (9.6)	1.3 (1.8)	4.3 (5.7)
Arvicola terrestris	2.3 (2.3)	0.0 (0.0)	0.0 (0.0)	1.0 (1.0)
Pitymys lusitanicus	3.0 (3.5)	0.0 (0.0)	0.0 (0.0)	1.3 (1.5)
Mus musculus	1.1 (1.1)	0.0 (0.0)	0.0 (0.0)	0.5 (0.5)
Sorex coronatus	0.9 (1.1)	0.0 (0.0)	0.0 (0.0)	0.9 (2.1)
Crocidura russula	0.7 (1.1)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)
Sciurus vulgaris	0.0 (0.0)	0.0 (0.0)	1.8 (1.8)	0.5 (0.5)
Lepus sp.	0.3 (1.1)	0.0 (0.0)	0.0 (0.0)	0.1 (0.5)
Domestic goat	0.9 (1.1)	3.1 (3.8)	0.0 (0.0)	1.2 (1.5)
Birds	0.3 (1.1)	3.5 (3.8)	3.2 (5.4)	2.0 (3.1)
Feathers	0.3 (1.1)	3.5 (3.8)	3.2 (5.4)	2.0 (3.1)
Reptiles	4.9 (11.6)	0.8 (1.9)	0.0 (0.0)	2.4 (5.7)
Podarcis muralis	1.8 (4.6)	0.0 (0.0)	0.0 (0.0)	0.8 (2.1)
Podarcis sp.	1.5 (1.1)	0.0 (0.0)	0.0 (0.0)	0.1 (0.5)
Lacerta schreiberi	2.2 (3.5)	0.0 (0.0)	0.0 (0.0)	0.9 (1.5)
Coronella girondica	0.4 (2.3)	0.0 (0.0)	0.0 (0.0)	0.2 (1.0)
Lacertidae	0.0 (0.0)	0.8 (1.9)	0.0 (0.0)	0.2 (0.5)
Amphibians	0.0 (0.0)	3.7 (3.8)	0.0 (0.0)	0.9 (1.0)
Rana temporaria	0.0 (0.0)	1.9 (1.9)	0.0 (0.0)	0.9 (1.0)
Rana sp.	0.0 (0.0)	1.7 (1.9)	0.0 (0.0)	0.4 (0.5)
Insects	8.8 (29.0)	18.6 (36.5)	17.0 (32.7)	13.8 (32.1)
Coleoptera	8.7 (27.9)	15.1 (28.8)	14.2 (27.2)	12.0 (28.0)
Orthoptera	0.0 (0.0)	2.7 (5.7)	0.0 (0.0)	0.7 (1.5)
Hymenoptera	0.0 (0.0)	0.8 (1.9)	0.3 (1.8)	0.3 (1.0)
Unknown insects	0.1 (1.1)	0.0 (0.0)	2.3 (3.6)	0.7 (1.5)
Plant material	6.1 (9.3)	19.1 (32.4)	57.3 (78.1)	24.2 (35.2)
Sorbus aucuparia	0.0 (0.0)	0.0 (0.0)	55.6 (72.7)	15.9 (20.7)
Crataegus monogyna	4.3 (4.6)	0.0 (0.0)	0.0 (0.0)	1.9 (2.1)
Rubus ulmifolius	0.0 (0.0)	3.5 (5.7)	0.0 (0.0)	0.9 (1.5)
Rhamnus alpinus	0.0 (0.0)	2.7 (5.7)	0.0 (0.0)	0.7 (1.5)
Prunus sp.	0.0 (0.0)	2.9 (3.8)	0.0 (0.0)	0.7 (1.0)
Rosa sp.	0.0 (0.0)	0.0 (0.0)	0.3 (1.8)	0.1 (0.5)
Unknown fruit	0.3 (1.1)	3.5 (3.8)	0.0 (0.0)	1.1 (1.5)
Gramineae	0.1 (1.1)	0.0 (0.0)	0.0 (0.0)	0.1 (0.5)
Other plant material	1.3 (2.3)	6.4 (13.4)	1.3 (3.6)	2.6 (5.6)

Insects were common food items and were most prevalent in summer forming 18 % of the diet. Beetles comprised 87 % of all insect remains. Reptiles and birds were rarely taken during the three seasons as each formed less than 5 % of the diet volume.

As in Minorca, seasonal pine marten diets varied greatly in the Cantabrian Mountains as significant differences were found between all three periods ($P < 0.0001$, df = 5).

Feeding niche breadth

Standardized feeding niche breadth indices were calculated for both pine marten populations. The annual diet of the Minorcan pine marten consisted of five food categories; it exhibited the most generalized feeding pattern resulting in a niche breadth index of 0.754. Cantabrian pine marten foods composed five categories and the 3-season diet was markedly less generalized as the niche breadth measured 0.380. Sampling duration and intensity in Minorca appeared to have no effect on the feeding niche breadth. When the island data were analyzed with the sample period and size equal to the Cantabrian data, Minorcan niche breadth indices remained high, 0.751 and 0.793, respectively.

The niche breadth index from combined Cantabrian/Pyrenean food habits data (0.469) was higher than data presented herein for the Cantabrian population but well below the island indices. Data from the Pyrenees resulted in the lowest index of all (0.186).

Prey size

The prey size index for Minorcan pine martens measured 66.4 (a total of eight prey items consumed) compared to 23.7 for Cantabrian martens even though the latter exploited a greater number (N = 13) of prey species. A larger prey size index resulted (80.5; eight prey items) when the island data were analyzed for the same duration as the Cantabrian; however, a lower index was obtained (49.9; six prey items) when sample sizes were identical.

All three prey size indices for Minorcan pine martens were larger than those from the Pyrenees (12.0) and the combined Cantabrian/Pyrenean (47.4) data set.

Prey species consumed by Minorcan pine martens during the 12-month period were significantly larger (98.7 ± 3.7 [SE] g, N = 803) than those found in the Cantabrian diet (31.4 ± 2.9 [SE] g, N = 148) ($P < 0.0001$, Mann-Whitney U test). The same was true when sampling periods and sizes were equalized (98.0 ± 4.1 [SE] g, N = 618 and 77.0 ± 7.4 [SE] g, N = 126, respectively; $P < 0.0001$). There was no significant difference between the mean prey size in the three variations of the Minorcan diet ($P > 0.10$).

The average prey size from the insular population also was significantly larger ($P < 0.0001$) when compared to Pyrenean (44.3 ± 6.6 [SE] g, N = 91) and Cantabrian/Pyrenean (40.7 ± 6.7 [SE] g, N = 162) food habits data. Prey sizes were not significantly different among the three mainland populations ($P > 0.05$).

Distributions of body weight across categories of prey size were different between pine martens from Minorca and the mainland (Fig. 2). Prey weight distributions among the three different Minorcan diet analyses were not significantly different ($P > 0.10$, df = 3, Kolmogorov-Smirnov test); the greatest proportion of prey items were from the 101–300 g category. Prey weight distributions from the Cantabrian, Pyrenean, and combined Cantabrian/Pyrenean diets were significantly different from those from Minorca ($P < 0.001$) as more than 75 % of the mainland prey species weighed between 16–50 g. There were no significant differences in weight distribution among the three mainland diets ($P > 0.10$).

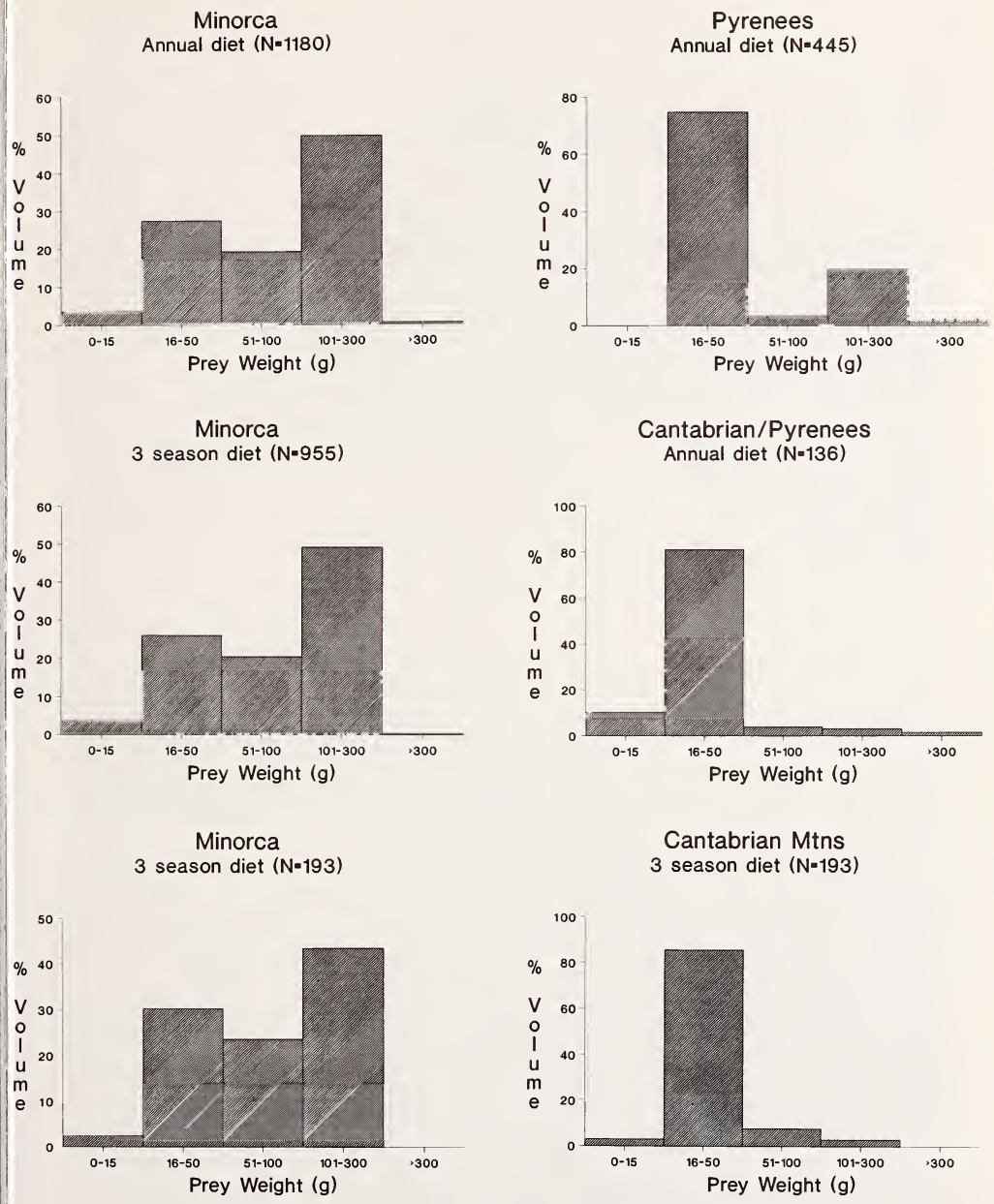

Fig. 2. Prey weight distributions from pine marten diets in Minorca and mainland Spain

Discussion

Feeding ecology

Interesting differences in diet can be seen between the two populations. The most striking result from the diet data is the nearly completely balanced use of food resources by pine martens in Minorca compared to the Cantabrian Mountains. Pine marten diet composition from the latter was comparable to diets reported in the Pyrenees (Ruiz-Olmo and López-Martín 1992) and Swiss Jura (Marchesi and Mermod 1989). The uniformity observed in the Minorcan pine marten diet may be explained by the insular environment and reduced competition whereby generalist feeders have been reported to capitalize on the increased availability of different kinds of foods and expanded resource base (see Lawlor 1982).

Reduced interspecific competition and increased food availability in insular communities generally selects for large individuals. Conversely, limited food supplies on small islands should select for small individuals (Wassersug et al. 1979; Lawlor 1982). Recently, a study of the geographic variation of adult pine martens (male and female combined) from Minorca, Majorca, and the Cantabrian Mountains revealed that Minorcan martens were significantly larger than the other two (6.2 % and 2.8 % larger, respectively), greater than any previously known population and proposed as a new subspecies, *M. m. minoricensis* (Alcover et al. 1986). Moreno et al. (1988) suggested that the Minorcan pine martens large size may be a result of higher predation on mammals and birds compared to Majorca, caused by the lack of competition with genets.

Several authors have pointed out the relationship between carnivore size and the size and abundance of their prey (Rosenzweig 1966; Case 1978; Simms 1979; Gittleman 1985; Vezina 1985). Erlinge (1987) reported that body size was positively correlated with prey size in European stoats (*M. erminea*). Shifts in body size in response to abundant prey have also been documented for other mustelids (McNab 1971; Powell and Brander 1977; King and Moody 1982; Monakhov 1989), canids (Schmitz and Kolenosky 1985; Geist 1987; Schmitz and Lavigne 1987; Thurber and Peterson 1991) and felids (Iriarte et al. 1990). Prey size indices and mean prey weights reported herein, however approximate, were significantly larger from Minorca than the Cantabrian Mountains, Pyrenees, and combined Cantabrian/Pyrenean data set.

Rabbits, rats and Herring gulls were important food items in Minorca unlike the other populations. Of some 37 faeces identified with Herring gull remains in Minorca, adult plumage appeared in 73 % (N = 27) while the rest were juveniles (Clevenger 1991). Similarly, King and Moody (1982) found a positive correlation between the size of introduced New Zealand stoats and the proportion of lagomorphs in the diet.

Lomolino (1985) reasoned that competitive release is a major factor responsible for insular gigantism in mammals, thereby suggesting that body size may be constrained by the presence of larger competitors (McNab 1971; Lawlor 1982). In communities where similar sized or larger competing species are absent, mean body size would be expected to increase (Rosenzweig 1968). On islands such as Minorca where the number of competitors is reduced, the range of food resources used by pine martens (its niche breadth) is amplified, greater prey sizes become available, which thereby may facilitate a shift to a larger mean body size (see Schoener 1967; Roughgarden 1972; Hespenheide 1975; Lister 1976). Prey species diversity is lower in insular vs. mainland environments, nonetheless overall prey abundance and availability may be greater in the former. Size differences between New Zealand and British stoats were explained by differences in overall prey size distribution for the two populations, although more species occur in Britain (King and Moody 1982).

Body size variation among continental and insular weasel populations showed no support for character displacement (Ralls and Harvey 1985; Erlinge 1987); however, in the Pacific Northwest large body sizes of American pine marten (*M. americana*) were

reported on islands with reduced interspecific competition (Giannico and Nagorsen 1989). In the same population (Nagorsen et al. 1991), a subsequent study did not reveal anything in the winter diet which could account for the distinct cranial morphology, but the authors noted that their one-season data were speculative. The large body size and absence of competitors in Minorca compared to mainland populations is concordant with this insular body size trend and supported by the diet and feeding ecology data presented herein.

Foster (1963) reported that island stone marten (*M. foina*) in the Mediterranean were smaller than individuals from the mainland. Dwarfism also has been documented among genets and the presently extinct stone marten from the Balearic Island of Ibiza (Delibes 1977; Delibes and Amores 1986). If resource limitation is a major factor affecting insular body size of mammals, then differing levels of resource abundance (or competition) on Mediterranean islands may explain these trends. Information on variations in prey abundance among island and continental populations, and how conspecifics partition these resources is lacking. Answers to these questions will be necessary before critical tests can be carried out investigating island-mainland body size trends.

Like other marten studies have shown, food choice is determined by what is abundant and accessible (Weckwerth and Hawley 1962; Brainerd 1990). Minorcan pine marten concentrated on seasonally abundant foods or those that had the greatest energy return, evidenced by the high proportion of birds during May–June, and insects and fruit during July–December. The generalist feeding pattern was congruent with other European studies (Lockie 1961; Nyholm 1970; Pulliainen 1981; Warner and O'Sullivan 1982; Marchesi and Mermod 1989).

The highest consumption of mammals occurred between January–April, while predation was lower the remainder of the year. Seasonal data on small mammal abundance and availability from Minorca are forthcoming and I suspect like other studies have shown, that rodent population levels do not peak until late summer or autumn (Goszczynski 1977; Erlinge et al. 1983, 1984; Alibhai and Gipps 1985; Flowerdew 1985). If so, then pine marten may exploit small mammals these months because other foods (birds, insects, fruit) are more scarce. Birds were taken all year-round, however, they were most prevalent in the diet during May–June, which earlier was shown to coincide with the hatching and fledgling period for most passerines in Minorca.

Mammals were the most important Cantabrian pine marten food during the 3-season period and were most prevalent in spring and summer. Other studies have also shown the importance of mammals in the species diet (Lockie 1961; Nyholm 1970; de Jounge 1981; Pulliainen 1981; Reig and Jedrzejewski 1988; Jedrzejewski et al. 1989; Marchesi and Mermod 1989). Wood mice were taken most, contrary to the aforementioned studies where microtine rodents predominated. The high incidence of woodland rodents suggests that Cantabrian pine marten forage primarily in beech/oak forests and less frequently in open habitats. In the Spanish Pyrenees woodland rodents were also preferred during spring and summer (Ruiz-Olmo and López-Martín 1992). In autumn fruits replaced mammals in the Cantabrian diet which was found in other pine marten studies ((Lockie 1961; Marchesi and Mermod 1989).

In this paper I have reported on pine marten feeding ecology from one insular and one mainland population, in addition to food niche breadths and prey size selection from other mainland populations in Spain. More basic diet data is needed from island and mainland populations to conduct critical testing to determine if gigantism is a general phenomenon among insular pine martens and carnivores in general.

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Zusammenfassung

Vergleichende Nahrungsökologie des Baummarders (Martes martes Linné, 1758) bei einer Insel- und einer Kontinentalpopulation in Spanien

An Kotproben wurde die Zusammensetzung der Nahrung des Baummarders (*Martes martes*) bei einer Insel- (Menorca, Balearen) und einer Kontinentalpopulation (Kantabrisches Gebirge) über einen Zeitraum von einem Jahr bestimmt und miteinander verglichen. Dazu dienten folgende Parameter: Nahrungsspektrum, Breite der Nahrungsnische, Beutegrößenindex und Verteilung der Beutegewichte. Kleinsäuger, Vögel, Früchte und Insekten stellten die wichtigsten vier Nahrungskomponenten in beiden Populationen dar. Auf Menorca waren alle vier über das Jahr verteilt in ausgewogener Weise bedeutend, während im Kantabrischen Gebirge Kleinsäuger und Früchte jahreszeitlich dominierten. Darüber hinaus waren die Inselmarder durch eine deutlich größere Breite der Nahrungsnische gekennzeichnet. Sie nutzten alle Nahrung im Jahr annähernd gleichartig im Gegensatz zu den Mardern des Kantabrischen Gebirges und gegenüber Vertretern aus zwei weiteren kontinentalen Populationen. Beutegrößenindex und mittlere Beutegröße waren auf der Insel ebenfalls größer. Für Baummarder von Menorca ist im Vergleich mit Individuen vom Kontinent eine deutliche Zunahme der Körpergröße festgestellt worden. Dieser „Inselgigantismus" wird in Zusammenhang mit erweiterter Nahrungsabundanz auf Menorca und reduzierter interspezifischer Konkurrenz diskutiert.

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