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THE RESPONSE OF EUROPEAN PINE MARTEN (*MARTES MARTES* L.) FEEDING TO THE CHANGES OF SMALL MAMMAL ABUNDANCE

ABSTRACT: The European pine marten (*Martes martes*) is commonly classified as an opportunistic predator. If this is the case, the species ought to show seasonal differences in the small mammal composition of its scats – the types of prey taken depending on their abundanc. In addition, it ought to consume the food that requires lower energy cost for their acquisition in each season. The feeding strategy of the European pine marten was studied in northwestern Spain by analyzing 209 scats collected between July 2004 and June 2005, and by seasonally trapping small mammals to obtain information on their abundance. The study area (5,722 ha) was located in a mountainous region (1,707–880 m a.s.l.) and covered with brushwood and deciduous forest (oak, birch, holly and pine). Molecular analysis of scats (PCR-RFLP) was performed to rule out the presence of the stone marten (*Martes foina* L.). The frequency of occurrence and biomass of the small mammals (the main prey species) preyed upon each season were compared. The pine marten consumed significantly more small mammals in the seasons in which their abundance was the lowest (winter and spring). In the autumn, when the highest number of small mammals was detected, the pine marten did not increase its predation of them. These results indicate that the European pine marten is not an opportunistic predator. Rather, the feeding strategy adopted by the species seems to be intermediate between that of an opportunist and specialist predator.

KEY WORDS: European pine marten, abundance, opportunist, scats, small mammals, specialist

1. INTRODUCTION

In Europe, the diet of the European pine marten (*Martes martes* L., 1758) is varied, and includes mammals, fruits, birds and insects (De Marinis and Masseti 1995), although small mammals are the year-round main prey items (Marchesi and Mermod 1989, Zalewski *et al.* 1995). Fruits, birds and insects are consumed preferably in autumn, spring, summer (Marchesi and Mermod 1989, Clevenger 1993, Jędrzejewski *et al.* 1993). In Scandinavia the European pine marten takes squirrels (*Sciurus vulgaris* L., 1758) (Storch *et al.* 1990) and hares (*Lepus* sp.) (Helldin 1999) when small mammals are scarce. In Poland, carrion (mainly roe deer *Capreolus capreolus* L., 1758) and birds' eggs are important during the spring (Zalewski *et al.* 1995). In the Balearic Islands, garbage seems to provide an alternative food source during periods of prey shortage (Moreno *et al.* 1988).

The European pine marten is commonly defined as an opportunist predator since its diet is very varied (Marchesi and Mermod 1989, Clevenger 1994, Helldin 1999). However, it is important to notice that the latter authors did not analyze prey abundance extensively. The only study to date that suggests a certain degree of predatory specialization on the part of this species was performed at Bialowieza National Park (Poland), where the bank vole (*Clethrionomys glareolus* Schreber, 1780) was the main prey, even though the yellow-necked mouse (*Apodemus flavicollis* Melchior, 1834) is the most abundant species in the study area (Jędrzejewski *et al.* 1993, Zalewski *et al.* 1995).

A species is considered a trophic specialist when it feeds almost entirely on one prey species, and when it shows this preference regardless of the prey's availability. Such predators are said to show a type II (hyperbolic) functional response (Holling 1959). An opportunist, however, consumes the food that is most available in each season and area, changing its diet depending on food availability. When the abundance of one prey type diminishes, opportunist predators begin to take a more abundant species; they therefore show a type III functional response (S-shaped) (Holling 1959, Glasser 1982, Angelstam *et al.* 1984, Erlinge 1986, Futyma and Moreno 1988).

The aim of the present study was to test the hypothesis that the European pine marten is an opportunist species. If it is an opportunist it ought to show significant seasonal differences in the consumption of small mammals (its main prey), changing what it takes according to abundance. An increase in small mammal consumption would be expected in seasons in which such prey is more abundant. In addition, in each season, the food items that require lower energy cost for their acquisition ought to be those most consumed.

2. STUDY AREA

The study was conducted over a 5,722 ha area at Os Montes do Invernadeiro Natural Park, NW Spain (UTM 29T 064633-643 and 467462-472). The topography of the area is mountainous with steep slopes. The altitude varies between 880 m and 1,707 m (Barja 2001). The climate is continental, with cold winters and hot summers. The annual average temperature and precipitation were 1,185 l m^{-2} and 10.4°C, respectively during the study period.

The study area occupies a transitional zone between the Mediterranean and Eurosiberian regions (Castroviejo 1977). This is manifested by the alternation between Mediterranean plant communities and relict Atlantic forests (Castroviejo 1977). Scrubland dominates the plant community, mainly heather (*Erica australis* L.), prickled broom (*Pterospartum tridentatum* L.) and sandling (*Halimiun lasianthum* Lam.). Original deciduous forest subsists in the valleys and along watercourses, and is formed mainly by associations of oak (*Quercus robur* L.), birch (*Betula celtiberica* Rothm. & Vasc.), holly (*Ilex aquifolium* L.) and rowanberry (*Sorbus aucuparia* L.) (Barja 2001). Large extensions are occupied by repopulated forests of Scot pine (*Pinus sylvestris* L.). The fauna is diverse, including carnivores such as the otter (*Lutra lutra* L., 1758), badger (*Meles meles* L., 1758), European polecat (*Mustela putorius* L., 1758), stoat (*Mustela erminea* Linnaeus, 1758), European common weasel (*Mustela nivalis* L., 1766), genet (*Genetta genetta* Linnaeus, 1758), wildcat (*Felis silvestris* Schreber, 1775), red fox (*Vulpes vulpes* L., 1758), and a large population of wolves (*Canis lupus* L., 1758) (Barja 2001).

3. MATERIAL AND METHODS

3.1. Collection and analysis of scats

Scats were collected monthly from July 2004 to June 2005 by establishing transects along roads. The use of roads by the European pine marten and other carnivores (wolf, red fox, wildcat) has been reported; these species frequently defecate on them, the scats acting as scent-marks (Pulliainen 1982, Robinson and Delibes 1988, Barja *et al.* 2005, Barja 2005a). Twenty-five transects 300 m in length were inspected every month. In order to include the territory of several individuals, and to ensure that the samples were representative, transects were established in four different zones of the study area set far apart from one another. In each zone the transects were separated by at least one kilometer. Transects were established in optimal zones for the species, taking into account the results obtained in the study area on habitat selection and distribution in this species (Barja 2005b).

Pine marten scats were differentiated from those of other sympatric carnivores (wildcat, red fox and wolf) by their size and shape. To rule out the presence of the stone marten (*Martes foina* Erxleben, 1777) in the study area, 90 fresh scats were collected in the four zones where the transects were later set out. The DNA in the fecal residues was then identified using the PCR-RFLP technique (Ruiz-González *et al.* in press): all sampling were of European pine marten. Camera traps (155 camera-traps per night) were also set up, and visual surveys and searches for dead animals also made, resulting in the presence of the stone marten in the area being ruled out.

The scats were cleaned in the laboratory following conventional procedures (Reynolds and Aebischer 1991). After drying, the different macroscopic components were separated, weighed and identified. The hairs, teeth and bones found were used to identify the prey items. The cuticle patterns of the hairs were compared to those in reference manuals (Faliu *et al.* 1980, Teerink 1991) and with reference hairs collected in the study area. Their macroscopic characteristics were also compared with those in a museum collection (Museo Nacional de Ciencias Naturales of Madrid).

The date of collection, UTM grid position, and the age of all collected scats were noted. Scat age: fresh (deposition-4 days old), medium age (5 days-1 month old) and old (> 1 month old) provided an estimate of the defecation date and allowed the seasonal variation of the diet to be analyzed. Fresh feces were characterized by their strong smell, the presence of a layer of mucus, and the lack of signs of dehydration. Medium-age feces had lost their scent and the layer of mucus, but maintained their characteristic shape. Old feces had no smell and had lost their characteristic shape. To analyze seasonal variation, the months of the year were grouped into seasons: spring (April–June), summer (July–September), autumn (October–December) and winter (January–March). To avoid the replication of samples, scat positions were noted using a global positioning system (GPS) apparatus.

When the species diet is studied by analyzing the scats, it is necessary to consider that the relative importance of the food types changes during the digestion process of the predator (Lockie 1960). Therefore, the obtained proportion of each food type in the dry scats is not real. Thus, to correct this it is necessary to use some correction factors (fresh weight of a food multiplied by the dry weight of the remains of this food type found in the scats). This methodology was proposed by Lockie (1960) in a study conducted in European pine marten, where the weight variation of the different food types during the digestion process of this species were analyzed. In the present study, to estimate the ingested biomass of each food type, we multiplied the dry weight of each food type by its correction factor. The following Lockie's correction factors (1960) were used: small mammals – 22, rabbits and hares – 43, other large and medium-sized mammals – 61, birds – 37, beetles – 5, butterflies and moths – 12, berries – 14, and lacertids – 8.5.

3.2. Live trapping of small mammals

Live trapping is the method that reflects sufficiently the number of small mammals in an area (Gurnell and Flowerdew 1990, Luiselli and Capizzi 1996, Powell and Proulx 2003). To determine the abundance of small mammals in the study area, a live trapping campaign was undertaken each season (August 2004, November 2004, January 2005 and May 2005) in the most representative habitats of the study area (deciduous forest, mature pine forest and brushwood) (Barja 2005b). In each habitat, three trapping sites far from one another were selected. A grid containing 25 Sherman traps, separated by 10 m and covering an area of 0.25 ha, was set up at each sampling point. In each habitat the traps were left out for 3 consecutive nights and checked every 12 h. The total effort was 2,700 traps per night. Bread impregnated with oil was used as bait. All animals captured were identified and the date noted.

3.3. Data analysis

To determine the relationship between the consumption of small mammals by the pine martens and their seasonal abundance, the number of scats with the small mammal remains every season (*ObsF*) was quantified. Since the scat number collected in each season was different (Spring: 67, Summer: 56, Autumn: 54, winter: 32), the number of scats with the small mammal remains every season was corrected (*ObsF**: corrected number of scats with small mammal remains):

$$ObsF^* = ObsF \; x \; I_c \quad (1)$$

$$I_c = \bar{N} / N \quad (2)$$

where I_c is the applied correction index, N is the total number of scats analyzed per season, and $\bar{N}$ the mean number of scats analyzed per season.

The expected percentages of scats with small mammal remains (*ExpF%*) in each season were calculated according to the following formula:

$$ExpF\% = A_s \; x \; 100 / A_t \quad (3)$$

Where A_s is the seasonal number of captured small mammals and A_t the total number of captured small mammals in the study area.

The expected frequencies (*ExpF*) of scats with small mammal remains per season were calculated with the following formula:

$$ExpF = \Sigma \; ObsF^* \; x \; ExpF\%/100 \quad (4)$$

The Shannon-Weaver diversity index (Shannon and Weaver 1949) was used to calculate dietary diversity from the observed frequencies in each season.

Since the variables were not normally distributed, they were analyzed by non-parametric statistical tests. The χ^2 test was used to test the differences between the number of scats with small mammal remains per season (*ObsF**) and the expected number of scats with the small mammal remains per season (*ExpF*). In contingency tables where more than 20% of the expected frequencies were <5, the Monte Carlo's exact test was used. Yates' correction was used for 2 × 2 tables. Significance was set at $\alpha < 0.05$.

4. RESULTS

A total of 209 scats were analyzed. Mammals were found to be consumed over other prey types (50% of the ingested biomass), followed by fruits (28%), birds (21%), insects (0.8%) and reptiles (0.2%). Rodents were the most important mammal prey, accounting for 65% of the ingested biomass of mammals, followed by insectivores (22%) and carrion (roe deer, wild boar and badger) (13%). The differences in the predation frequencies with respect to the different mammal species were significant ($\chi^2 = 67.6$, d.f. = 2, 121, $P < 0.001$). Of the mammals taken, small mammals (rodents – except squirrels – and insectivores) made up 83% of the ingested biomass, mainly *Apodemus* sp. (46%), followed by *Glis glis* L. (11%), *Talpa occidentalis* Cabrera (7%) *Clethrionomys glareolus* (7%), *Crocidura* sp. (6%), *Neomys* sp. (6%), *Sorex* sp. (6%) *Arvicola* sp. (4%), *Eliomys quercinus* L. (3%), *Microtus* sp. (2%), *Mus* sp. (1%) and other not identified insectivores (1%) ($\chi^2 = 253.5$, d.f. = 11, 106, $P < 0.001$). The rowanberry (*S. aucuparia*) made up some 96% of the ingested fruit biomass.

During the trapping period, 201 small mammals were captured. The wood mouse (*A. sylvaticus*) was the most abundant species (95%), followed by the yellow-necked mouse (*A. flavicollis*) (3%), the pygmy shrew (*Sorex minutus* L., 1766) (1%), the greater white-toothed shrew (*Crocidura russula* Hermann) (0.5%), and the garden dormouse (*E. quercinus*) (0.5%). The differences between the different species captured were significant ($\chi^2 = 716.8$, d.f. = 4, 201, $P < 0.001$). The abundance of small mammals varied from one season to another. The greatest abundance of small mammals occurred in autumn (64.4 individuals ha^{-1}), followed by summer (22.2 individuals ha^{-1}), winter (3.6 individuals ha^{-1}) and spring (0 individuals ha^{-1}) (Fig. 1) ($\chi^2 = 16.3$, d.f. = 3, 201, $P < 0.001$).

The seasonal consumption of small mammals was not related to their abundance (Fig. 1). The differences between the expected (*ExpF*) and observed (*ObsF**) seasonal frequencies were significant ($\chi^2 = 16.3$, d.f. = 3, 105, $P < 0.001$). In spring and winter, when the abundance of small mammals was low, the pine marten showed a preference for this type

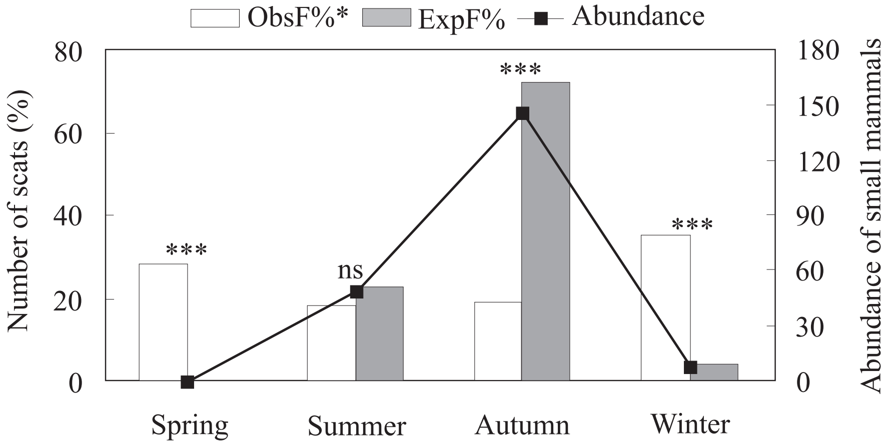

Fig. 1. Percentage of scats of European pine marten with small mammal remains (*ObsF%**, equation 1) per season, expected percentages (*ExpF%*, equation 3) and abundance of small mammals. The expected percentages of scats with small mammal remains (*ExpF%*) in each season were calculated multiplying the seasonal number of captured small mammals (A_s) × 100 and related to the total number of captured small mammals (A_t) (see method section). *** – P <0.001, ns – P> 0.05.

of prey (spring: 53% of the ingested biomass, winter: 60% of the ingested biomass) (Spring: χ^2 = 789.6, d.f. = 1, 30, P <0.001; winter: χ^2 = 243.0, d.f. = 1, 38, P <0.001). In summer, the consumption of small mammals was related to their abundance in the environment (24% of the ingested biomass), with no significant differences between observed and expected frequencies (χ^2 = 1.0, d.f. = 1, 20, P> 0.05). In autumn, although the abundance of small mammals was at its highest, the pine marten did not increase its predation of them (31% of the ingested biomass) (Fig. 1) – in fact it showed a preference for rowanberries (χ^2 = 41.0, d.f. = 1, 21, P <0.001).

The greatest dietary diversity and the lowest dominance values were obtained in spring (Shannon-Weaver index H = 1.37, Dominance D = 0.28) and winter (H = 1.33, D = 0.32); the lowest diet diversity and the highest dominance values corresponded to autumn (H = 1.01, D = 0.44). In summer, the food diversity diminished (H = 1.21, D = 0.34).

5. DISCUSSION AND CONCLUSIONS

In the study area, the diet of the European pine marten was varying, confirming the species to have an flexible feeding character and to be an efficient predator of small mammals. The species also appears to detect easily the birds' nests and young squirrels, and to take rowanberries before they fall. Mammals, however, were found to be the main prey, in agreement with what is indicated by other authors (Pulliainien 1980, Marchesi and Mermod 1989, Clevenger 1993, Jędrzejewski *et al*. 1993, Zalewski *et al*. 1995). The predator mainly focused on the genus *Apodemus*, the most abundant in the study area and a fundamental resource for this and other medium size carnivores such as the wildcat (I. Barja – unpublished). As this prey (mainly *A. sylvaticus*) is basically found in forests, it indicates a preferential use of this habitat type by the pine marten in the study area. This has been mentioned in previous studies conducted in the same area (Barja 2005) and in other parts of Europe (O'Sullivan 1983, Marchesi and Mermod 1989, Brainerd 1990).

A specialization towards taking small mammals was noticed; these preys were taken selectively although present in low densities. When a prey type is consumed with a higher frequency than that expected for its abundance, this reveals a behavior typical of a specialist species that does not change its food preferences even when that food is harder to find (Holling 1959, Begon *et al*. 1986, Jędrzejewski and Jędrzejewska 1993, O'Donoghue *et al*. 1998). In the present study, the pine marten showed no reduction in its preference for small mammals – mainly *Apodemus* sp. – in the seasons when they were more scarce (winter and spring), even though squirrels, different forest birds, insects, reptiles and carrion (roe deer and wild boar, *Sus scrofa* L.) were all available. This absence of a preference change may in part be due to the weakness of small mammals during the colder months. The winter of 2004–2005 was especially cold and dry in the study area, and influenced the physical conditions of the small mammals caught during the trapping period. This reduced the effort required of the predator to pursue and capture them. In autumn, when the abundance of small mammals in the study area was at their highest, the pine marten did not increase its predation of them. In fact it showed a preference for rowanberries, probably because this food provides an advantage in terms of energy optimization. When the pine marten consumes the berries the manipulation time diminishes (there is no pursuit phase as there is with animal prey), meaning a better energy balance for the predator (Kacelnik and Bernstein 1994).

The results of this study show that the feeding strategy adopted by the European pine marten is intermediate between that of an opportunist and specialist predator. Previous studies have classified the species as a strict opportunist. Small mammals constitute its main prey and they are consumed although present in low densities. The pine marten probably has a crucial influence on small mammal populations in forest areas, especially on the genus *Apodemus*.

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