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Reduction of potential food interference in two sympatric carnivores by sequential use of shared resources

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ABSTRACT

The common genet (*Genetta genetta*) and the stone marten (*Martes foina*) are two species that overlap extensively in their distribution ranges in southwest Europe. Available diet data from these species allow us to predict some interference competition for food resources in sympatric populations. We checked the food interference hypothesis in a sympatric population. The diet of both predators was analyzed through scat collection. Seasonal differences in biomass consumption were compared between both species in those items considered as key resources according to biomass consumption. Strawberry tree fruits can be considered as key resource exclusively for genets whereas fungi, blackberries and rabbits are keys for stone martens only. For other key resources consumed by both species (wood mouse and figs) we suggest that a possible mechanism to reduce diet overlap could be the sequential use of these resources: no intensive exploitation by both species of the same key resource during the same season was detected. Figs and wood mouse were used alternatively. Although strawberry tree fruits and blackberry are exclusive key resources of one of the species, their consumptions showed the same pattern. Diet niche overlap in our study is low compared with other carnivore communities suggesting that exclusive use of some key resources and sequential use of shared ones is an optimal scenario to reduce overall competition for food resources.

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1. Introduction

Direct and indirect interaction between species produces strong effects in the dynamics of populations and the structure of communities (Sih et al., 1985). Competition plays a key role in interaction processes (Schoener, 1974; Schoener, 1982; Keddy, 1989), but we need to show an effect on fitness to demonstrate the existence of competition (Keddy, 1989). Unfortunately the evidence of depressive effects of competi-

tion in populations of vertebrates is anecdotal, with a very limited number of experiments (Hakkarainen and Korpimäki, 1996 and references therein). Most of the evidence of existence of competition comes from patterns of character displacement on morphological traits, which have been explained as evidence of past competition between species (reviewed in Schluter, 2000).

The study of current competition in the field may be studied as a three-step process (MacNally, 1983) including: 1) evidence of resource overlap, 2) evidence of exploitative or interference interactions, 3) evidence of depressive effects on fitness. Most of the studies on competition between vertebrates were centered on the first step, as it is easily per-

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formed. Although resource overlap is not necessarily linked to competition (Wiens, 1977), something impossible to assert without a detailed knowledge of the ratio between availability of preys and number of consumers (Wiens, 1977; MacNally, 1983), there is some agreement that it is a necessary first step in any study of current competition between species (Schoener, 1974; Jones and Barmuta, 1998).

In carnivores there is some correlative evidence of the strong effect of competition on their populations and communities (Rosenzweig, 1966; Palomares et al., 1996). Most of this evidence was based on preliminary studies on the patterns of resource overlap. Thus, the study of resource overlap between sympatric species may be a useful way to deepen the knowledge of interactions and potential current competition of different carnivore species.

Competition between species is more probable when species that overlap their geographic ranges show similar body size and feeding habits. The common genet (*Genetta genetta* L. 1758) and the stone marten (*Martes foina* Erxleben, 1777) are two species with similar body sizes that overlap extensively in their distribution ranges in southwest Europe (Mitchell-Jones et al., 1999). In particular, both species have similar distribution patterns in Central Spain (Virgós and Casanovas, 1997; Virgós and Casanovas, 1998; Virgós et al., 2000). Data available from common genet and stone marten diets allow us to suggest that in this area some interference competition for food may exist between these predators (Clevenger, 1994; Virgós et al., 1999). In the northern Iberian Peninsula and southern France, the common genet has been considered a specialist predator of rodents (Livet and Roeder, 1987). Nevertheless, at southern latitudes arthropods may represent an important part of the diet, whereas fruits are relevant in some seasons (Virgós et al., 1999). The stone marten feeds on a wide variety of foods, fruits forming the main part of the diet, but small mammals and birds are important secondary preys (Clevenger, 1994). Thus, both species are food generalists with small mammals and fruits as the main key resources, but they shared a large proportion of them, at least in some seasons. Interestingly, and in support of this hypothesis of interference competition for food, data from diet studies in sympatric and allopatric populations of genets and a congeneric of stone marten—the pine marten (*Martes martes* L., 1758)—in the Balearic Islands showed that food habits of pine martens are very different in sympatry and allopatry. On islands where two species are sympatric, pine martens consumed preferably on plant material, especially fruits, whereas on islands where genets are not present, martens are more prone to prey on small mammals and other vertebrates. However genets prey mostly on small mammals in both situations (Moreno et al., 1988; Clevenger, 1993, 1995, 1996).

In areas where two species live sympatric, several mechanisms may mitigate the overlap in resource use and then the competition between them: food segregation and habitat segregation were the most relevant (Schoener, 1974), but mitigation may also be possible due to differences in competitive ability in different habitats (e.g. Kotler and Brown, 1999 and references therein) or to temporal segregation, for instance differences in circadian activity (Schoener, 1974; Jones et al., 2001). Temporal segregation in the use of resources

may be also possible through a sequential use of the shared resources, but this alternative has not been considered so far. In the case of genets and stone martens, reduction of competition or interference interactions is not probable by habitat differences, at least in most of the distribution range where both species exploited similar habitats (Virgós and Casanovas, 1997; Virgós and Casanovas, 1998). Microhabitat differentiation (e.g. Rosenzweig, 1987 for small mammals) could be possible but has so far not been checked. Circadian activity of both species was very similar, and thus segregation following a diel temporal scheme is not very probable (Genovesi et al., 1997; Munuera and Llobet, 2004). Food divergence or sequential use of this resource could be an alternative to allow coexistence of both species in sympatric areas. However, despite their abundance and the large number of diet studies of these species in the Mediterranean, to our knowledge no studies have been undertaken to compare the diet of sympatric common genet and stone marten populations in this region, and only one has been carried out in the Euro Siberian region (Carvalho and Gomes, 2004), where diet patterns are different from the Mediterranean (Clevenger, 1994; Virgós et al., 1999). The aim of this study is to describe the year-round overlap pattern in shared key resources and to analyze the patterns found according with known resources availabilities in the study area. Specifically (1) we compared the seasonal patterns of diet diversity and consumption of food resources. (2) We studied the trophic niche overlap, which is expected to be high between these species (Carvalho and Gomes, 2004), and its change through the seasons. (3) We compared the temporal use of key food resources along seasons by both species, comparing if these are used simultaneously by genets and stone martens.

This diet information is the base for future research on feeding ecology and potential competitive interactions between these species in the large areas of sympatry in the south-western part of the Mediterranean region.

2. Methods

2.1. Study area

We performed the study in Montes de Toledo (Province of Toledo, Central Spain) (39°35'N, 4°41'W). The study area was about 120 km² in size and most of it was included within the Cabañeros National Park. The altitude range is 750–1250 m a.s.l. and the annual rainfall was 640 mm whereas temperatures varied between 3.6 °C in average in December and 25.3 °C in August during the study. The scrub habitats are dominated by holm oak (*Quercus ilex*) and gum cistus (*Cistus ladanifer*) (50% of total surface), with mono-specific patches of Pyrenean oak (*Q. pyrenaica*) (25%), cork oak (*Q. suber*) (10%) and pine (*Pinus* spp.) plantations (10%) (Vaquero, 1997). In addition, in some wet areas, the scrubland is more diverse and several species with fleshy fruits like Strawberry tree (*Arbutus unedo*) and Blackberries (*Rubus* spp.) are common. The ripening season extends from October to January in the former species and between July and October in the latter (Vaquero, 1997). There are also many kitchen gardens

and meadows on the river-banks (5%), where figs (*Ficus carica*) are widespread but always in low number of feet (1–4) per patch what becomes it a very located resource. This species extends its ripening season from June to September in our study area (Vaquero, 1997). This vegetation pattern and habitat characteristics are typical for both the Iberian Peninsula and many other Mediterranean habitats of southern Europe (Peinado and Rivas-Martínez, 1987).

2.2. Sample collection

Between October 1998 and December 2000, 152 common genet and 142 stone marten scats were analyzed in this study. In order to optimize the laboratory work, the scats ultimately analyzed were randomly selected from the bigger pool of those collected, respecting seasonal and spatial proportions. The faeces were collected every 2 weeks: common genet scats were collected from nine monitored latrines and stone marten ones were collected along four established transects that ranged in length from 3 to 5 km and were spaced 2–8 km. The latrines and transects sampled were spaced throughout the study area in order to be representative of the local population and to record its possible variability.

After soaking the faeces in water for 24–48 hours, these were broken down and the solid remains graded in size using a water jet and a sieve. Food items were identified by microscopic analysis and compared to seeds, feathers and skins collections and by using identification keys. Single characteristics (e.g. teeth, beaks or stings) were used to individualize the preys. Twenty-five fruits of each multi-seed fruit species (strawberry tree fruits, figs, blackberries and grapes *Vitis vinifera*) were collected from the study area, opened, and their seeds counted to establish the average number of seeds per fruit. When analyzing the scats, the number of seeds in each were counted to extrapolate the number of fruits of each species consumed per scat. In the particular case of European rabbits (*Oryctolagus cuniculus*) teeth were used to estimate ages and sizes (Calzada et al., 2003). Food items were identified to species level whenever possible.

For the analyses, we pooled the data into four seasons: autumn (September–November), winter (December–February), spring (March–May) and summer (June–August). The identified food items were ascribed to one these five categories: a) vegetative material, b) invertebrates, c) reptiles, d) birds or e) mammals. The biomass of each prey item was calculated using prey weights from individuals collected in the study area and further data from references (Delibes, 1974; unpublished data from the authors). Because these species only may consume 200 g each time (Delibes, 1974; Cuesta, 1994), we consider this number as the top biomass value per scat when large preys like carrion or rabbit were present. The diet was expressed quantitatively as percentage of consumed biomass [$PB = (\text{biomass of food item } i / \text{total biomass}) \times 100$]; additionally we also presented frequency of occurrence [$FO = (\text{number of scats with the food item } i / \text{total number of scats}) \times 100$] in Appendices A and B. Frequency of occurrence was only used to ensure our work could be compared with other studies where FO values were widely used, but they were not used in the statistical analyses of the present study.

In comparative studies with sympatric species that include diets and diversity indices, it is very important to define levels of analysis more closely in order to understand the underlying process shaping the patterns observed (Serafini and Lovari, 1993). We defined “key resources” a priori as those that exceed 10% in mean biomass in any season (Appendices A and B). Key food resources, which are not necessarily limiting resources, represented those resources very important to shaping life-history traits of the species, and in carnivores are those food resources largely consumed, that were strongly related to life-history traits such as territory size, body condition, sociality, or reproductive output (Gompper and Gittleman, 1991). Thus, in our study, these key food resources are figs, strawberry tree fruits and wood mouse for genet, and fungi, figs, blackberries, wood mouse (*Apodemus sylvaticus*) and rabbits for stone martens. We excluded carrion as “key resource” as we consider its consumption is incidental: there are no dumps in the surrounding area and all the carrion in the study area comes from wild ungulates.

2.3. Statistical analyses

We used two-way ANOVA on PB data from the two species to test seasonal (considering both species together) and species differences in consumption. The seasonal difference in the consumption of resources between both species was tested through the interaction term of the ANOVA.

Trophic niche breadth was calculated using Levins (1968)'s index with the five food general taxonomic categories. This index varies from 0 to ∞ , 0 being the minimum value of niche breadth. Trophic niche overlap was calculated using Pianka's index (1973). This index varies from 0 to 1, 0 being the minimum overlap value.

3. Results

3.1. Overall diet pattern

Within animal preys, the only food key resource for genets was wood mouse (54.7% of mean biomass) (Appendix A). Especially relevant was the consumption of figs (15.2%); less important were strawberries (3.7%), although this latter represented 14.6% during autumn. Other fruits potentially consumed both for genets and stone martens were of minor overall relevance in mean biomass.

In the case of stone martens fungi dominated the diet of stone martens throughout the year (21.9% in mean biomass) (Appendix B). Within fruits, the main key food resource was figs (15.7%) and blackberries (year-round 3.9%; but 15.6% in summer). The rest of the species showed lower values. Overall consumption of fruits by stone martens was 6.6% of mean biomass, a value close to the genet (5.5% of mean biomass). As in the case of genets, the main prey item within small mammals for stone martens were wood mouse which accounted for 15.8%.

Table 1 – Trophic niche breadth (Levins' index) and trophic niche overlap (Pianka's index) between stone marten and common genet in Cabañeros National Park (Central Spain)

Season	Stone marten	Genet	Overlap
Autumn	1.49	1.66	0.33
Winter	1.46	0.72	0.19
Spring	1.92	1.15	0.58
Summer	2.29	1.77	0.20

3.2. Trophic niche breadth and trophic niche overlap

The stone marten always had a wider trophic niche than the common genet, other than for autumn (Table 1). The trophic niche was broader in summer for both species, while the lowest values were in winter. The diet overlap was relatively low (range 0.19–0.33) throughout the year, except in spring (0.58) when wood mouse reached 24.4% in the diet of stone marten, the largest value for this species (Table 1).

3.3. Key resources

For key resources we also detected large differences between both species for fungi, wood mouse and rabbit (Table 2). Fungi consumption is only detected for stone martens, with large consumption in the autumn–winter seasons. During summer stone martens did not consume this resource (Fig. 1). In the case of wood mouse, the pattern was very different in that genets consumed large amounts of this prey all year-round except for summer, when stone martens consumed higher proportions than the genet (Fig. 1). Rabbit consumption was higher in stone martens than in genets, especially during spring, and to a lesser extent in summer. In autumn and winter the consumption of rabbits was very

Table 2 – Results from two-way ANOVA's with species and season as fixed factors and the different key resources as response variables

Food resource	df	F	P
<i>Fungi</i>			
Species	1,282	36.58	< 0.001
Season	3,282	8.95	< 0.001
Species × season	3,282	9.05	< 0.001
<i>Figs</i>			
Species	1,282	0.26	0.61
Season	3,282	9.65	< 0.001
Species × season	3,282	7.25	< 0.001
<i>Strawberry tree fruit</i>			
Species	1,282	2.33	0.13
Season	3,282	3.82	0.01
Species × season	3,282	5.62	< 0.001
<i>Blackberries</i>			
Species	1,282	2.08	0.15
Season	3,282	6.18	< 0.001
Species × season	3,282	2.72	0.04
<i>Wood mouse</i>			
Species	1,282	38.97	< 0.001
Season	3,282	7.38	< 0.001
Species × season	3,282	8.37	< 0.001
<i>Rabbits</i>			
Species	1,282	4.95	0.03
Season	3,282	2.68	0.05
Species × season	3,282	2.21	0.09

low in both species (Fig. 1). We did not detect statistical differences in the consumption of figs, strawberry tree fruits and blackberries (Table 2), and then the large differences detected in the vegetative material item appear to be due to the high differences observed in fungi consumption rather than to differences in fruit consumption. Genets consumed large amount of figs in summer and stone martens in autumn (Fig. 1). For strawberry tree fruits, consumption is relatively low except for genets in autumn and to a lesser extent for stone martens in winter. Blackberry consumption was focused on the summer season, with a higher consumption for stone martens, although this difference was not statistically significant (Fig. 1).

3.4. Sequential use of key resources

Although we have not detected differences in the consumption of several key resources between genets and stone martens, a possible mechanism of reducing diet overlap could be the sequential use of the same resource. We tested this alternative by looking at the interaction term of the ANOVA analyses performed.

Significant interaction terms were detected for fungi, figs, strawberry tree fruits, wood mouse and blackberry consumption. In the first, the significant interaction term can be explained by the large differences observed between both species in autumn and winter and the lower differences in the rest of seasons (Fig. 1). In the case of figs, the interaction term was highly significant due to a different importance of this resource for each species according to the season (sequential use). Genets consumed figs mainly in summer whereas stone martens showed very low consumption (Fig. 1). In contrast, stone martens consumed higher proportions of figs during autumn whereas genets considerably reduced the consumption of this resource (Fig. 1). A similar pattern was found for strawberry tree fruits, although less evident than that observed for figs. Genets consumed large amounts of this resource during autumn whereas stone marten did not consume it (Fig. 1), however in winter genets did not consume fruits of this species, while stone martens included it in moderate proportions in its diet (Fig. 1). For wood mouse, the significance of the interaction term was due to a higher consumption of this species for stone martens than for genets in summer, while during the rest of seasons genets consumed a much higher proportion of this species than did stone martens (Fig. 1). Finally, the interaction term was significant for blackberry consumption as a consequence of the large difference observed during summer, when stone martens consumed large proportions of this fruit, and the very similar consumption the rest of year, but with a slighter higher consumption for genets during autumn, when stone martens did not consume this resource (Fig. 1).

4. Discussion

We define key resource a priori as that resource accounting for more than 10% in mean biomass in any season for any of these two sympatric carnivores. Thus, we have a total of six

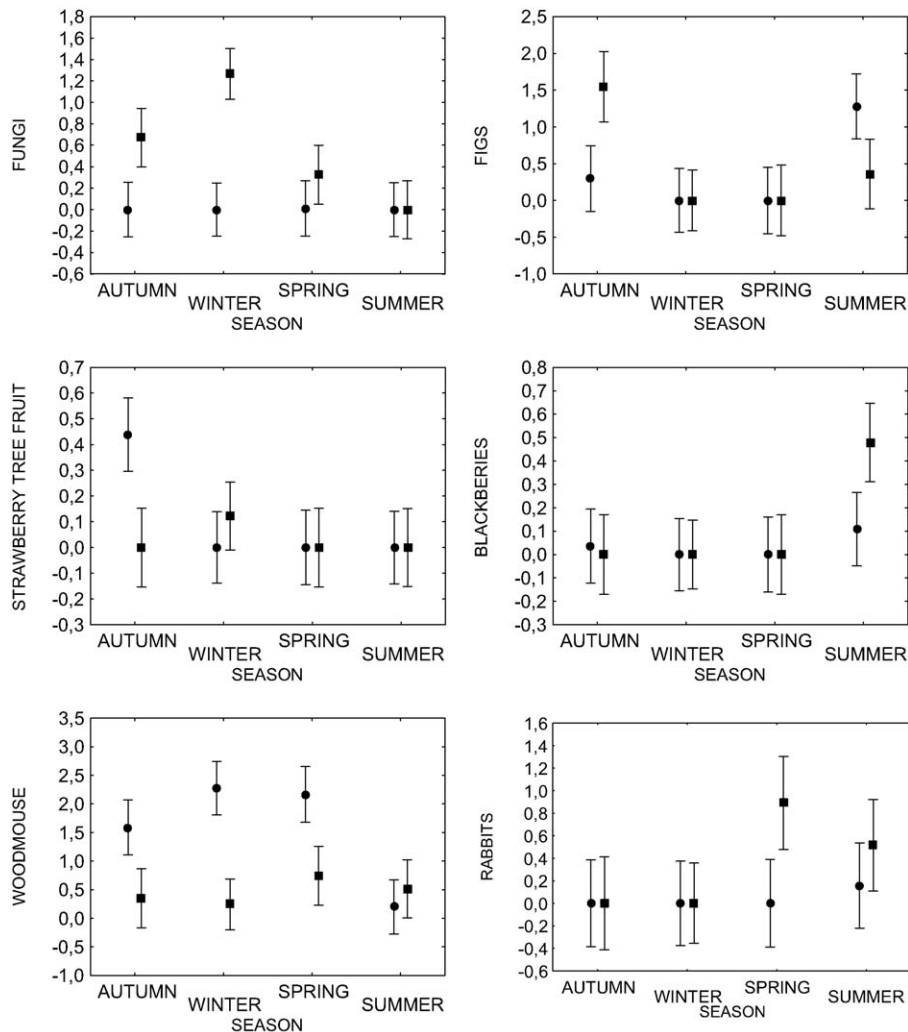


Fig. 1 – Means (squares and circles) and 95% confidence intervals (bars) indicating the seasonal consumption of the key food resources defined in this study for genets and stone martens. Stone marten values were represented by squares and genet ones by circles.

key resources. One of them (strawberry tree fruits) was exclusive to genets, three were exclusive to martens (fungi, blackberries and rabbits) and, finally, two were important both for genets and stone martens (figs and wood mouse). Trophic competition should be negligible in those key resources exclusive of one species (Carvalho and Gomes, 2004), but in the two key resources important for both species there is potential food interference, in which case trophic competition could be minimized by the sequential use of these resources.

Diet niche overlap in our study is low compared with other carnivore communities (e.g. Jaksić and Delibes, 1987; Serafini and Lovari, 1993; Clevenger, 1995; Baghli et al., 2002; Padiál et al., 2002; Carvalho and Gomes, 2004), suggesting that exclusive use of several food resources (e.g. fungi or blackberries) and sequential use of the other key resources is an optimal scenario to reduce overall competition for food resources (Schoener, 1974; Keddy, 1989).

According to the competition theory, the high overlap in the diets among sympatric species should be higher when a

key resource is abundant and this is the same for both species (Schoener, 1982), but this is not true between genets and martens in our study area. On the other hand, other research shows that populations of generalist species may specialize by means of behavioral responses to variation in abundance of their main prey, hence reducing their niche breadth (Futuyma and Moreno, 1988; West-Eberhard, 1989). The scarcity of the main resource can be overcome with alternative strategies such as increasing the searching efficiency, spending more time searching or changing their feeding areas (e.g. Ward and Krebs, 1985; Fietz and Ganzhorn, 1999; Kotler and Brown, 1999). This seems to have been the case in our study.

Studies on the diet of common genet are relatively numerous in the Mediterranean areas (reviewed in Virgós et al., 1999), and most of them agree that the wood mouse is the main prey according to biomass. Nevertheless, Virgós et al. (1999) have also shown that genets are able to concentrate their feeding activity on other resources when wood mouse availability is low, or other resources are more profitable, or

both. The latter may be the case in the scrublands of Central Spain when we compared figs and wood mouse consumption throughout the seasons.

Data from our work indicates that the common genet based its diet primarily on consumption of the wood mouse. Nevertheless, populations of this species are lower in summer (Moreno and Kufner, 1988) and then its consumption by genets dramatically decreased. Figs mature between summer and the middle of autumn (Vaquero, 1997), and they are an alternative and profitable resource for genets. Thus, during summer figs are the main food item for genets, compensating for the reduction in the wood mouse availability at this season. Fig consumption can not be considered as “incidental” because genet changes its searching strategy, leaving the scrubland and going to market gardens in order to get figs to replace wood mice. In autumn, as wood mouse population increases due to reproduction (Moreno and Kufner, 1988), genets return to prey on wood mouse on scrubland as their main food resource, and figs are not consumed despite their high availability during the first half of autumn (Vaquero, 1997). From this result, it could be suggested that genets prefer wood mouse to figs, and only the low availability of the former may lead genets to a seasonal specialization on figs. Other researchers have proposed that fruit specialization of other carnivores such as stone martens could be a response to a decline in protein ingestion from small mammals (Serafini and Lovari, 1993; Genovesi et al., 1996; Pandolfi et al., 1996) and this could be the case of the genets in our study area.

Although genets preferred wood mouse to any fruit species, the common genet was selective when feeding on fruits. Figs are eaten in summer and strawberry tree fruits in autumn. Blackberries, whose maturing period overlaps with figs and strawberry tree fruits (Vaquero, 1997), are consumed less than figs or strawberries despite its large field availability (Vaquero, 1997). This situation has also been observed for other carnivores (e.g. Serafini and Lovari, 1993; Gil-Sánchez, 1996; but see Delibes, 1978) and is possibly due to fruit characteristics such as scent, flavor, size and pulp content, which may influence its choice by carnivores (Herrera, 1987). Also important is the distance among consecutive stems of every species on the field, or even the productivity per species: this is very important to optimize the searching activity (e.g. Ward and Krebs, 1985; Fietz and Ganzhorn, 1999). Both figs and strawberry tree fruits are bigger, have more pulp content and their distributions are more concentrated in the field than blackberries.

In relation to the stone marten, the data indicate a very complex pattern of food use. Several authors have proposed the relative specialization of this species on fruits being small mammals also important (reviewed in Clevenger, 1994; Pandolfi et al., 1996). Our data partially supports this hypothesis: fruits and small mammals dominated the diet of stone martens, but fungi (autumn and winter) and rabbits (spring and summer) also represented key resources for the species. Fungi could represent a very suitable and abundant source of proteins and other resources for stone martens during cold winters, and can perhaps replace the relatively low availability of fleshy fruits during this season. Particularly noteworthy is the capture of rabbits by the stone mar-

ten, despite being very scarce in the study area (Authors, unpub. data). Genet can capture rabbits (Virgós et al., 1999) but in our research this prey is scarce in its diet.

Figs are the main fruit species both for genets and stone martens, but the pattern of consumption differed in both species. Figs represented the bulk of the diet of stone martens in autumn, whereas in summer its importance is lower. In genets the opposite was observed. Figs are available in both seasons, when one could expect a similar consumption in both seasons, but genets and stone martens selectively consumed large proportions of figs at different seasons. The strawberry was also consumed by stone martens, although it is only in winter when consumption reached some minor importance, whereas in autumn, when availability is higher (Vaquero, 1997), there is no consumption of this species. In other areas where strawberry is available it was included in a relatively significant amount in the diet of stone martens in both seasons (Amores, 1980). Strawberry is a large fruit, with characteristics in size and pulp/seed ratio similar to other important fruits consumed by the marten species. In this case, the low proportion of this species in the diet of stone martens is paradoxical, especially when observing the relatively large ingestion by genets during autumn. One possible explanation could be the existence of interference for food between both carnivore species, which is highly probable between predators of similar size (Rosenzweig, 1966; Jaksić et al., 1981; Caro and Stoner, 2003).

The existence of interference for food was supported by several factors:

First, stone marten begins the consumption of figs—a cultivated species—in autumn, not in summer when figs are already available (Vaquero, 1997). In autumn, genet stops its consumption because it preys on largely available and preferred wood mouse in the scrubland. In this season, the lack of consumption of strawberries for stone martens could be due to its preferential use of cultivated areas (Lodé, 1994) where figs are present. In contrast, genets consumed large proportions of strawberry tree fruits in autumn in the scrubland where wood mouse has higher densities (Camacho and Moreno, 1989). In winter, when figs are not available, stone marten start searching other resources (especially fungi) in the scrubland and can find strawberries because feet of this species are distributed in the scrubland. In this season, genets did not consume this fruit, perhaps due to the large availability of wood mouse, which allowed them to avoid interference for strawberry fruits with stone martens. This sequential use of the same resources minimizes overlap and probably food competition for a limiting resource (figs or strawberries) between both species.

Second, in contrast to genets, blackberries—which are widespread in the field (Vaquero, 1997)—were consumed in relatively large amounts by stone martens, a pattern observed elsewhere (Delibes, 1978; Serafini and Lovari, 1993; Lodé, 1994). Nevertheless, in other Mediterranean areas the consumption of blackberries is very low (Amores, 1980; Gil-Sánchez, 1996; Pandolfi et al., 1996). The low consumption of blackberries in these areas could be due to differences in availability between locations or because ripening of several fruit species overlapped and stone martens may prefer some species to others. For example, Gil-Sánchez (1996) suggested

that low consumption of blackberries was due to its temporal overlapping with fig availability and the greater preference of stone martens for the latter. In our study area, figs and blackberries also showed overlapping ripening times, but in contrast to data from south-eastern Spain (Gil-Sánchez, 1996), stone martens consume blackberries fruits in large amounts during summer, when figs are highly available (the main item in the genet diet during summer, see above). Thus, two potential explanations could explain the large consumption of blackberries in summer compared to the data presented by Gil-Sánchez (1996): i) the preference for blackberries or figs depending on environmental availability, in which case when blackberry or figs are highly available in some patches, then stone martens specialize in them; ii) other processes such as the above-mentioned food interference with other frugivorous species may change the value of a particular fruit species from one location to another. We did not know the availability of blackberries in the location studied by Gil-Sánchez (1996), and thus we cannot reject the first alternative. Nevertheless, the author indicated that the species is abundant in the study area. We suggest that the food interference hypothesis is highly possible, because genets consumed figs in large amounts during summer (see above), when stone martens appear to avoid this highly profitable resource, searching for alternatives ones, including blackberries.

Third, wood mouse is the main small mammal consumed by stone martens, but its importance is very low compared to the genet diet, and the seasonal consumption of wood mouse not coincides with that of genets. The large value was found in spring—when fruits are scarce—with low proportions during winter and autumn, when wood mouse is very abundant (Moreno and Kufner, 1988). Surprisingly, the consumption of wood mouse in summer, when availability is very low, is similar to autumn and winter and a higher than in the case of genets is observable. It could be suggested that consumption of wood mouse by stone martens was not related to availability, as in the case of genets. The hypothesis of feeding interference appears again as a possible explanation: in this season, genets prefer to feed on figs because are quite predictable and profitable because generate an optimum energy outcome compared with the always difficult to hunt, and now scarce, wood mouse. On the contrary, although wood mouse has now lower populations, stone

marten moves its hunting activity to this prey to avoid interference with genet.

The possible exclusion of food patches of one of the species by the other would require a detailed knowledge of microhabitat use of both species. Unfortunately, the studies regarding the use of space and other ecological aspects of genets and stone martens living in sympatry or rejection behavior observations are almost nonexistent. Thus we can not conclude that stone martens are forced from their core areas by genets during the limiting seasons (especially fig patches in summer) as seems to occur in Balearic Islands between genet and pine marten (a stone marten's sibling species) with year-round diet at island level (Moreno et al., 1988; Clevenger, 1993, 1995, 1996). Nevertheless, a preliminary recent study (Mangas et al., 2005) is consequent with this hypothesis since genets and stone martens do not coincide in 1×1 km squares sampled in a pinewood in Central Spain. Future more exhaustive research may elucidate the potential spatial interactions between these species according to food availability and dispersion, and its impact on other key life-history traits of both species.

Altered patterns of resources can not be claimed as certainty of competition but supported the existence of resource partitioning to allow coexistence (MacNally, 1983). This coexistence could then be possible due to the large variations in the relative seasonal abundance of alternative food resources (e.g. figs–wood mouse–fungi) and the high patchiness of the Mediterranean environments which allow species to inhabit the same area but exploiting different food patches (Wiens, 1976; Hakkarainen and Korpimäki, 1996).

Our data supported potential food interference between genets and stone martens as an explanation of the food patterns found. The relative low seasonal overlap between both species seems to be a consequence of a sequential use of shared food key resources that minimizes this overlap.

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Appendix A

Food items expressed as percent biomass in common genet scats from Cabañeros National Park (Central Spain), 1998–2000 (percentage frequency of occurrence in parentheses).

Food category/food item	Autumn		Winter		Spring		Summer		Mean
	37		39		37		39		
Number of scats	37		39		37		39		
Vegetative material	28.2	(51.5)	1.1	(5.2)	1.0	(8.3)	57.5	(33.3)	22.0
Fungi	–	–	–	(–)	0.4	(2.8)	–	(–)	
<i>F. carica</i>	9.9	(27.0)	–	(–)	–	(–)	50.7	(28.2)	
<i>Rubus ulmifolius</i>	1.2	(5.4)	–	(–)	–	(–)	4.3	(7.7)	
<i>A. unedo</i>	14.6	(21.6)	–	(–)	–	(–)	–	(–)	
Other fruit	2.5	(5.4)	1.1	(5.2)	0.6	(5.6)	2.5	(–)	
Invertebrates	2.1	(70.3)	0.9	(48.7)	4.0	(72.2)	14.4	(94.9)	5.3
<i>Buthus occitanus</i>	0.4	(8.1)	–	(–)	–	(–)	4.7	(61.5)	
<i>Scolopendra cingulata</i>	–	(–)	–	(–)	0.3	(5.6)	1.5	(23.1)	
Orthoptera	0.6	(29.7)	0.1	(7.7)	–	(–)	4.8	(64.1)	
Coleoptera	1.1	(48.6)	0.8	(48.7)	2.4	(66.7)	2.6	(76.9)	
Other invertebrates	–	(–)	–	(–)	1.3	(11.1)	0.8	(7.7)	
Reptiles	–	(–)	–	(–)	0.5	(5.6)	0.6	(7.7)	0.3
Birds	13.1	(35.1)	9.3	(38.5)	12.5	(27.8)	9.1	(12.8)	11.0
<i>Erithacus rubecula</i>	1.3	(8.1)	1.9	(10.3)	3.0	(11.1)	–	(–)	
<i>Turdus merula</i>	6.5	(8.1)	–	(–)	–	(–)	6.3	(5.1)	
<i>Parus major</i>	1.4	(5.4)	2.9	(10.3)	2.3	(5.6)	–	(–)	
Other passerines	0.7	(2.7)	0.9	(2.6)	1.1	(5.6)	–	(–)	
Unidentified passerines	3.2	(13.5)	3.6	(12.8)	6.1	(13.9)	2.8	(7.7)	
Mammals	56.6	(64.8)	88.7	(87.2)	82.0	(72.2)	18.4	(23.1)	61.4
<i>Crocodyra russula</i>	0.4	(2.7)	–	(–)	0.8	(2.8)	1.3	(5.1)	
<i>Microtus duodecimcostatus</i>	2.3	(5.4)	2.4	(5.1)	3.8	(2.8)	–	(–)	
<i>A. sylvaticus</i>	53.1	(64.8)	84.4	(87.2)	73.6	(72.2)	7.8	(12.8)	
Other small mammals	0.8	(5.4)	1.9	(5.1)	–	(–)	–	(–)	
<i>O. cuniculus</i>	–	(–)	–	(–)	–	(–)	6.3	(5.1)	
Carrion	–	(–)	–	(–)	3.8	(2.8)	3.0	(2.6)	

Appendix B

Food items expressed as percent biomass in stone marten scats from Cabañeros National Park (Central Spain), 1998–2000 (percentage frequency of occurrence in parentheses).

Food category/food item	Autumn		Winter		Spring		Summer		Mean
	32		43		32		33		
Number of scats	32		43		32		33		
Vegetative material	80.3	(100.0)	70.4	(81.3)	9.1	(46.9)	33.5	(39.4)	48.3
Fungi	21.6	(65.6)	58.8	(67.4)	7.0	(28.1)	–	(–)	
<i>F. carica</i>	50.8	(28.1)	–	(–)	–	(–)	11.8	(12.1)	
<i>Rubus ulmifolius</i>	–	(–)	–	(–)	–	(–)	15.6	(12.1)	
<i>A. unedo</i>	–	(–)	5.3	(2.3)	–	(–)	–	(–)	
Other fruit	7.9	(9.4)	6.3	(11.6)	2.1	(18.8)	6.1	(21.2)	
Invertebrates	7.0	(71.8)	10.7	(67.4)	3.7	(75.0)	19.9	(72.7)	10.3
<i>Buthus occitanus</i>	–	(–)	–	(–)	0.6	(6.3)	1.4	(12.1)	
<i>Scolopendra cingulata</i>	–	(–)	1.3	(7.0)	1.6	(9.4)	7.7	(27.3)	
Orthoptera	3.1	(59.4)	0.3	(7.0)	0.1	(6.3)	0.6	(12.1)	
Coleoptera	1.9	(40.6)	7.0	(58.1)	1.4	(62.5)	1.7	(45.5)	
Other invertebrates	2.0	(15.6)	2.1	(4.7)	–	(–)	8.5	(12.1)	
Reptiles	1.3	(3.1)	–	(–)	2.1	(5.4)	–	(–)	0.9
Birds	–	(–)	8.3	(7.0)	10.5	(9.4)	9.6	(11.1)	7.1
<i>Erithacus rubecula</i>	–	(–)	2.1	(2.3)	–	(–)	–	(–)	
<i>Turdus merula</i>	–	(–)	–	(–)	4.9	(3.1)	–	(–)	
<i>Parus major</i>	–	(–)	3.0	(2.3)	2.9	(3.1)	–	(–)	
Other passerines	–	(–)	–	(–)	–	(–)	–	(–)	
Unidentified	–	(–)	3.2	(2.3)	2.7	(3.1)	9.6	(9.1)	
Mammals	11.4	(9.4)	10.6	(4.7)	74.6	(34.4)	37.0	(18.2)	33.4
<i>Crocodyra russula</i>	–	(–)	–	(–)	–	(–)	3.4	(6.1)	
<i>Microtus duodecimcostatus</i>	–	(–)	–	(–)	2.7	(3.1)	–	(–)	
<i>A. sylvaticus</i>	11.4	(9.4)	10.6	(4.7)	24.4	(15.6)	16.8	(6.1)	
Other small mammals	–	(–)	–	(–)	–	(–)	–	(–)	
<i>O. cuniculus</i>	–	(–)	–	(–)	28.0	(9.4)	16.8	(6.1)	
Carrion	–	(–)	–	(–)	19.5	(6.3)	–	(–)	

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