Spatial distribution models in a frugivorous carnivore, the stone marten (*Martes foina*): is the fleshy-fruit availability a useful predictor?

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Abstract
Fleshy-fruit availability is rarely used as a predictor in stone marten (*Martes foina*) habitat models, despite its frugivorous carnivore diet. Data on stone marten occurrence, habitat structure and fleshy-fruit species abundance was collected along 2 km long survey routes within 2 x 2 km sample plots (n = 30). Two different spatial scales were considered: 1) the entire survey route; and 2) 200 m segments within each 2 km survey route. Data analyses included Poisson General Linear Models (GLM) and Generalized Linear Mixed Models (GLMM) for the first and second approaches, respectively.
Strawberry tree (*Arbutus unedo*) availability was significantly and positively correlated to stone marten occurrence at both spatial scales, particularly for the large-scale model. At the larger scale, a lower correlation to the traditional habitat structure variables was observed. Tree cover was the most important variable in the small-scale model, but strawberry tree availability was also an important predictor. Stone marten abundance was low in areas of high tree cover and absence of strawberry trees; emphasising the prominent role of strawberry trees *per se* in the abundance of stone martens. Our results indicated that including fine, field-derived estimates of key food resources for species can increase the utility of habitat models.
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Keywords
Arbutus unedo; Generalized Linear Mixed Model; niche models; mutualisms; sign surveys; stone marten

Introduction

The stone marten (*Martes foina*) is widely distributed throughout the Mediterranean basin and is the most common marten species in central Europe (Libois and Waechter, 1991; Mitchell-Jones et al., 1999). In most of central Europe, the species is primarily

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associated with human environments (Skirnisson, 1986; Libois and Waechter, 1991; Herrmann, 1994; but see Goszczynski et al., 2007). However, in the Mediterranean region, the species prefers forests and mosaics of forests, shrubs and rocky habitats rather than human environments in forest-dominated landscapes (Sacchi and Meriggi, 1995; Genovesi et al., 1997; Virgós and Casanovas, 1998; Virgós et al., 2000).

Interestingly, despite their abundance and habitat preferences, few studies to address differences in stone marten habitat associations across the range of the species have been conducted. The majority of the work reported has been based on radio-tracked individuals over small geographic areas (Skirnisson, 1986; Herrmann, 1994; Genovesi et al., 1997; Rondinini and Boitani, 2002). Studies over large areas have rarely been performed (Sacchi and Meriggi, 1995; Virgós and Casanovas, 1998; Virgós et al., 2000), and of those, sampling has covered only a small fraction of available habitats in Mediterranean regions.

Plant species characteristic of the Mediterranean are largely fleshy-fruit producers, which may be the primary food resource for stone martens (Clevenger, 1994; Genovesi et al., 1996; Pandolfi et al., 1996; Barrientos and Virgós, 2006). Stone martens can consume a large amount of fruit when available, and the species is considered the most frugivorous carnivores in Europe (see Rosalino and Santos-Reis, 2009). Pandolfi et al. (1996) demonstrated that fruits are a crucial part of marten diets and compensate energy deficiencies in seasons with low small mammal availability or other alternative food sources. Therefore, fruits can be considered a key food resource for stone martens, even in regions where prey species are most often consumed.

The influence of key food resources on the abundance and distribution of other carnivores has been well documented (e.g. earthworms and badger, Woodroffe and Macdonald, 1993; fish and otters, Kruuk, 1995; rabbits and lynx, Palomares et al., 2001; wolves, Paquet et al., 2006). However, little data is available for stone martens, although it has been shown that home-ranges and spacing patterns are mainly shaped by the distribution and abundance of food resources (Powell, 1994). Recently, Mortelliti and Boitani (2008), showed the pivotal importance of fruit availability to explain stone marten distribution in a fragmented landscape.

In the present study, we tested the applicability of habitat models in several broad contexts. First, we determined if the importance of fruit availability as a resource could be extended over continuous scrubland landscapes, covering large areas of southern Europe. It is vital to develop habitat models built over different landscape scenarios to assist managers and conservationists (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Elith et al., 2006); and a priority to develop habitat models that include factors such as potential predators, main food resources, mutualists, and habitat structure (Austin, 2002; Araújo and Guisan, 2006; Austin, 2007). For example, researchers have developed different habitat suitability models used in forestry and other human intervention planning at the landscape scale for different *Martes* species in North America (e.g. Buskirk and Powell, 1994; Carroll et al., 1999; Slauson et al., 2007). However, these studies have used habitat structure or composition as surrogates of important food or shelter resources. The situation is even worse for the Paleartic *Martes* species, and particularly for stone martens. Only one study included food availability or presence as a predictor of stone marten habitat use (Mortelliti and Boitani, 2008),

but it was developed in a fragmented scenario, and fruit availability was measured as a composite cover of fruiting species rather measuring specific species. In this work, several of the preferred food resource species were measured in some detail. The habitat model served to improve stone marten management and knowledge regarding species habitat requirements over a distinct part of their geographic range.

In this study, we describe the habitat associations of stone martens in typical scrubland communities of west-central Spain at two spatial scales. We used both variables related to habitat structure and several variables related to the availability of key fleshy fruit species incorporated in the diet of stone martens.

Material and methods

Study area

The study was conducted in the Monfragüe National Park in Cáceres Province (west-central Spain; fig. 1) during the spring of 2004 (period end March-end May). Monfragüe is typical of the Mediterranean vegetation in central Spain; comprised of woodlands dominated by cork oak (*Quercus suber*), with a large diversity of shrubs including strawberry trees (*Arbutus unedo*), *Cistus* spp., *Phyllirea angustifolia*, and *Erica* spp. (Peinado and Rivas-Martínez, 1987). Other fleshy fruits species include blackberries (*Rubus* spp.) and wild rose (*Rosa* spp.), which are scarce and exhibit a patchy distribution. Fleshy-fruit species were not bearing fruit during the period of sampling. In addition to woodlands, in some areas, eucalyptus (*Eucalyptus globulus*) and pine (*Pinus* spp.) plantations, deforested areas (mainly due to activity to remove eucalyptus), and dehesas (formations with scattered cork oaks and holm oaks (*Quercus ilex*)
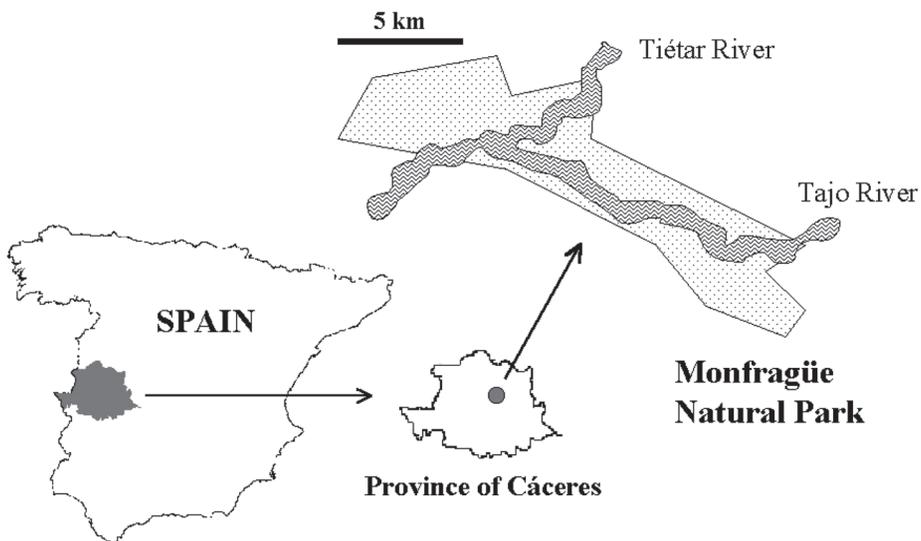

Figure 1. Location of the study area. Monfragüe National Park, Iberian Peninsula, Cáceres Province. Reprinted from Lozano et al. (2007), © Elsevier, 2007.

without an understory shrub layer) dominate the landscape. Moreover, land use by humans has also modified the potential vegetation, most notably free-ranging livestock in the dehesas. Climate is typical Mediterranean, with hot and dry summers, mild winters, and moderately rainy autumns and springs (Font, 1983).

Sampling protocol

Monfragüe was divided into plots of 2 × 2 km following UTM (Universal Transverse Mercator) coordinates. A total of 30 plots were sampled, which homogenously covered approximately 85% of the total surface area of the park. In each plot, stone marten scat was searched over a 2 km survey route. The survey routes were along paths of 2-5 m widths, and routes with car traffic were avoided. Most of the park is closed to the public, so paths and roads are rarely used. Survey routes were typically placed in the middle of the plot, and placed so all representative habitats were covered.

Stone marten scat was identified from other sympatric species such as red foxes (*Vulpes vulpes*) and dogs (*Canis familiaris*) by shape, size, and smell. When identification of a particular scat was not definitive, the sample was not considered in deriving the occurrence index to avoid bias in abundance estimates (see Sadlier et al., 2004 for similar recommendations). Scat sign surveys have proven the most reliable and efficient method to detect stone martens in Mediterranean landscapes (Barea-Azcón et al., 2007).

Each survey route was divided into 200-m length segments that yielded 10 segments per route to derive an occurrence frequency index (He and Gaston, 2000; see also a similar methodology in Lozano et al., 2003, 2007). In each segment, the presence or absence of stone marten scat was recorded, which allowed the derivation of a simple occurrence index as follows: number of segments with scat/10. This index mitigated the potential bias of an index based on scat density (discussed in Virgós et al., 2000). The potential bias produced by sampling during different seasons (e.g. Andelt and Andelt, 1984) was avoided by restricting sampling to spring.

During survey route sampling, a series of variables related to species habitat quality was counted or estimated: tree cover, shrub cover < 50 cm height, shrub cover >50 cm height, rock cover, average tree height, and average shrub height. The availability of four fleshy-fruit species typically consumed by stone martens was further evaluated: an estimate of the number of strawberry trees and cover of blackberry and wild rose shrubs and juniper trees (Sacchi and Meriggi, 1995; Genovesi et al., 1996; Pandolfi et al., 1996; Genovesi et al., 1997; Virgós and Casanovas, 1998; Virgós et al., 2000; Barrientos and Virgós, 2006). All variables, with the exception of fleshy-fruit availability, have formerly been used in *Martes*-habitat models to reflect habitat quality in terms of shelter, food or both (Buskirk and Powell, 1994; Thompson and Harestad, 1994). We made visual estimates of all variables (excluding strawberry tree number) in a 15 m radius circle every 200 m. The average value for each variable in the survey route was obtained from the 200-m estimates. The availability of strawberry trees (indicated by the number of trees) was recorded in the 15 m radius circle in each 200 m segment. The number of different tree species was also determined. Prior to sampling, the three

individuals who performed the fieldwork completed a trial to assume consistency in sampling estimates.

Because the survey routes were uniformly distributed throughout the park, and estimates were consistently apportioned over the survey routes, we assumed the habitat characteristics measured in the field were representative of the segments and the survey routes, as well as the landscape composition of the entire park.

Statistical analyses

Habitat selection is hierarchical and occurs from the home range of an organism to the landscape scale (Johnson, 1980; Wiens et al., 1987). Therefore, the factors shaping the occurrence of stone martens at two spatial scales were analyzed: the entire 2 × 2 km plot and the 200 m segment within each survey route. Thus, the first scale represented the surface inhabited by several individuals, and 150 ha was considered the mean home-range for the species in the Mediterranean landscape (Rondinini and Boitani, 2002). This area was used to characterize landscape elements linked to a different number of potential individuals. In contrast, the 200 m scale represented selection of particular individuals within their home range during daily foraging habits.

The first spatial scale was analyzed applying a traditional approach based on a regression-like Generalized Linear Model (GLM), where the dependent variable was the occurrence frequency index for the entire survey route and the average of the variables measured or estimated in the field were predictors. A model with Poisson errors and a log link function was employed (MacCullagh and Nelder, 1989) and model selection was performed by backward elimination. In order to avoid multicollinearity problems between predictors, we previously selected a subset of predictors with no significant correlations among them. Although some caution has been expressed about the use of stepwise procedures to select the best models (e.g. Burnham and Anderson, 2002; Graham, 2003), a recent simulation study showed that stepwise methods performed similarly to novel algorithms for subset selection (Murtaugh, 2009). Despite we used the most traditional stepwise procedure, we checked if additional dropped variables can support well the data by using AICc as criterion to select variables and models, and we did not found significant differences with the models obtained by using stepwise methods.

Selection was accomplished by a matrix correlation with all possible correlations among predictors, and between predictors and the stone marten occurrence frequency index. When several predictors were significantly correlated, those with the best correlation with the response variable were selected for further backward multiple regressions.

Finer spatial scale analyses were conducted using the number of scats in each segment as the response variable and measured variables as predictors. A Generalized Linear Mixed Model (GLMM), where each segment was a random factor (MacCullagh and Nelder, 1989) was applied, because each 200 m segment was not independent of the others in the same survey route. Furthermore, a Poisson error and a log link function in the GLMM were chosen due to scat count data. Model selection was

undertaken following model simplification procedures and parsimony (MacCullagh and Nelder, 1989; Crawley, 1993). Thus, non-significant terms were sequentially removed from the maximal model and terminated only when significant terms were retained in the model (Crawley, 1993). The significance of retaining or dropping each predictor was validated when a change in deviance was applied when it was removed, which was distributed as a Chi-square. For the GLMM analysis, only predictors not correlated with each other were used; and those with the best correlation with the response variable were selected for further model simplification procedures.

Statistical analyses were performed with the STATISTICA 6.0 package for Windows to obtain large-scale habitat models and matrix correlations, and the GLIMMIX macro for SAS V8 for small-scale habitat models.

Results

Results indicated the stone marten is relatively common in Monfragüe with scat in 19 of the 30 plots sampled. The abundance index in areas where it was located fluctuated between 0.2 and 0.9 (mean ± SE for all plots; 0.22 ± 0.05). Strawberry trees were detected in 18 of the 30 plots.

Strawberry trees were common in two plots where stone marten scat was not recorded. It is interesting to note that in six of the plots lacking strawberry trees, we did not observe stone marten scat. In the remaining plots without strawberry trees, but with stone marten presence (6-plots), stone marten abundance was low (0.2 in all cases; one plot with an intermediate value of 0.4). In order to ascertain the statistical significance of these data, we performed a G-test using abundance of stone marten as rows and the presence or absence of strawberry trees as columns. Stone marten abundance index was categorized as low equal to an abundance index below 0.5 (half of the segments with the presence of the species), and high equal to an abundance index above this value. We observed a significant effect of strawberry tree presence on stone marten abundance in the plots (G = 7.71; 2 d.f.; p = 0.02).

Predictors from highest to lowest correlation with stone marten abundance were as follows: strawberry tree number, tree cover, shrub cover > 50 cm, shrub height, *Rosa + Rubus* cover, shrub cover < 50 cm, tree height (all species) and rock cover. Some predictors showed significant inter-correlations (see table 1), therefore our initial model was performed with backward eliminations and exhibited the following predictors: strawberry tree number, tree cover, *Rosa + Rubus* cover and shrub cover < 50 cm.

At the large-spatial scale, Poisson multiple regression (GLM) with stone marten occurrence values (abundance index) in each route retained one variable in the final model after the backward elimination procedure; the total number of strawberry trees along the survey routes (r = 0.69; p < 0.001). Stone martens exhibited the highest occurrence on survey routes located in areas where the greatest number of strawberry trees was recorded (fig. 2).

A similar result was observed at the finer scale, when data were analyzed using GLMM with the values from each 200 m segment. The most informative variable

Table 1.
Correlation matrix indicating different predictors used to characterize stone marten habitat selection.

|	Shrub cover < 50	Shrub cover > 50	Rock cover	Tree height	Shrub height	Number of strawberry trees	*Rosa + Rubus* cover
Tree cover	r=0.15 p=0.44	r=0.22 p=0.24	r=0.53 p<0.01	r=0.40 p=0.03	r=-0.04 p=0.85	r=0.04 p=0.84	r=-0.12 p=0.52
Shrub cover < 50		r=-0.09 p=0.65	r=0.37 p=0.05	r=0.33 p=0.08	r=-0.06 p=0.73	r=0.23 p=0.22	r=0.09 p=0.62
Shrub cover > 50			r=0.06 p=0.74	r=0.02 p=0.91	r=0.59 p<0.001	r=0.48 p<0.01	r=0.18 p=0.33
Rock cover				r=0.63 p<0.001	r=-0.23 p=0.22	r=-0.14 p=0.45	r=-0.13 p=0.51
Tree height					r=-0.19 p=0.31	r=-0.07 p=0.71	r=-0.10 p=0.60
Shrub height						r=0.75 p<0.001	r=0.28 p=0.13
Number of strawberry trees							r=0.36 p=0.05
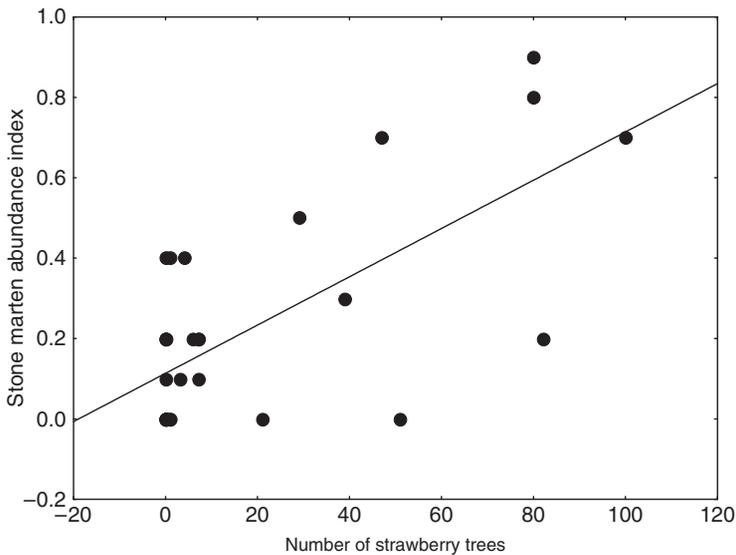
Figure 2. Positive association between stone marten abundance index and strawberry tree number in each plot.

was tree cover, but strawberry tree number was also retained in the model (table 2). Stone marten scat was more commonly recorded in segments with high tree cover and a higher number of strawberry trees. Consequently, the number of strawberry trees was included in both spatial scales, indicating the value of tree species for stone martens.

Table 2.
Variables retained in the final model from a backward stepwise model using a Generalized Linear Mixed Model (GLMM) with scat number as the response variable and specific predictor values in each 200 m segment. The predictor signs were based on partial regression coefficients.

Predictors	F value	df	p	Sign of the relationship
Tree cover	17.62	1.26	< 0.001	+
Number of strawberry trees	6.08	1.26	0.01	+

Table 3.
Results of the 2-way Poisson ANOVA with the stone marten abundance index as the response variable and tree cover and strawberry tree number categorized as fixed factors. The quartile distribution of continuous variables was used to assign categories to the predictors. The last two quartiles for the tree cover factor (areas of high tree cover) were applied in the analysis.

Factors	df	Wald statistic	p
Tree cover categorized	1	2.20	0.14
Number of strawberry trees categorized	2	10.53	<0.01
Tree cover x strawberry number	2	0.35	0.84

Despite the importance of tree cover in the final GLMM model, the greater influence of fruit availability for stone martens was supported by two results of the study: 1) tree cover and strawberry tree number were not correlated, i.e. plots exhibited both high tree cover and low strawberry tree number; and low tree cover and high strawberry tree number (table 1); and 2) if tree cover was the most important variable, similar stone marten abundance should be found in areas with high tree cover but varied strawberry tree abundance. To evaluate this latter possibility, a two-way Poisson ANOVA was performed with stone marten abundance index as the response variable and strawberry tree number and tree cover as fixed factors. Both predictors were categorized using the quartile distribution, and a Poisson ANOVA conducted, but restricting the analysis to areas with high tree cover (third and fourth quartile of the distribution). The Poisson ANOVA revealed a clear effect of strawberry tree number on stone marten abundance, despite similar tree cover values (table 3). Indeed, the stone marten abundance index was higher in areas with a high number of strawberry trees within the same tree cover category (fig. 3).

Discussion

Although some authors question the use of signs to derive habitat models for carnivores (e.g. Davison et al., 2002; Harrington et al., 2008), several recent studies indicate the reliability and suitability of this method when performed by experienced field researchers (Sadlier et al., 2004; Webbon et al., 2004; Prugh and Ritland, 2005).
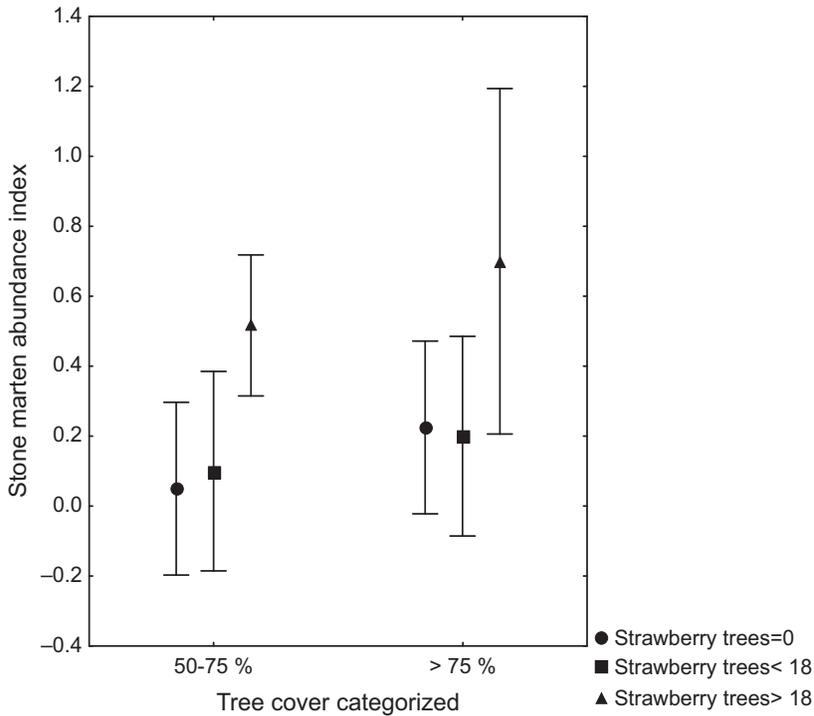
Figure 3. Interaction plot showing the stone marten abundance index in areas of high tree cover (categorized according to quartile distribution of the continuous variable) for three levels of strawberry tree number (categorized according to the quartile distribution of the continuous variable –the last two quartiles combined).

Properly trained and skilled individuals can easily identify stone marten scat from other sympatric carnivores. Barea-Azcón et al. (2007) demonstrated how scat surveys outperform other techniques, such as camera-trapping or scent stations to detect the species in Mediterranean environments. Based on our long-term experience in scat identification and the usefulness of this method to detect stone martens, we are confident our results are reliable and robust.

Stone marten distribution and occurrence was primarily determined by strawberry tree abundance both at the 2 × 2 km plot scale and at the finer 200-m segment scale. This association was detected in spring, when strawberry tree fruits were not available for stone martens. It is likely the value of this fruit as a key food source shapes stone marten home range distribution, even in seasons when the fruit is not available. Indeed, it has been shown for Marten species, which home-ranges location at the landscape scale is mainly explained by the spatial distribution of key food resources (and also mates) (see Powell, 1994 for a review). These resources can fluctuate among seasons, but if the food resource is very important for the species, their seasonal availability can influence spatial distribution of annual home ranges such as has been shown for stone martens (Genovesi et al., 1997) and other marten species, in which home range fidelity

is large (Phillips et al., 1998; Zalewski and Jedrzejewski, 2006). Subsequently, the distribution of strawberry tree patches is critical for stone marten distribution in an annual basis despite seasonal changes in fruit availability.

Strawberry trees are an integral component of mature Mediterranean scrublands (Peinado and Rivas-Martínez, 1987). Therefore, it is probable strawberry trees play a major role in the distribution of stone martens in large areas of the Mediterranean basin. The stone marten is a food generalist, able to consume the most available resources both seasonally and spatially (Clevenger, 1994; Lodé, 1994; Genovesi et al., 1996; Pandolfi et al., 1996). Despite the wide food spectrum of the species, some degree of specialisation on fruits has been shown (Serafini and Lovari, 1993; Clevenger, 1994; Genovesi et al., 1996; Gil-Sánchez, 1996; Pandolfi et al., 1996). Strawberry trees offer a large and pulp-rich fruit to stone martens and other frugivorous species (Herrera, 1989), which explains the observed facultative specialisation. Field data in similar regions indicated that the fruits are consumed, but with apparent moderate differences among regions (Amores, 1980; Barrientos and Virgós, 2006). The preference for strawberry tree fruits could have increased in Monfragüe and other Mediterranean areas, where the availability of other fruit species is low. For example, in the study area stone martens were less likely to forage on species with low occurrence, such as blackberries, wild rose or juniper trees. In other areas, where figs or *Prunus* are abundant, the stone marten may specialize on these species (Gil-Sánchez, 1996; Barrientos and Virgós, 2006) and may change the relative suitability for strawberry trees. In a situation with low diversity of fruit species, and the high-energy value of large strawberry tree fruits, the stone marten dependence on this resource should be predictable.

The link between strawberry trees and stone martens was not only found at the 2×2 km plot level, but also at the smaller scale within 200 m segment plots which suggested stone martens were more frequent in plots with higher availability of strawberry trees, and the species intensively used areas with increased numbers of strawberry trees. It can be argued that strawberry tree habitats supply other important resources to stone martens, not only a seasonal food supply, but also increased shelter availability (greater shrub cover and shrub height) or increased density of prey species in shrub areas, which reinforces the role of this habitat use for stone martens during the non-fruiting season. Indeed, tree cover was an informative variable in the fine-scale habitat model. These results supported trees as a source of shelter in stone marten habitat selection. However, the presence of strawberry tree fruit increased habitat quality for the species more than serving a shelter function. Our data indicated that areas with similar tree cover without strawberry trees had lower stone marten occurrences. The latter result supports the hypothesis that strawberry tree distribution and occurrence is closely associated with stone martens, despite its potential role as shelter (i.e. strawberry tree fruit dictates stone marten distribution).

The importance of fruit to determine stone marten distribution has previously been reported by Mortelliti and Boitani (2008) in a fragmented landscape of central Italy. The authors indicated that within the size and isolation of patches, the within-patch quality (mainly defined by the availability of fleshy fruits) can improve the likelihood of patch occupancy. Indeed, our results can be extended to other landscapes of different species composition and community structure, emphasising the pervasive role of

distribution and abundance of fleshy fruits in shaping the distribution and abundance of stone martens.

Most Mediterranean landscapes are now threatened by human activities. Mutualistic interactions may be disrupted by habitat transformation or fragmentation (Aizen and Feisinger, 1994; Santos et al., 1999; Traveset, 2002; Jordano et al., 2007). For example, long-distance dispersal and colonization success of some fleshy-fruit plant species may be constrained by a decline and subsequent absence of carnivores (Santos et al., 1999; Jordano et al., 2007). Because predators may suffer local or regional extirpation as a consequence of combined effects of habitat loss and predator control (Gittlemann et al., 2001; Virgós and Travaini, 2005), species such as strawberry trees may be threatened.

In addition, the large removal of typical scrublands to reduce fire effects (e.g. Mangas et al., 2007) can produce a strong reduction in the availability of key food species for stone martens and other frugivorous carnivores. Conservation policies must consider these subtle interactions when management actions are planned and executed.

The results of this study have shown that the inclusion of food availability estimates can increase the utility of habitat models to conserve and manage species, facilitating a more clear and mechanistic explanation of species abundance patterns along environmental gradients. One question raised by this study is the strong relationship between stone martens and *Arbutus unedo* (strawberry tree) fruits. Studies in other locations with high availability of cultivated or other preferred wild fruits (e.g. *Rubus*, *Prunus* or *Juniperus*) are necessary to test if the observed association between stone marten distribution and abundance of preferred fruit species is a generality among *Martes foina*.

Acknowledgements

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