



A comparison on the response to forest fragmentation by medium-sized Iberian carnivores in central Spain

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Abstract. We studied the use of forest fragments by five medium-sized carnivore species in 280 forest fragments on the two Iberian plateaus. We looked for indirect evidence (faeces, tracks, dens) of fragment use (occurrence) by the species and analysed whether occurrence could be related to four groups of variables: local (vegetation structure and patch size), landscape (distance to possible colonisation sources), regional (fragment location on the northern or southern plateau) and the vegetation type of the fragments. We analysed the differential response of species according to their life-history and behavioural traits. The relationship between use by each species and the factors studied was analysed using stepwise logistic regressions. Results indicate that three factors are crucial to explain fragment use: fragment size, geographic location and vegetation type. Large fragments are used more than smaller ones, the northern plateau is more suitable than the southern plateau, and holm oak and broad-leaved oak forests are more used than pine woods. The effects and magnitude varied slightly among species, depending on habitat requirements or life-history traits. Data indicate that conservation strategies in fragmented environments must take into account elements functioning at different spatial scales, and that it is essential to consider each case within a characteristic regional context.

Introduction

Forest fragmentation adversely affects many forest vertebrates (Opdam 1991; Andrén 1994; Bender et al. 1998). Mammalian studies on this subject have mainly focused on small mammals (Verboom and van Apeldoorn 1990; Tellería et al. 1991; Van Apeldoorn et al. 1992; Tew and Macdonald 1993; Oehler and Litvaitis 1996), and there is a lack of studies on carnivore species. However, due to their relatively large size, these species may be more vulnerable to processes of habitat deterioration (Laurance 1991). This lack of information is particularly important since many of these animals are endangered or affecting other key species such as game or threatened ones.

This study explores the patterns of fragment use by medium-sized Iberian carnivores of central Spain. In particular, it analyses the role of factors that may affect fragment occupation by these species at different spatial scales (Kotliar and Wiens 1990; Brown and Litvaitis 1995). The use of each fragment by a species may

depend on factors that act on a local scale (e.g. forest area and physiognomic structure), and also on factors that act at landscape scale (e.g. distances to possible sources of animals for colonisation), or on its regional abundance because populations in fragments may interact with larger populations (Gilpin and Hanski 1991). It is interesting to know, therefore, the relative importance of the different factors given that conservation measures for these animals may be ineffective if not applied at the appropriate scale (Hansen et al. 1993). Conversely, we suggest that different carnivore species may show a contrasted response to fragmentation according to their different life-history traits. Red foxes are able to survive in very deforested landscapes, so they could be less susceptible to forest lost than other species. On the other hand, badgers are very constrained by the presence of good soils to dig their setts (Roper 1993), and this probability is enhanced in large forests with high environmental heterogeneity (Freemark and Merriam 1986). So, we expect that badgers may be more constrained by large forests than other species due to this particular behavioural trait. Wildcats, genets and stone martens need a high availability of shelter and food (especially woodmouse and microtines in the case of genets and wildcats). As abundance of rodents is very high in small forests (Tellería et al. 1991), we cannot expect these species to be limited in fragment size by this factor. Moreover, it is probable that these species may be recorded both in large and small fragments, although they may prefer large forest because of their necessity of shelter. Finally, both genets and stone martens show a rather termophilic affinity (Delibes 1983), whereas badger is more abundant in wet areas (Virgós and Casanovas 1999). So, we expect genets and stone martens to show higher occurrence in the south than in the north, and the opposite in the case of the badger.

The Iberian plateaus are a good system for studying medium-sized carnivore distribution in fragmented forests at different spatial scales. This group of mammals is still relatively rich in Spain, although it is usually concentrated in the best conserved mountain areas where forests are common (e.g. Delibes 1983). In contrast, north and south plateaus are intensively farmed with patchily distributed forests across the landscape (Santos and Tellería 1998). The plateaus differ in climatic conditions and predominant land uses. The northern plateau is rainier and cooler than the southern plateau, two traits which in Mediterranean climates positively affect primary productivity and the abundance of primary and secondary consumers (Oksanen et al. 1981). Moreover, the northern plateau is devoted to cattle raising, whereas hunting on small game species is common in the south fragments, which is associated with intensive predator control activities. It is, therefore, possible that these uses give rise to differences in regional abundance of mammals and that these differences affect their ability to colonise or survive in the fragments.

The specific aim of this study is to analyse whether the use of fragments by medium-sized carnivore species is linked to (a) their location in the northern or southern plateau (regional effect), (b) landscape structure at local scale, especially fragment distance to other forests (landscape effect), (c) the size and physiognomic and botanical features of each fragment (fragment effect), (d) the vegetation type (tree dominant cover) of each fragment and (e) the particular life-history traits of each species studied. Supposing that several of these factors are linked to fragment

use, we were interested in finding out the relative importance of each one in order to draw conclusions that can be applied to the conservation of medium-sized carnivores.

Material and methods

Study area

The Iberian plateaus are a characteristic plain area of Spain divided by the mountains of the Central System. The northern plateau is higher (800 m asl.), wetter and cooler than the southern plateau (above 600 m asl.) (Font 1983). Both areas are dominated by extensive cereal farming, with isolated remains of the old Mediterranean forest (holm oak forests, mainly *Quercus ilex*) and conifer plantations (mainly *Pinus pinea*, *P. pinaster*). These forests present an intensely fragmented distribution pattern in which small fragments are common in the landscape (Santos and Tellería 1998).

A total of 280 forest fragments distributed among eight different archipelagos (a group of neighbour fragments in a particular area) in the two plateaus were sampled: 169 and 111 on the northern and southern plateaus, respectively (see archipelago location in Figure 1). Selection of the forests was made using recent aerial photographs (1:20000). Two independent criteria were taken into account for this selection: (a) its usefulness in the gradient of patch sizes (0.1–>100 ha); (b) each forest patch should be separated from other patches (at least 25 m) by an agricultural matrix (devoted to intensive cereal crops). The distribution of sizes, isolation and vegetation type in each archipelago is given in Table 1.

Species selection and sampling

We chose the five commonest medium-sized carnivore species of the Iberian Peninsula and we assume that they need woodland or scrubland areas to survive, even though they use the ecotones and peripheral deforested areas to feed. These species use rather large home ranges, so that they may regularly visit several fragments, and so locating them in a particular forest indicates the current use of this fragment but does not necessarily imply the stable presence of an isolated population. The selected species were: red fox (*Vulpes vulpes*), badger (*Meles meles*), stone marten (*Martes foina*), genet (*Genetta genetta*) and wild cat (*Felis silvestris*). We also included rabbit (*Oryctolagus cuniculus*) for its potential role in carnivore distribution because it is an important prey for many carnivore species in Spain (Jaksic and Soriguer 1981).

We searched for indirect evidences of use in each forest studied (tracks, faeces and dens/burrows). This method has been proposed by several researchers (e.g. Clevenger 1993; Staender 1998) as a good alternative to trapping or scent-stations indexes in carnivore-habitat studies conducted at landscape or regional scales. The latter methods are too expensive and time-consuming to be an adequate option in

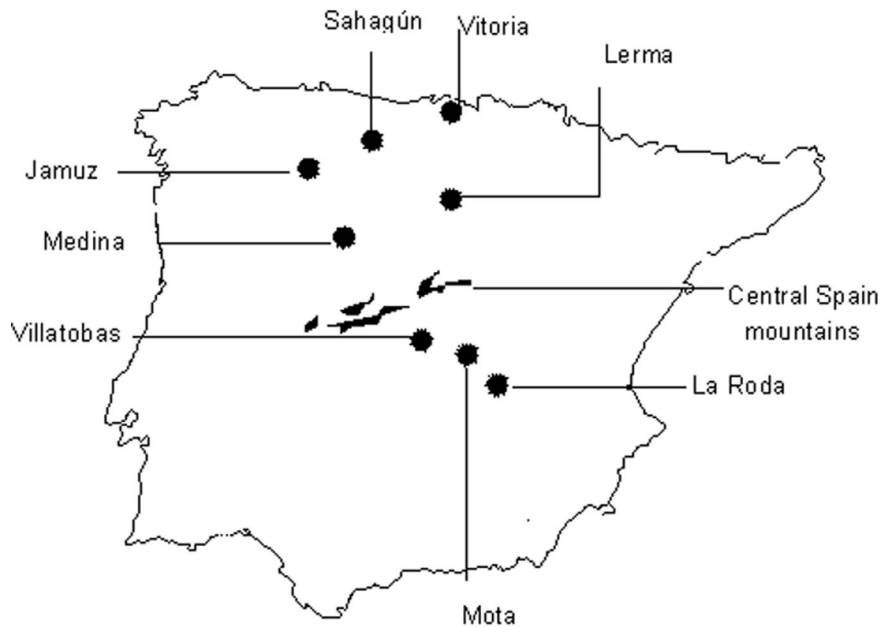


Figure 1. Location of eight forest archipelagos in the two Iberian plateaus containing the study forest fragments.

large-scale studies. In addition, other authors have indicated the good fit between faeces or dens recording and population density or frequency of occurrence (e.g. Cresswell et al. 1989; Cavallini 1994; Staender 1998). The fragments were visited from May to August of 1994. One visit per patch was made during this study period, providing a snapshot of the current use of these fragments for each species. This procedure allowed us to describe the pattern of fragment use for the individuals of different species over a range of sizes, degrees of isolation and habitat features.

The fragments were sampled using survey routes along roads and paths of similar width (to locate scats of stone marten, red fox, wildcats and rabbits) and cross-country (out of the paths) to locate badger setts and genet latrines. In fragments under 2 ha, the whole area was exhaustively surveyed for sign search (both in paths and cross-country). In fragments over 2 ha, path and cross-country routes were surveyed alternatively in each forest. We sampled survey routes of 500 m long. The routes were 1 m wide in paths and roads and 10 m wide cross-country. In particular, the genet latrines and dens (for badgers) were searched in the same type of habitat features along the survey routes: fences, edges, rocks, slopes, riverbanks. We attenuated the problems associated with the use of signs as a measure of current use by sampling under similar climatic conditions (late spring and summer) and searching for signs with the same protocol across habitats. The first attenuates the problem with differences in decay rates over seasons. The second alleviates the problem of differences in detectability in different habitats.

Table 1. Forest archipelagos studied in the Iberian plateaus.

Archipelago	N	Location	Habitat type	Inter-fragment distance	Distance to nearest continuous forests	<1 ha	1–10 ha	10–50 ha	50–100 ha	>100 ha
Jamuz	41	North	Holm oak	116.34 (25–520)	14.90 (6.0–21.4)	19	15	5	1	1
Lerma	29	North	Holm oak	97.24 (25–495)	10.20 (1.1–21.8)	13	4	6	2	4
Sahagún	38	North	Broad-leaved	48.95 (25–220)	4.09 (0.2–29.0)	13	15	5	2	3
Vitoria	22	North	Broad-leaved	202.73 (25–460)	1.48 (0.6–3.3)	6	9	7	0	0
Medina	39	North	Pine	72.56 (25–280)	23.09 (18.3–29.8)	10	21	4	3	1
Villatobas	39	South	Holm oak	101.28 (25–760)	41.3 (28.4–45.3)	15	16	4	3	1
Mota	31	South	Holm oak	88.06 (25–440)	10.8 (6.6–17.4)	11	8	7	3	2
La Roda	41	South	Pine	174.88 (25–460)	28.05 (22.3–30.9)	14	16	7	1	3

For each archipelago are given: Number of forest patches (N), geographic location (plateau), habitat type (dominant tree species), mean and range of inter-fragment distances (in m), mean and range of distances (in km) from forest higher than 1000 ha, and number of forest fragments in each size category.

The number of these survey routes in each forest fragment follows an approximately logarithmic relationship with fragment size, in order to homogeneously cover the whole patch. Thus, the number of routes varied from 2 in the 2–3 ha fragments to a minimum of 10 in fragments over 100 ha.

Fragment features

The fragments were characterised at the three spatial scales of the study by using a series of factors that could potentially affect mammal use. Firstly, regional effect involved classification into two groups according to location on the northern or southern plateau. Secondly, for landscape effect isolation was quantified in relation to possible colonisation sources (distance to nearest fragment, distance to forests greater than 100 ha, and distance to forests greater than 1000 ha in the mountains or riparian woods). The measurements were made on aerial photos (1:18000) in the case of the first two estimates and on LANDSAT images (1:100000) for the third variable. For fragment effect, the size of each fragment was determined in hectares on photos 1:18000, and vegetation type was determined in the field according to the dominant type of tree in each fragment (holm oak wood *Q. ilex*; broad-leaved forests: Pyrenean oak woodland *Q. pyrenaica* and/or Portuguese oak *Q. faginea*; and pinewood *P. pinaster* and *P. pinea*). Vegetation structure was quantified in 25 m radius circles by visually estimating the cover of variables that could be of potential importance to the different species for food, shelter, or both: tree cover, shrub >50 cm cover, shrub <50 cm cover and herb cover (see Morrison et al. 1992; Santos and Tellería 1998).

Analyses

The occurrence of species in each fragment was used as a dependent variable in a stepwise logistic regression analysis (forward Wald method; Hosmer and Lemeshow 1989) in which location (in north or south plateau), distances, size, vegetation structure variables, and vegetation type (dominant tree species, see above) for each fragment were used as predictors. The vegetation type and the plateau were included as 'dummy' variables (Neter et al. 1985). In order to reduce collinearity in multiple logistic regression analysis, we analysed the potential association between continuous predictor variables through Pearson correlations, then we used the different subsets of independent variables to run stepwise multiple logistic regression and to evaluate the adequacy of the different models from a deviance analysis among *G*-statistics values from the final models (Manly et al. 1993). In these analyses, all possible two-way interactions between variables were considered.

All the variables were transformed before the analyses by logarithmic (fragment size and isolation) and angular (vegetation covers) transformation. The logistic regression analyses were carried out with the statistical package SPSS 6.0 and the remaining analyses were done with Statistica 4.5.

Table 2. Pearson correlation matrix among the different variables used in this study.

Variable	Distance nearest fragment	Distance fragment > 100 ha	Distance forest > 1000 ha	Size of the nearest fragment	Fragment size	Herb cover	Shrub cover	Shrub < 50 cm cover	Tree > 50 cm cover
Distance nearest fragment	0.038	$P = 0.532$	$0.050 P = 0.406$	0.047	$P = 0.436$	-0.098	$P = 0.103$	0.073	$P = 0.226$
Distance fragment > 100 ha		0.102	$P = 0.088$	-0.108	$P = 0.071$	0.156	$P = 0.009$	-0.257	$P < 0.001$
Distance forest > 1000 ha			0.145	$P = 0.048$	0.119	$P = 0.892$	0.008	$P = 0.892$	-0.247
Size of the nearest fragment				0.190	$P = 0.001$	-0.007	$P = 0.902$	0.059	$P = 0.329$
Fragment size						-0.180	$P = 0.002$	0.164	$P = 0.006$
Herb cover								-0.365	$P < 0.001$
Shrub < 50 cm cover								0.294	$P < 0.001$
									0.090
									$P = 0.132$
									-0.269
									$P < 0.001$
									0.147
									$P = 0.014$
									-0.210
									$P < 0.001$
									0.031
									$P = 0.605$
									-0.236
									$P < 0.001$
									0.105
									$P = 0.080$
									-0.277
									$P < 0.001$
									-0.255
									$P < 0.001$

Shrub > 50 cm cover

Results

Correlations among variables

Only three variables did not show significant correlations between them: fragment size, distance to nearest forest greater than 1000 ha and distance to nearest fragment. All vegetation structure variables were correlated with some or all of the above-mentioned variables, so they were not included in the following analyses (see Table 2). We examined relationships of these three variables with geographic location and vegetation type (fixed factors), which should be also included in the regression analysis, with protected ANOVA after MANOVA analysis (Scheiner 1993). MANOVA results indicated that there were significant differences between plateaus ($\chi^2 = 0.77$; 2276 d.f.; $P < 0.001$) and vegetation types ($\chi^2 = 0.33$; 6550 d.f.; $P < 0.001$). The protected ANOVA for each dependent variable indicated that only the distance to nearest forest greater than 1000 ha showed statistical differences both for geographic location and vegetation type (Table 3). Southern forest fragments were further from large forests than northern ones (26.19 ± 8.84 vs. 13.05 ± 12.50 km), and broad-leaved forests were less isolated than holm oak and pine ones (3.13 ± 4.6 vs. 18.64 ± 12.93 and 25.57 ± 3.41 km). Therefore, the distance to forests greater than 1000 ha was not independent of vegetation type and geographic location, so both in least squares and logistic stepwise multiple regressions we checked two independent models including variables non-intercorrelated: (1) fragment size (local effects), distance to nearest forest (local effects), geographic location (regional effects) and vegetation type; (2) fragment size (local effect), distance to nearest fragment (local effect) and distance to nearest forest greater than 1000 ha (landscape effects).

Species occurrence in forest fragments

The five species studied presented an unequal pattern of use among fragment sizes (Table 4). The model that included fragment size, distance to nearest fragment, vegetation type and geographic location (model 1) performed better than the model with fragment size, distance to nearest fragment and distance to nearest forest greater than 1000 ha for all species (model 2; see deviance analyses in Table 5).

Table 3. Results of the protected ANOVA performed with geographic location (plateau) and habitat types (holm oak, broad-leaved oak and pine forests) as factors, and fragment size, distance to nearest fragment and distance to nearest forest greater than 1000 ha.

Variable	F value	d.f.	Significance P
Distance to nearest fragment	2.173 (Plateau)	1278	0.14
	0.098 (Habitat type)	2277	0.91
Distance to nearest forest >1000 ha	81.103 (Plateau)	1278	<0.001
	279.224 (Habitat type)	2277	<0.001
Fragment size	1.258 (Plateau)	1278	0.26
	1.029 (Habitat type)	2277	0.36

Table 4. Number of fragments used by the study species according to fragment size (in brackets, number of surveyed fragments in each size category).

Species	<0.5 ha (n: 60)	0.5–2 ha (n: 85)	2–5 ha (n: 43)	5–10 ha (n: 17)	10–50 ha (n: 45)	>50 ha (n: 30)	North Plateau (n: 169)	South Plateau (n: 111)	Total (n: 280)
<i>Vulpes vulpes</i>	15	28	14	9	30	29	84	41	125
<i>Meles meles</i>	0	2	0	1	3	9	14	1	15
<i>Martes foina</i>	1	5	2	1	5	9	18	5	23
<i>Genetta genetta</i>	0	4	1	1	5	5	14	2	16
<i>Felis sibiricus</i>	2	10	2	0	3	7	22	2	24

Table 5. Diagnostic results from logistic regressions for the two different models considered and for each species considered: concordance between observed and predicted values (%) ((a) overall, (b) presence correctly predicted, (c) absence correctly predicted), G -model, P -values and deviance analysis (obtained from the expression $G_{\text{model 1}} - G_{\text{model 2}}$ with d.f._{model 1} - d.f._{model 2} degrees of freedom).

	<i>Vulpes vulpes</i>	<i>Meles meles</i>	<i>Martes foina</i>	<i>Genetta genetta</i>	<i>Felis silvestris</i>
Model 1	69.29(a)	97.14(a)	92.86(a)	94.64(a)	91.79(a)
	59.20(b)	53.33(b)	13.04(b)	18.75(b)	4.17(b)
	77.42(c)	99.62(c)	100(c)	99.24(c)	100(c)
	$G_4 = 74.48$	$G_3 = 55.07$	$G_4 = 38.23$	$G_4 = 39.64$	$G_3 = 22.51$
	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$
Model 2	71.79(a)	96.43(a)	92.14(a)	94.29(a)	91.43(a)
	58.40(b)	33.33(b)	8.7(b)	0(b)	0(b)
	82.58(c)	100(c)	99.61(c)	100(c)	100(c)
	$G_2 = 66.31$	$G_2 = 45.09$	$G_2 = 31.78$	$G_1 = 14.44$	$G_2 = 12.03$
	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P = 0.002$
Deviance	$G_2 = 8.17$	$G_1 = 9.98$	$G_2 = 6.45$	$G_3 = 25.2$	$G_1 = 10.48$
	$P = 0.017$	$P = 0.0015$	$P = 0.04$	$P < 0.001$	$P = 0.0012$

Particularly, model 1 was largely more suitable than model 2 for genets and wildcats, species with strong differences between models both in G values and percent of concordance (Table 5).

In addition, both models showed low percentages of concordance for the species presence (high omission rate), with exceptions. Intermediate levels of omission errors were found in badgers and red foxes from model 1. The 0% correct assignment for presence data in genets and wildcats from model 2 is noticeable. Because of their low predictive power and low G values, we concentrate on the results from model 1 (Table 5).

A regional effect was found for red foxes, badgers and wildcats, which showed higher occurrences on the north than on the south plateau. Fragment size was an important factor linked to occurrence in red foxes and genets. In all these cases, species occurrence was higher in large than in small fragments. Vegetation type also explained the occurrence of red foxes and genets, finding higher values in holm oak and broad-leaved forests than in pine fragments for red foxes and the opposite pattern for the genet. A relatively important part of the occurrence pattern of badgers, stone martens, genets and wildcats was explained by two-way interactions between some predictors. The occurrence of badgers was higher in large oak forests than in small or large pine ones (habitat \times size interaction). The occurrence of stone martens was explained by two interactions: habitat \times size and habitat \times distance to nearest fragment. Stone martens showed higher occurrences in large oak fragments than in large or small pine fragments. The second interaction indicated that stone martens were more frequent in fragments near other patches in holm oak woodlands than in both near and isolated broad-leaved and pine forests. However, this pattern could be spuriously affected by the low power of the model (Table 5). Genets were more frequent in large pine fragments compared to both large and small oak fragments. For wildcats, the occurrence was higher in large holm oak forests than in both large and small broad-leaved or pine fragments. In summary, fragment size,

Table 6. Summary of the selected variables in the final models from the stepwise logistic regressions (forward Wald) for each species considered.

Species	Variable	B	P	R
<i>Vulpes vulpes</i>	Size	1.221	<0.001	35.02
	Plateau	0.710	<0.05	8.87
	Habitat		<0.05	7.5
	'Holm oak'	0.755	<0.05	
	'Broad-leaved'	0.750	0.07	
<i>Meles meles</i>	Size × Habitat		<0.001	42.85
	Size × 'Holm oak'	2.498	<0.001	
	Size × 'Broad-leaved'	1.852	<0.001	
	Plateau	0.854	<0.01	20.07
<i>Martes foina</i>	Habitat × distance to nearest forest >1000		<0.01	17.15
	'Holm oak' × distance	-0.668	0.07	
	'Broad-leaved' × distance	0.857	<0.01	
	Habitat × size		<0.001	33.7
	Holm oak × size	1.814	<0.001	
	Broad-leaved × size	0.498	0.15	
<i>Genetta genetta</i>	Size	1.368	<0.001	31.97
	Habitat		<0.001	29.81
	Holm oak	-3.198	<0.001	
	Broad leaved	-2.193	<0.01	
	Plateau × distance to nearest forest >1000	-1.263	<0.01	22.04
<i>Felis silvestris</i>	Plateau	2.370	<0.01	21.23
	Habitat × size		<0.01	19.10
	Holm oak × size	0.846	<0.01	
	Broad-leaved × size	-0.111	0.78	

regional location and vegetation type effects were important variables for all the species, while landscape effects only affected stone marten occurrence. Variables included in the final model for the different species are given in Table 6.

Discussion

Regional and landscape effects

Forest location on the northern or southern plateau is an important factor in determining the likelihood of the different species to use the fragments. This may be related to a hypothetical higher regional abundance of carnivore species on the northern plateau. The greater suitability of northern forests has been demonstrated in other vertebrates (birds: Tellería and Santos 1993; roe deer: Virgós and Tellería 1998), and it has been shown that badger abundance is lower in southern than in northern areas of the mountains of central Spain (Virgós and Casanovas 1999). Although genets and stone martens are termophilic species and they should be more abundant in the south than in the north plateau, the data indicated the opposite

pattern. This presumed southwards decrease in abundance may be related both with the growing deterioration of the forests (perhaps linked to rarity of stone martens, genets and wildcats) and increased xericity in the south of the Iberian Peninsula (probably linked to badger rarity), where the formerly intense pressure (felling, charcoal making, cattle ranching) has brought about an increasing loss in the mesic tree cover in favour of xeric and rather shrubby species (Costa et al. 1995; Santos and Tellería 1998). This man-made change in the dominant vegetation has also occurred in the north, but in a less marked way. In any case, given that the populations of species established in the fragments are not independent entities, it seems logical to assume that differences in the regional abundance of the study species may determine differences in fragment colonisation rates and, therefore, in the richness of species using them. Hence, the lower use in the south compared to

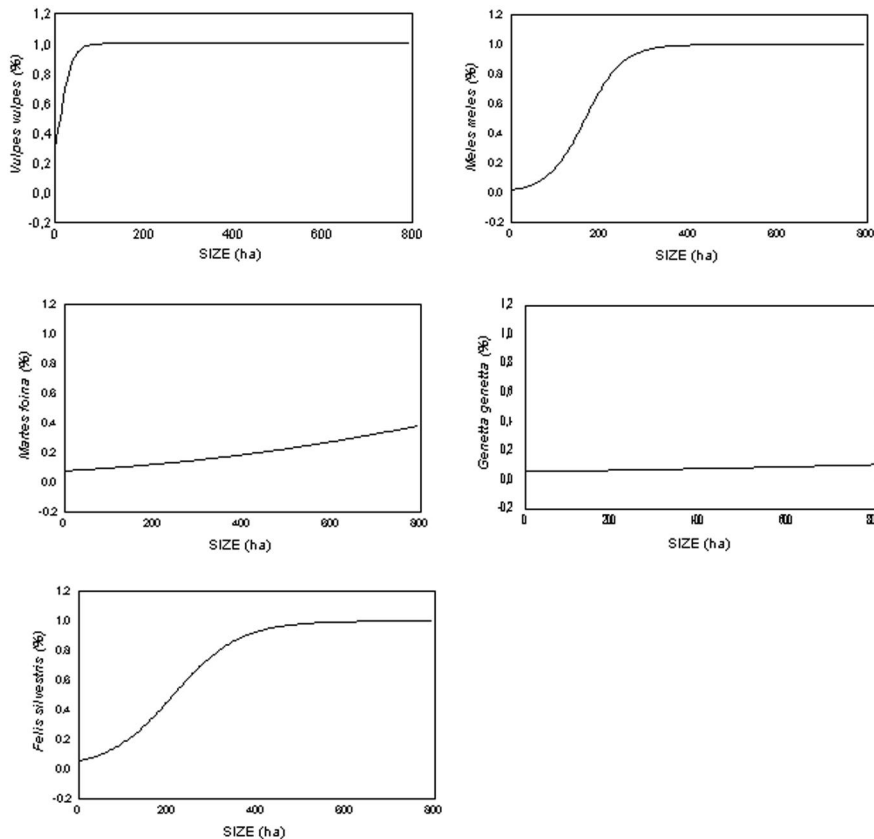


Figure 2. Graphs showing the percentage of fragment presence of the different carnivore species over a range of fragment sizes. Range interval for fragment size is large (200 ha) in order to indicate the different sensitivity of the species to increases in forest size above 200 ha (assumed as enough to maintain populations of the different species).

the north should be a result of the presumed low species density on regional forests (including the mountain forests) of the southern plateau.

However, the role of isolation from large forests in mountains or riparian woods (landscape effects) probably is not negligible to explain differences in occurrence between plateaus. Both predictors are confounded because northern fragments are less isolated than southern ones. The distance to nearest fragments greater than 1000 ha was an important variable in the second model and allowed to explain an important part of the occurrence variation for the different species. This is not surprising because carnivores are less mobile and less able to overcome habitat barriers than other species such as birds. From this point of view, the most isolated forests might be expected to be less used than the less isolated ones; a similar fact has been shown by a medium-sized ungulate species, the roe deer (*Capreolus capreolus*), in central Spain (Tellería and Virgós 1997). So, colonisation and rescue effects are more difficult in fragments in the southern parts than in their northern counterparts and they may partially explain the low occurrence of carnivore species in the south plateau. It could be suggested that both factors, regional habitat quality (xericity and shrubby structure) and isolation, may explain together the recorded pattern but the data and spatial contexts do not allow us to test their relative role.

In addition, most parts of southern forests are used as hunting grounds for small game and predators have been persecuted and killed for decades. Therefore, the regional effect is probably a combination of several underlying processes that interact to decrease the suitability of forest fragments in the south of the Iberian Peninsula. More experimental studies may help us to understand the proximate causes of this pattern and their relative importance.

Local effects

Fragment size was an excellent predictor of carnivore occurrence in fragments. This association between fragment size and occurrence has been largely shown for different vertebrate species (Andrén 1994; Bender et al. 1998). This fact may be explained because large fragments are able to maintain high populations of the species (Fahrig and Merriam 1994) that should be less prone to extinction (Pimm et al. 1988). This might be linked to greater use of these fragments and therefore to higher probability of locating signs of species presence. Moreover, the large fragments are more heterogeneous than small ones (Freemark and Merriam 1986), which favours the presence of different scarce resources for the species.

However, there is a surprisingly low use of the smaller fragments by true edge species, which could make appropriate use of the patch edges and the peripheral cultivated areas. In any case, sensitivity to size varied considerably according to species, although the incidence was clearly higher in fragments larger than 100–200 ha than in small fragments (see Figure 2 for incidence functions over large fragments). In accordance with our initial predictions, the species least affected by fragment size is the red fox, which is able to live in deforested agricultural environments provided that there are small remnants of bushes or trees where it can establish itself (Macdonald et al. 1981). Badgers and wildcats are also habitat

generalist species, although they respond less well to area reduction; both tend to disappear in fragments of similar size (Figure 2), with small differences in their rarefaction in fragments under 100 ha, but with a higher occurrence of wildcats in the small fragments. Badgers are omnivores, able to exploit a wide range of food resources (Roper 1994), but they need places to locate its setts (dens) from which to make routine movements (Roper 1993). Wildcats, however, appear to depend more on prey abundance than on availability of den sites (Stahl and Leger 1992). In this sense, the great abundance of small mammals and the presence of rabbits (the basic prey of wildcat; Stahl and Leger 1992) in small fragments and in ecotonal areas (Tellería et al. 1991; Tew and Macdonald 1993) might facilitate its more frequent appearance in small fragments, which has been suggested in our initial predictions.

Finally, stone marten and genet do not appear to be uniquely restricted to the larger fragments, in general being notably scarce in the forest fragments of the study area. This result is paradoxical given that the two species are recognised trophic and habitat generalists, well able to move over relatively broad territories (see Livet and Roeder 1987 for the genet; Libois and Waechter 1991 for the stone marten). It is possible that the thermal preferences of genets may restrict it to certain specific sites in central Spain (Delibes 1983; Virgós and Casanovas 1997), reducing its regional abundance and its probability of fragment occupancy. However, it is difficult to explain the rarefaction of the stone marten on the Iberian plateaus and their concomitant withdrawal to larger fragments. It could be suggested that the fragments show a lack of suitability due to their low rock cover and hilliness, two important habitat features for stone marten presence in central Spain (Virgós and Casanovas 1998; Virgós et al. 2000).

Vegetation type

The floristic composition of the tree cover does appear to determine certain differences among species, given that most of them were more frequent in oak than in pine forests, and so the species richness in pine forests was lower than in oak ones. An exception to the general low occurrence of the species in pine forests was the genet, a species more restricted by thermal conditions than by habitat or physiognomy (own unpublished data). The greater importance of both holm oak and broad-leaved forests compared to pine forests may be explained because conifer fragments are mostly plantations on agricultural lands. The relative youth of many of them (25–40 years) could negatively affect their use by the species due to the fact that they have not had time to be colonised by the study species. On the other hand, pine forest structure is less diverse (e.g. low shrub cover), providing probably less refuge and food for the involved species.

Conclusions

In summary, although our results should be interpreted with caution for wildcats, genets and stone martens due to the relatively low predictive power of the models,

the data support previous suggestions about the need to consider the conservation problems of species in fragmented habitats at different spatial scales (see also Kotliar and Wiens 1990; Hansen et al. 1993; Oehler and Litvaitis 1996). This involves limitations when planning any strategy to conserve these animals in the study area. For example, the two plateaus represent different scenarios from the perspective of carnivore use of fragmented forests. Their conditions depend on climatic factors and probably on historical and land-use factors that are difficult to manipulate in the short term or at a local level. However, fragment size seems to be a more easily manageable factor from the perspective of species conservation. Any forest alteration that tends to reduce overall size, or any reforestation plan on the plateaus that includes recovery of these mammals should take into consideration the basic need to maintain large forests (always over 100 ha) in order to ensure that these species are conserved. Conversely, reforestation with pine plantations seems to be a wrong decision if the interest is to maintain medium-sized carnivores in the region.

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