

Habitat selection by European badgers at multiple spatial scales in Portuguese Mediterranean ecosystems

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Abstract. Different habitat features can limit animal populations at different spatial scales. We examined habitat selection by Eurasian badger in a *montado* landscape in southern Portugal at four scales: core area (1 km²), home range (4 km²), social group territory (25 km²), and local population (100 km²). Our goals were to identify important habitats for conservation at each spatial scale (cell size) using candidate variables shown to be important by previous research. As expected, across all scales, badger occurrence was consistently and strongly correlated with dominance of cork oak and deciduous woodlands, and badgers seemed to avoid cultivated fields. Contrary to expectation, monocultures of conifers contributed positively to badger detection. The predictive ability of the models was poor at all scales, probably owing to our inability to include factors such as food, competitors, predators, undercover vegetation, and roads. Nonetheless, the models illustrate the importance to badgers of the *montado*, an ancient human-modified ecosystem that is threatened by current European Union agricultural conversion policies.

Introduction

Understanding habitat factors that limit populations is central to conservation (Krebs 2002). However, different habitat factors may be important at different scales (e.g. Wiens 1989; Block and Brennan 1993; Bissonette 1997). The scales at which animals select habitat can reveal the most important factors limiting a population, and the broader the scale the more important the factor (Rettie and Messier 2000). A nested hierarchical structure of habitat selection has been described, including: geographic ranges, home range, components within the home range, and specific resources at a site (Johnson 1980). However, it remains untested whether species with marked social structure follow similar patterns. We hypothesise that social species, such as the Eurasian badger (*Meles meles*), may have different habitat-selection patterns depending of the scale of analysis, especially in complex landscapes.

Badgers are widely distributed across Europe and Asia, with a southern limit in the Iberian Peninsula (Dobson 1998; Virgós and Casanovas 1999a; Revilla *et al.* 2001; Virgós 2001a; Johnson *et al.* 2002). Although solitary foragers at night, by day badgers in southern latitudes live in social groups of 2–8 animals (values from Portugal in Rosalino *et al.* 2004, 2005b) with a communal territory centred on the communal den or sett (Revilla *et al.* 2001; Rosalino *et al.* 2004). Previous studies across Europe suggest that the badger is a habitat generalist that prefers deciduous woodlands, natural pastures, wetlands and riparian areas

(Appendix 1). However, habitat-selection patterns may differ at the edge of a species' range, illuminating limiting factors that explain species' environmental tolerances (Virgós and Casanovas 1999a). Understanding habitat selection would enhance conservation of peripheral populations, such as those in south-western Europe.

In southern Portugal, traditional management has created a mosaic of the two dominant vegetation types: cork oak (*Quercus suber*) and holm oak (*Q. ilex*), wherein three rural activities (wood-gathering, livestock production and agriculture) are pursued in a single space. This human-altered but seminatural landscape, termed *montado*, has persisted for ~1300 years (Joffre *et al.* 1999) and occupies ~36% of Portugal, mainly in the south. It creates a mosaic of landscape elements that vary in tree density, understorey management practices, grazing intensity, and fallow periods (Pinto-Correia 2000). Partly as a result of European Union (EU) policies, the *montado* of southern Portugal is experiencing an increase in agricultural conversion, conversion to tree plantations, and improvement of the road network. These three changes may have negative impacts on badgers. Agricultural conversion replaces the *montado* with large areas of cereal plantations (wheat, rye, and oats). Plantations of non-native eucalyptus and pine for pulp and paper production are avoided by badgers during foraging (Bicik *et al.* 2000; Revilla *et al.* 2000). Finally, road improvement is believed to cause increased casualties and, by promoting habitat fragmentation, may

contribute to declining badger densities in the Iberian Peninsula (Virgós and Casanovas 1999a; Revilla *et al.* 2000; Virgós 2001a; Rosalino *et al.* 2004; Santos-Reis *et al.* 2005).

In this paper we describe habitat-selection patterns of Eurasian badgers at multiple spatial scales. We studied habitat associations of badgers in southern Portugal to identify the importance of *montado* and other habitat features to badgers.

Materials and methods

Data were collected throughout southern Portugal (Fig. 1), including the Natural Park of S. Mamede, the Natural Park of south-west Alentejo and Vicentine Coast, and two Special Protection Zones (Castro Verde and Moura-Mourão-Barrancos).

Cork oak and holm oak *montado* woodlands have an allopatric distribution and dominate the study area, including the protected areas. Within each dominant type, there is significant variation in tree density, understorey species (which included rockrose (*Cistus* spp.), Mediterranean broom (*Genista* spp.), lavender (*Lavandula* spp.), wheat, rye), livestock (sheep, goats, pigs and cattle), and fallow land (Firmino 1999; Joffre *et al.* 1999; Pinto-Correia and Mascarenhas 1999; Pinto-Correia 2000).

Data collection

Badger presence was categorised as 'detected' and 'not-detected', and were derived from ~1900 km of transect surveys conducted during 1990–2002. We overlaid a 1-km grid across a map of southern Portugal, and 2298 cells of 1 × 1 km square were systematically selected and surveyed by walking a transect counting signs of presence (Wilson and Delahay 2001; Sadlier *et al.* 2004; Barea-Azcón *et al.* 2007). Each cell typically contained ≤5 of the 19 land-cover classes (see *Proportion of each land-use type in the sampled areas*). We arranged transect segments such that transect length in each land-cover type was proportional to the cover of each land-cover type within the cell and there was 250–1000 m of transect in each land-cover type. Only 3% of the land-cover occurrences within cells were covered by transects 250–500 m long. Two experienced observers walked each transect. Surveys were conducted by 15 observers employed by the Center of Environmental Biology of the University of Lisbon (CBA), the Department of Biology of the University of Évora, the Institute for Nature Conservation (ICN) and the Center of Studies for the Iberian Avifauna (CEAI).

Badger detection was considered if a badger footprint, scat, latrine or sett was recorded in the cell. Because badger signs are easily recognised, we assume misclassification of presence signs to be negligible. When no badger sign was detected, the cell was classified as 'not-detected' to reflect the fact that badgers were not necessarily absent in these cells. Because animals are active year round and many individuals disperse from each sett for solitary foraging each night, we assume a negligible rate of false 'not-detected' cells.

Environmental variables

For each cell, we used existing GIS data layers to generate two types of explanatory variables:

Proportion of each land-use type in the sampled areas

Land-cover types were derived from the land-cover map produced by the National Center for Geographic Information (CNIG) based on aerial photography from 1990 (1-m resolution), photo interpreted (minimum mapping unit 1 ha) and field verified in 1991. CNIG classified land use into 668 units with varying dominant overstorey and understorey vegetation and tree and shrub cover. Because multivariate procedures demand a parsimonious set of explanatory variables, we ignored understorey conditions (which typically are cleared and regrow on a 3–5-year rotation such that conditions in any particular year would not be of use in our model) and overstorey canopy classes and merged some similar categories to produce coverage with 19 broad land-cover categories: cork oak woodland, holm oak woodland, six types of mixtures and densities of cork and holm oak woodlands, shrubland, non-native conifer and eucalyptus plantations, agricultural field, deciduous forest, orchards, natural pastures, water, rocky areas, urban land, and mining areas. These broader categories have a lower error rate than the original map, but some areas classified as *montado* in 1991 had probably been converted to cereal fields or eucalyptus and pine plantations by the time of our surveys. However, this was the only digital vegetation coverage available for such area and our field notes on vegetation conditions at locations where we found badger sign suggested that the land-cover map was highly accurate.

We then derived an *a priori* candidate set, which consisted of all those variables that were reported as important influences on badgers in the literature (Appendix 1). We also considered interactions among some explanatory variables, restricting our attention to 14 interactions biologically plausible for badgers in the *montado* agro-ecosystem, namely mixtures of cork and holm oak woodlands, shrubland and woodland, and orchards and water.

Proportion of soil type in the areas sampled

Soil type was derived from the digital map produced by the General Direction of Environment (DGA) and was categorised into six classes: cambisols, lithosols, luvisols, planosols, podzols and vertisols. We created a dummy variable for each soil type variable.

Statistical analysis

To evaluate the effect of landscape scale on models of badger distribution we used a nested methodology which we scaled up by merging the information from 1 × 1 km cells into non-overlapping cells of three sizes: 2 × 2 km, 5 × 5 km and 10 × 10 km. We used the 1 × 1 km cell to reflect selection at a scale smaller than an individual home range, and the 2 × 2 km cell to reflect the 4-km² sizes of individual home ranges (Van Apeldoorn *et al.* 1998; Rosalino *et al.* 2004, 2005b). The 5 × 5 km cell reflects selection at the level of the communal territory (Rosalino *et al.* 2004, 2005b), and the 10 × 10 km cell reflects the local population (Van Apeldoorn *et al.* 1998). For the 5 × 5 km and 10 × 10 km cells, we considered only those cells in which at least 20% of the 1 × 1 km cells had been surveyed for badger. Because in most of the cells, the surveyed 1 × 1 km cells are randomly distributed among the larger cells we believe that

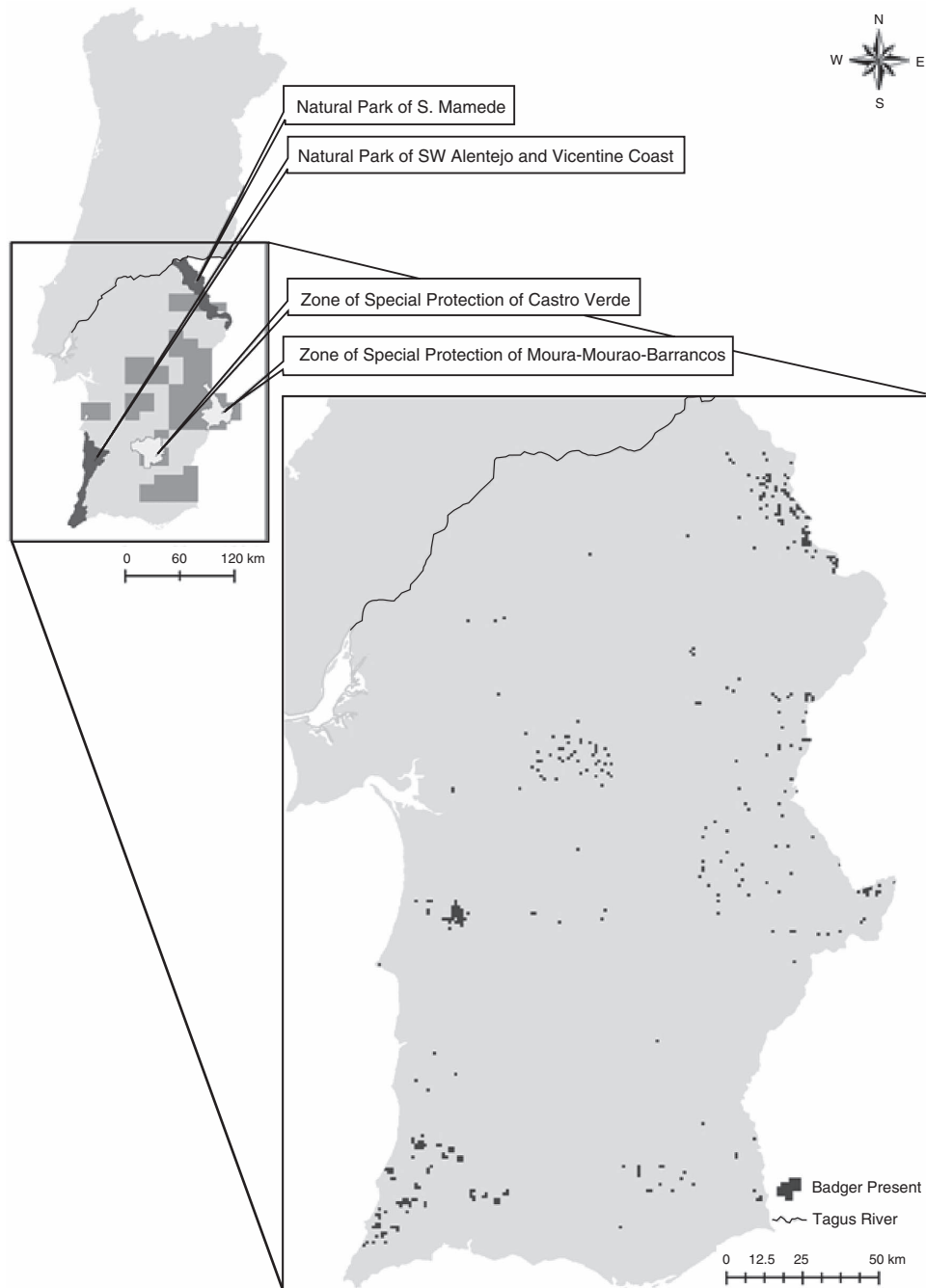


Fig. 1. Location of the study area in southern Portugal. Top left – map of Portugal with areas of data collection: dark grey – Natural Parks; medium grey – research project areas; and light grey – Zones of Special Protection. Bottom right – map of southern Portugal with badger-detection 1 × 1 km grid cells.

they are representative of the entire 5 × 5 and 10 × 10 km areas. At these cell sizes, badger detection was quantified as the proportion of surveyed cells in which badger sign was detected. At the 1 × 1 km and 2 × 2 km cells, badgers were considered either ‘detected’ or ‘not-detected’.

All variables were tested for normality and arcsine transformed. Pearson correlation coefficients were used to test for correlation between the dependent and independent variables

and between pairs of independent variables. Variables correlated with badger detection and non-collinear to other independent variables (multiple $R^2 < 0.5$) were candidates for model development and calibration (Hosmer and Lemeshow 2000).

At each spatial scale, we partitioned the data into two sets using ~80% of the cells for model development and 20% for model testing (Burnham and Anderson 1998). We used logistic regression for 1-km² cells ($n = 1879$ cells for development,

422 for testing) and 4-km² cells ($n = 851$ for development and 223 for testing) because the dependent variable was binary (detected/not-detected). At the scale of the 25-km² cell ($n = 152$ cells for development, 39 for testing) and 100-km² cell ($n = 36$ cells for development, 9 for testing), the dependent variable was a continuous variable (proportion of 1-km² cells in which badgers were detected); therefore we used multiple linear regression.

For both models, we used an *a priori* candidate set, which consisted of all those variables that were reported as important influences on badgers in the literature (Appendix 1). GIS analyses were performed using ArcView 3.2; statistical analyses were performed using SPSS and S+.

Stepwise logistic regression

We used backward-elimination stepwise logistic regression with a maximum of 100 iterations. At each step, the variable with the P -value of the Wald statistic exceeding 0.10 was removed from the model. At any step in which no variable with $P > 0.10$ was in the model, the variable with the lowest P value < 0.05 that was not already in the model was allowed to enter (Hosmer and Lemeshow 2000). To minimise misclassifications due to an unbalanced number of detection/not-detection, the classification cut-off was set equal to the proportion of cells in which badgers were detected in the full sample at that spatial scale.

Overall model performance was estimated through the Nagelkerke's R^2 value, and Hosmer and Lemeshow goodness-of-fit Chi-square (Hosmer and Lemeshow 2000; Pearce and Ferrier 2000). We assessed model accuracy using a confusion matrix, with model sensitivity (number of correctly predicted detections), specificity (number of correctly predicted not-

detections), errors of commission (predicted detections in cells where badgers were not detected) and errors of omission (predicted non-detections in cells where badgers were detected), and overall model predictability (Wright *et al.* 2000), using the 20% of cases not used in model development.

Stepwise multiple regression

At each step, the variable with the lowest P -value of the F -statistic (< 0.05) was entered into the model; a variable was dropped from the model when $P > 0.10$ (Zar 1999). We controlled for multicollinearity by excluding from the model any variable that had a multiple $R^2 > 0.50$ with variables included in the model. The dependent variable was tested for spatial autocorrelation before model development and when the final model was obtained using Moran's I statistic (Legendre 1993; Carroll and Pearson 2000; J. Prather, Northern Arizona University, pers. comm.). Model performance was evaluated by an overall adjusted R^2 and the significance of the coefficients in the model (Zar 1999). Model accuracy was assessed by regressing predicted versus actual percentage of 1-km² subcells occupied by badgers within each 5×5 km or 10×10 km cell, for the 20% of cells withheld from model development.

Results

Our surveys (Fig. 1) resulted in the detection of badger presence signs in 372 of the 2298 1-km² surveyed cells. Two variables – percentage of landscape occupied by deciduous woodlands, and percentage of landscape under pure cork oak – had a consistently positive influence on badger occupancy at three of the four spatial scales (Table 1). Three other variables were associated with badgers at two spatial scales, namely percentage shrub stands

Table 1. Standardised coefficients of variables in models of habitat selection by Eurasian badgers at four spatial scales, using various sets of candidate variables

A positive value indicates a positive correlation with badger occurrence. All coefficients are significant at $P < 0.1$. Stepwise procedures selected variables from a set of candidate variables that included all variables for which the literature suggested relationships. We used backwards-elimination logistic regression for the two smaller cell sizes and forward-entry multiple linear regressions for the larger cells

Variable	1 × 1 km cells	2 × 2 km cells	5 × 5 km cells	10 × 10 km cells
Conifer stands	2.5	3.2	0.31	-0.27
Cultivated field	-1.4	-2.0		0.31
Deciduous woodlands	7.6	11.8	0.25	
Natural pastures		-2.6		-0.23
Pure cork oak stands	2.4		0.58	0.89
Pure holm oak stands		-1.8		
Shrubs stands	1.5			0.28
Streams and rivers	3.9			
Cambisol			-19.0	0.31
Lithosol	-0.3		-26.4	
Luvisol			-26.2	
Planosol		2.9	-1.9	
Podzol			-7.2	
R^2	0.16	0.19	0.52	0.71
HL (P -value) ^A	5.5 (0.73)	5.98 (0.65)		
F -statistic (P -value) ^B			17.4 (<0.0005)	9.66 (<0.0005)

^ABased on the Hosmer and Lemeshow goodness-of-fit test. P -values > 0.05 indicate a well fitted model.

^BBased on F test statistic. P -values < 0.05 indicate a regression that is significantly different from its residues. d.f. = 11 for 5×5 km cell and 6 for 10×10 km cell.

(positive association, as expected), natural pastures (negative, contrary to expectation), and presence of lithosol soils (negative, as expected). Conifer stands were positively associated (contrary to expectation) with badgers at three scales, but negatively associated with badgers at the largest cell size. Cultivated fields had a negative association (as expected) at two scales, but a positive effect at the largest cell size. No other variable had a consistent effect at two or more spatial scales. No model included any interaction term.

Our analyses did not support expected positive influences of fruit trees, holm oak, luvisol, planosol, podzol and vertisol soils. We also did not find evidence for the expected negative influence of non-native eucalyptus plantations and cambisol soil.

The models explained a relatively low amount of variation in badger detection (Table 1). The models were better at predicting cells in which badgers were not detected than cells in which badgers were detected (Table 2).

Discussion

The three most important factors influencing the occurrence of badgers in southern Portugal were deciduous trees (positive), pure cork oak forests (positive), and conifer stands (positive).

The most important factor was coverage of deciduous trees. This is consistent with findings in England (Thornton 1988; Wright *et al.* 2000), Ireland (Hammond *et al.* 2001), The Netherlands (Van Apeldoorn *et al.* 1998), the Czech Republic (Bicík *et al.* 2000), and Spain (Virgós and Casanovas 1999a; Revilla and Palomares 2002) that badgers use deciduous forests. These authors concluded that badgers use these deciduous woodlands because of the moist environment, where water, shelter and food (especially earthworms) are abundant. Deciduous woodlands occupy only small portions (less than 20%) of 1-km² cells in southern Portugal, which would suggest that they are being actively sought by badgers. Badgers are using these areas for food (earthworms) and shelter as the soft soil promotes the easy digging of setts, a limiting factor for Mediterranean badgers (Virgós and Casanovas 1999a; Rosalino *et al.* 2004).

The second most important factor was the percentage of landscape in pure cork oak forests. Several studies in Spain suggest the importance of native forests to badgers (Virgós and Casanovas 1999a; Revilla *et al.* 2000, 2001; Revilla and Palomares 2001; Virgós 2001a), and Rosalino *et al.* (2004, 2005b) identified cork oak woodlands with understorey as

highly used by badgers in Portugal. Cork oak habitats occur in three different forms in southern Portugal: pure cork oak forest, mixed cork oak forest (i.e. mixed with other codominant trees, often including deciduous trees), and cork oak forest with agricultural crops in the understorey. A dense tree cover characterises pure cork oak forest. This vegetation type is maintained by removing patches of shrubs every 3–5 years to enhance cork production and quality, creating a mosaic of shrub/no shrub. Apparently, this human alteration to natural succession of pure cork oak stands does not cause badgers to avoid the altered areas; radio-tagged badgers in the study area did not change behaviour following shrub clearance (Rosalino *et al.* 2004), although shrub clearance can obstruct sett access. Similarly, stone martens and common genet in southern Portugal are not affected by shrub removal (Santos-Reis *et al.* 2004). However, it is important to emphasise that despite not avoiding shrub-cleared areas, these species use shrubs as shelter both in the study area (Rosalino *et al.* 2004; Santos-Reis *et al.* 2004) and elsewhere (Mangas *et al.* 2008). This result is consistent with previously reported positive associations of badgers with shrub cover (Mangas *et al.* 2008; Appendix 1), except for one study where a negative association was reported. The other two types of cork oak woodlands are also maintained by human influence. Human activities promote mixed cork oak forest by maintaining deciduous trees and other forest types interspersed within cork oak stands. Cork oak woodlands with cultivated fields are the result of the removal of the understorey and plantation for livestock forage.

The third most important factor in badger distribution in southern Portugal was plantations of non-native conifers. Conifer stands typically covered 4–7% of each 1 × 1 km cell where badgers occurred. The positive association of these plantations with badgers is somewhat surprising because Revilla *et al.* (2000) identified the replacement of Mediterranean scrubland by conifers and eucalyptus as a major threat to badgers. Moreover, radio-tagged badgers in southern Portugal did not use eucalyptus plantations (Rosalino, unpubl. data). However, studies from northern Spain (Virgós and Casanovas 1999b), Ireland (O’Corry-Crowe *et al.* 1996) and the UK (Cresswell *et al.* 1989) have shown that badgers may use these plantations for building their setts. In our case, we speculate that (1) in areas lacking additional forest structure, badgers may find in conifer plantations the only shelter available, (2) interspersed within the conifer plantations there may be additional food (insects or fruits) or other resources for badgers that are not resolved at the scale at

Table 2. Model accuracy for models of habitat selection of Eurasian badgers in southern Portugal, based on 422 cells set aside for model testing

AA, correctly predicted non-detection of badgers; AP, predicted non-detection when badger was detected; PP, correctly predicted detection of badgers; PA, predicted detection when badgers were not detected. Error of omission: the model predicted non-detection in cell where badgers were detected. Error of commission: the model predicted badger detection in a cell where badgers were not detected. The 1 × 1 km model had 75% overall correct classification, and the 2 × 2 km model had a 66% correct classification

Cell size	No. of cases				% Error	
	AA	PA	PP	AP	Omission	Commission
1 × 1 km	315	40	24	43	64.2	11.2
2 × 2 km	153	24	9	37	80.4	13.6

which this analysis was conducted, (3) the seeds or other tissues of these trees form the basis of a trophic chain from which badgers may ultimately benefit, (4) the landscape configuration of sites of the radio-tracking studies differed in some way from the larger sample of landscapes in this study, such that badgers might, in fact, use the plantations on much of southern Portugal. Clearly, more research is needed to clarify the effects of these plantations on badgers.

Shrub cover and watercourses, as expected, had a positive effect in badger detection although none of these effects were strong; nor were they evident at all spatial scales. Shrub cover has been identified as a key factor for badgers (Revilla *et al.* 2000, 2001; Revilla and Palomares 2001; Virgós 2001a; Mangas *et al.* 2008). Although badgers in the UK detect and capture prey where vegetation is sparse and short (Kruuk *et al.* 1979; Seiler *et al.* 1995), in southern Portugal shrub cover may function as shelter against high summer temperatures (Rosalino *et al.* 2005a). High summer temperatures also make water an important resource in southern Portugal. Even though badgers may acquire their water from food items, they also require access to water. Virgós (2001b) reported badger preference for riparian areas, especially when no forested habitat was found in the surroundings.

We found negative effects of natural pastures, cultivated fields and lithosols in badger presence. Again, none of these effects were strong, nor were they evident at all spatial scales. Natural pastures have been reported to positively affect habitat-selection patterns by badgers throughout the Iberian Peninsula (Virgós and Casanovas 1999a; Revilla *et al.* 2000; Revilla and Palomares 2001; Rosalino *et al.* 2005b) and other European countries (e.g. the UK, The Netherlands). Badgers have been associated with pastures and cultivated fields (Van Apeldoorn *et al.* 1998; Wright *et al.* 2000; Hammond *et al.* 2001) and perceived as agricultural pests due to burrowing and destroying early stages of cereal plantations in their foraging activities. Plantations seem to provide an important component of badgers' diet, insects in Mediterranean areas (Rosalino *et al.* 2005a), and earthworms at other European locations. However, pastures and cultivated fields also increase badgers' exposure to humans; the lack of shelter (a key factor in badger ecology in Mediterranean landscapes: Rosalino *et al.* 2004; Mangas *et al.* 2008) may make these areas less amenable for use by badgers. In addition, soils in southern Mediterranean regions are drier and harder to dig than soils in northern locations, which may further restrict badgers' use of pasture lands. Badgers prefer to burrow and build setts in softer soil types (Bicík *et al.* 2000; Hammond *et al.* 2001), thus the high rock composition of lithosols may explain the avoidance of these areas. However, we did not find any consistent and meaningful influence of other soil types on badger detection. Since soil type seems to be a key factor for the establishment of badger setts (Bicík *et al.* 2000; Hammond *et al.* 2001), further research is recommended to clarify this aspect of badger ecology.

Our models failed to support several other predictions suggested by the literature (Appendix 1). For instance, we expected a positive response to fruit orchards because fruits are important foods for badgers in southern Portugal (Rosalino *et al.* 2005a), but our models failed to identify this variable. Additionally, holm oak forest has also been reported to be negatively correlated with badger abundance (Virgós and

Casanovas 1999a). These forests are associated with arid soil, summer drought, and closed structure (Virgós and Casanovas 1999a), but we failed to detect any influence on Portuguese counterparts.

Contrary to suggestions that important habitat factors may vary with the scale of the model (Wiens 1989; Bissonette 1997), deciduous trees and pure cork oak were the most important variables across scales in our study. However, Virgós and Casanovas (1999a) found that important factors did vary with scale in another Mediterranean landscape. We believe this difference reflects the fact that our study area was a relatively more homogeneous cork oak woodland compared with the heterogeneous landscape studied by Virgós and Casanovas (1999a).

Our results also indicate an increase in explanatory power at larger cell sizes, which may be an effect of the resolution of the available datasets. The resolution of the predictor variables may not allow the resolution of fine-scale habitat-selection features (shelter and food); however, a recent comparison of models derived from field-based and remotely derived habitat data shows that the latter produced better results, probably because the remotely derived data incorporated multiple sources of variability that compensated for the lower resolution of some of the habitat features (Newton-Cross *et al.* 2007). Thus, these results seem to better reflect the social structure of badgers. Badger setts are shared by 4–15 individuals, and the social group maintains a collective home range that is ~20 km² in size, compared with the 4.5 km² for individual home ranges (Rosalino *et al.* 2004, 2005b). Thus strongest selection may be evident at the 5 × 5 km scale, an area within which the social group needs to find all requisite resources.

In our models, habitat factors explained a relatively small fraction of the variation in badger occurrence, which is consistent with a recent review on badger modelling (Newton-Cross *et al.* 2007). We think that this reflects the fact that the Eurasian badger is a habitat generalist (e.g. Van Apeldoorn *et al.* 1998; Virgós and Casanovas 1999a; Bicík *et al.* 2000; Wright *et al.* 2000; Virgós 2001a, 2002; Johnson *et al.* 2002; Rosalino *et al.* 2004). Morrison *et al.* (1998) suggest that low *R*² values in models can also result from (1) errors in measuring animal occurrence and non-detection, (2) sampling animal occurrence and non-detection during seasons or years that do not reflect actual distribution of the species, (3) errors in measuring the explanatory variables, or (4) failure to measure some important habitat variables.

The first three possibilities seem unlikely to be significant causes of model failure because (1) the observers were well trained, and badger sign is easy to detect and difficult to confuse with sign of other species, (2) data were collected over several years on a species that is active in all seasons, and (3) habitat maps were produced by photo-interpretation by the CNIG, with follow-up field verification, and were highly detailed (668 categories). However, the soils map used was of lower resolution than the habitat map, introducing a certain level of error in that small soil patches were not reflected in the map.

Doubtless, our models were subject to the fourth potential problem, namely omission of important variables. For instance, we did not consider two factors that may affect badger distribution, namely food abundance (Virgós 2001a, 2002;

Johnson *et al.* 2002; Rosalino *et al.* 2005a) and road density (Clarke *et al.* 1998; Wright and Fielding 2002). Because prey abundance changes rapidly and shows marked spatial variation, it is impossible to analyse in a GIS model such as this one. For example, other studies have successfully incorporated the effect of prey abundance on habitat selection by carnivores (Beier and Drennan 1997; Drennan and Beier 2003). Unfortunately, at the time we were constructing the model, limited suitable GIS road layers existed for this study area. We opted not to incorporate them into the model because they would add error due to the different mapping units. Furthermore, because the land-cover classification included roadside trees as a separate class, adding a road layer would be redundant. Nonetheless, this candidate variable did not emerge as important in our analyses, indicating either that it is not a good surrogate for the effect of roads or that roads are not an important factor. Finally, Santos Reis *et al.* (2004) suggest that competitors and predators do not play an important role on badger distribution patterns.

Despite the limitations of our models, the clear conservation lesson from our study is the importance of deciduous trees and pure cork oak to conserving badger populations in southern Portugal. Management and decision-making should favour natural vegetation and preference for pastoral activities to maintain the historically human-altered, sustainable and unique landscape and land-use, the *montado*. Furthermore, our results illustrate the importance of the *montado*, an ancient human-modified ecosystem that is threatened by current EU agricultural conversion policies.

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Appendix 1. Habitat variables for the Eurasian badger identified in the available literature from The Netherlands, the Czech Republic, the UK, Ireland, Spain and Portugal

Most closely related explanatory variable in our models	Significant variables in the study	Reported influence on badgers ^A	Badger response variable in the study	Geographical location	Study
Coniferous forest	Coniferous forest	+	Badger setts	Czech Republic	Bicik <i>et al.</i> (2000)
	Conifer plantations	–	Territory	Southern Spain	Revilla <i>et al.</i> (2000)
	Conifer forest	+	Badger setts	Northern Spain	Virgós and Casanovas (1999b)
	Conifer woodlands	+	Badger setts	Ireland	O’Corry-Crowe <i>et al.</i> (1996)
Cork oak forest	Cork oak with understorey	+	Badger territory	Southern Portugal	Rosalino <i>et al.</i> (2005)
Cultivated fields	Arable lands	+	Badger sett	The Netherlands	Van Apeldoorn <i>et al.</i> (1998)
Deciduous woodland	Deciduous and mixed woodland	+	Badger sett	The Netherlands	Van Apeldoorn <i>et al.</i> (1998)
	Deciduous forest	+	Badger occurrence	Czech Republic	Bicik <i>et al.</i> (2000)
	Deciduous woodland	+	Badger sett	Northern England	Wright <i>et al.</i> (2000)
Eucalyptus plantations	Eucalyptus plantations	–	Badger occurrence	Czech Republic	Bicik <i>et al.</i> (2000)
	Eucalyptus plantations	–	Territory	Southern Spain	Revilla <i>et al.</i> (2000)
Fruit trees	Fruit trees	+	Badger territory	Southern Portugal	Rosalino <i>et al.</i> (2005)
Holm oak forest	Holm oak forest cover	+	Badger abundance	Central Spain	Virgós and Casanovas (1999a)
Soil type	Loamy soil	+	Badger occurrence	Czech Republic	Bicik <i>et al.</i> (2000)
	Stony and clay soil	–	Badger occurrence	Czech Republic	Bicik <i>et al.</i> (2000)
	Soil type	Varied ^B	Badger numbers and setts	Ireland	Hammond <i>et al.</i> (2001)
Pastureland	High quality pasture	+	Badger numbers and setts	Ireland	Hammond <i>et al.</i> (2001)
	Grassland	+	Badger sett	Northern England	Wright <i>et al.</i> (2000)
	Pasturelands	+	Territory	Southern Spain	Revilla <i>et al.</i> (2000)
	Pastures	+	Badger territory	Southern Portugal	Rosalino <i>et al.</i> (2005b)
	Pastures	+	Territory	Southern Spain	Revilla and Palomares (2001)
Shrubs	Lentiscus scrubland	+	Territory	Southern Spain	Revilla <i>et al.</i> (2000)
	Mediterranean scrubs	+	Territory	Southern Spain	Revilla and Palomares (2001)
	Shrub cover	+	Badger sett	Southern Spain	Revilla <i>et al.</i> (2001)
	Shrub cover	+	Badger sett density	Central Spain	Virgós (2001a)
	Scrubland	+	Badger presence	Southern Spain	Mangas <i>et al.</i> (2008)
	Shrub cover	–	Badger presence	Northern Spain	Virgós and Casanovas (1999a)
Streams and rivers	Riparian areas	+	Badger territory	Southern Portugal	Rosalino <i>et al.</i> (2005b)
	Riparian areas	+	Detected signs	Spain	Virgós (2001b)
	Wetlands	+	Territory	Southern Spain	Revilla <i>et al.</i> (2000)

^A ‘+’ (positive) and ‘–’ (negative) relationships at $P < 0.05$ in the referenced study.

^B Cambisol and lithosol negative influence; luvisol, planosol, podzol and vertisol positive influence.