

# Habitat quality predicts the distribution of a lizard in fragmented woodlands better than habitat fragmentation

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## Keywords

deciduous and evergreen forests; food abundance; fragment size; fragment isolation; *Psammodromus algirus*; thermal quality.

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## Abstract

Organisms often face a higher risk of local extinction in fragmented than in continuous habitat. However, whether populations are affected by reduced size and connectivity of the habitat or by changes in habitat quality in fragmented landscapes remains poorly investigated. We studied the regional distribution and microhabitat selection of the lacertid lizard *Psammodromus algirus* in a fragmented landscape where the existence of deciduous and evergreen woodlands brought about variation in habitat quality. Lizards never occupied any fragment smaller than 0.5 ha. However, above that limit fragment size no longer predicted lizard occurrence, which was explained by woodland type instead, with lizards being more frequently found in deciduous than in evergreen woodlands. Lizards selected microhabitats that had structural features favouring thermoregulation, foraging and predator avoidance, and we identified better conditions for thermoregulation and food acquisition in deciduous than in evergreen woodlands. Our results support the idea that variation in habitat quality can sometimes override the effect of habitat fragmentation on animal populations. We consider the implications of our study for the conservation of Mediterranean lizards, discussing our results in a broader context framed by previous studies conducted in nearby areas.

## Introduction

The negative effects of habitat loss and fragmentation on biodiversity have been widely acknowledged after three decades of theoretical and empirical research (Turner, 1996; Fahrig, 2003; Henle *et al.*, 2004a). Habitat destruction is now accepted as the principal cause of the extinction crisis we are witnessing (Laurance & Bierregaard, 1997; Harrison & Bruna, 1999; Noss, Csuti & Groom, 2006). However, the negative impact of habitat fragmentation is better supported by its pervasive consequences for organisms, such as local extinction in fragmented habitats (Turner, 1996; Henle *et al.*, 2004b), than by explicit attempts to understand the processes causing biodiversity loss (McGarigal & Cushman, 2002; Fahrig, 2003; Ries *et al.*, 2004). Besides, the study of habitat fragmentation has traditionally favoured a few model organisms (principally vascular plants, birds and mammals; Opdam, 1991; Bierregaard *et al.*, 1997; McCollin, 1998; Fazey, Fischer & Lindenmayer, 2005) or particular habitats (mostly temperate and tropical forests; Laurance & Bierregaard, 1997; Schmiegelow & Mönkkönen, 2002), which has resulted in a serious unawareness of the consequences of fragmentation for most organisms. Biased knowledge of the effects of habitat fragmentation is parti-

cularly disappointing for conservation purposes, because the responses to habitat fragmentation greatly vary between organisms, habitat types and geographic locations (Crome, 1997; Santos, Tellería & Carbonell, 2002; Lindenmayer & Fischer, 2007).

For example, ectothermic vertebrates may show different responses to fragmentation compared with endothermic birds and mammals. Previous research has reported both sensitivity (Scott *et al.*, 2006) and resistance (Kitchener *et al.*, 1980; Burbidge & Mckencie, 1989) of lizard populations to habitat fragmentation, with greater ability of generalist species to persist in fragmented habitat (see Smith *et al.*, 1996). Variable vulnerability of lizards to habitat fragmentation could be related to their special biological features. Lizards often suffer high predation and impaired thermoregulation when refuges are scarce (Martín & López, 1999a), which probably reduces lizards' ability to use inhospitable habitat between isolated habitat patches and, as a consequence, hampers population connectivity in fragmented landscapes (Stamps, Buechner & Krishman, 1987). Restricted dispersal could increase the risk of local extinction of lizards in habitat fragments, which would cause regional extinction in areas subjected to prolonged habitat fragmentation (Burkey, 1989; Cooper & Walters,

2002; Henle *et al.*, 2004b). However, ectothermy also helps lizards reduce space and energy requirements, perhaps favouring population persistence in small habitat patches (Pough, 1980). In that case, lizards might maintain viable populations in isolated fragments for longer than birds and mammals (Hinsley *et al.*, 1996; Henle *et al.*, 2004b), which could favour their persistence in fragmented landscapes despite their reduced colonization ability.

Microhabitat selection could be a main mechanism explaining the persistence of lizard populations in fragmented habitat. However, both the patterns and the fitness consequences of microhabitat selection may vary in space and time in relation to variation in predation risk, food availability, opportunities for thermoregulation and other components of habitat quality (Martín & López, 1999b, 2002). Such variation may in turn have demographic consequences (Díaz *et al.*, 2005a), which combined with stochastic processes may lead to variable population density or even occurrence, among fragments of different size or quality.

The consequences of habitat fragmentation for European lizards are largely unknown (for exceptions see Boudjemadi, Lecomte & Clobert, 1999; Díaz *et al.*, 2000, 2005a; Le Galiard, Ferrière & Clobert, 2005). We analysed the relationships between fragmentation, habitat quality, regional distribution and microhabitat selection in the large psammomorph *Psammotriton algirus*, a lacertid lizard widespread in Iberian woodlands (Carretero *et al.*, 2002). The large psammomorph is a generalist species that occupies a wide range of Mediterranean forested and shrubby habitats, even if such habitats are degraded (Carretero *et al.*, 2002). Wide habitat use is a typical feature of so-called 'soft-edge' species, which are largely resistant to fragmentation (Stamps *et al.*, 1987). However, the large psammomorph also shows traits typical of species that are sensitive to fragmentation ('hard-edge' species; Stamps *et al.*, 1987). In particular, it faces strong predation pressure by various vertebrate species (Valverde, 1967; Martín & López, 1990), which seems to strongly influence microhabitat use in this species (Díaz, 1992; Díaz, Cabezas-Díaz & Salvador, 2005b).

We analysed the relative importance of habitat fragmentation (i.e. reduced size and connectivity of available habitat) and habitat suitability on the distribution and microhabitat selection of the large psammomorph, in an area covered by two woodland types that presumably differ in habitat quality for lizards (evergreen and deciduous oak forests). Remarkably, a previous study of the distribution of the large psammomorph in the close vicinity of our study area uncovered hard-edge responses of lizards to forest fragmentation, revealing that lizards had an extremely low probability of maintaining viable populations in fragments smaller than 90 ha (Díaz *et al.*, 2000). The discovery of lizard populations in woodlands far below this size in the same geographic location (the study area in this paper; see Díaz *et al.*, 2005a) raises the question as to what extent lizards can display variable responses to fragmentation at the landscape scale. Therefore, comparing our results with the study by Díaz *et al.* (2000) is also an explicit objective of this study.

## Materials and methods

### Study area

We studied lizard populations in an  $11 \times 12$  km<sup>2</sup> agricultural landscape (Fig. 1) located around Lerma, northern Spain (42°5'N, 3°45'W; 850 m a.s.l.). In this area, forests cover <10% of their former range, being fragmented into patches of variable size interspersed among cereal fields. Forest remnants in this area are dominated by either deciduous Pyrenean oaks *Quercus pyrenaica* or evergreen Holm oaks *Quercus ilex*, which are assumed to be habitats of different quality for the large psammomorph. In central Spain, the large psammomorph is more abundant in Pyrenean oak than in Holm oak forests (Díaz & Carrascal, 1991a; Díaz, 1997), and experimentally released juvenile psammomorphs grew up faster in Pyrenean oak than in Holm oak forests (Iraeta *et al.*, 2006).

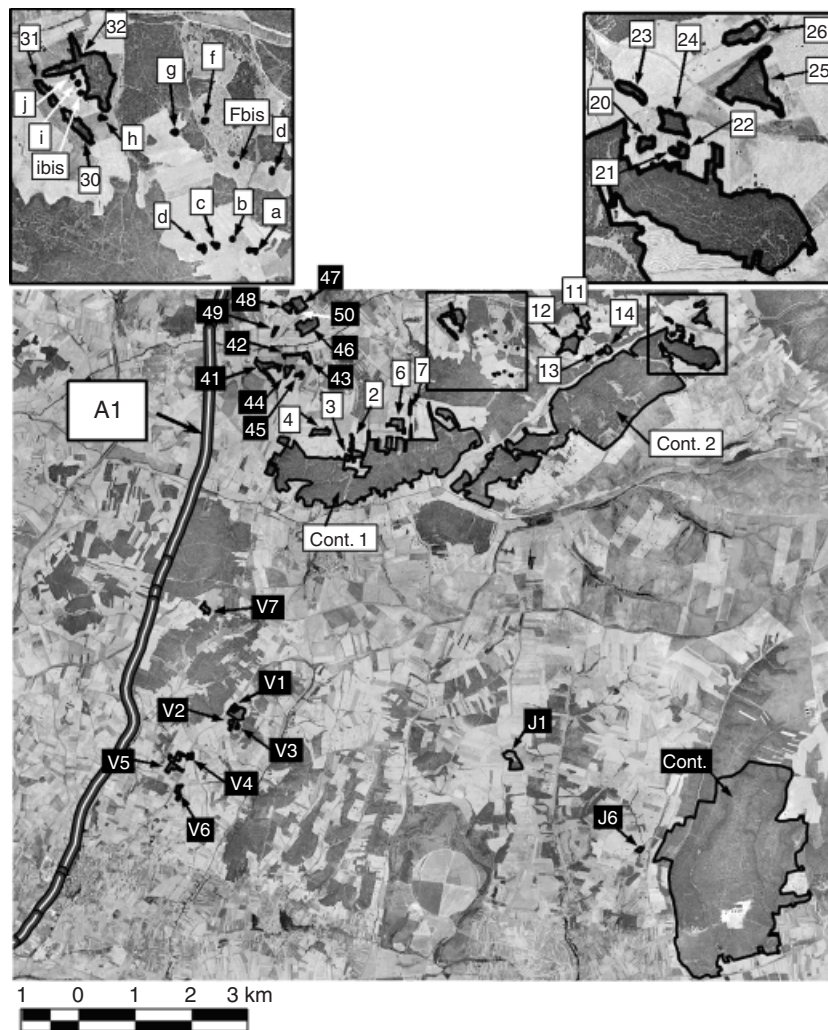
### Structural features of woodlands

We surveyed 50 forest fragments (19 Holm oak and 31 Pyrenean oak woodlands; Supplementary Material Appendix S1) during the lizard activity seasons (April–September) of 2001 and 2002. We measured the size of each fragment and two indices of their isolation relative to other woodlands: the distance to the closest woodland larger than 200 ha (hereafter continents, all of which house large lizard populations; Supplementary Material Appendix S1) and the distance to the closest fragment larger than 0.5 ha. We also measured the proportion of ground covered by trees (vegetation above 2 m high), shrubs (woody plants below 2 m high), 30-cm-high plants (hereafter ground-level vegetation cover) and leaf litter. All these cover variables had previously been found to be potentially important for the large psammomorph (Carrascal & Díaz, 1989; Díaz & Carrascal, 1991a; Díaz *et al.*, 2000). Vegetation cover was estimated on 25-m-radius plots (0.2 ha) according to Prodon & Lebreton (1981). Sample size increased with woodland size in such a way that sample sizes per woodland ranged between one single plot for fragments smaller than 0.2 ha and 25 plots in the larger forests (c. 6.5 ha; see Supplementary Material Appendix S1).

### Habitat quality in deciduous and evergreen woodlands

At the start of the lizard activity season in 2002 (in April 23), we measured thermal quality and food abundance in four representative woodlands (two Pyrenean oak fragments of 1.0 and 5.2 ha, and two Holm oak fragments of 0.9 and 4.1 ha; see Díaz *et al.*, 2005a). We accounted for within-fragment variation in these components of habitat quality by sampling several plots regularly spaced in each fragment (five or 10 plots depending on fragment size).

We measured environmental operative temperatures ( $T_e$ : the equilibrium temperature of inanimate objects with similar heat-transfer properties as lizards; Bakken & Gates,



**Figure 1** Map of the study area showing the location, size and shape of the woodlots and continents studied. Deciduous and evergreen forests are shown in white and black squares, respectively. The location of the motorway (State road A1) that sets the western limit of the study area is also shown. Two sectors of the study area (framed on the map) have been magnified.

1975; Bakken, 1992), using copper tubes that were built and calibrated to mimic the thermal properties of non-thermoregulating lizards (for further details, see Díaz & Cabezas-Díaz, 2004). The thermal quality of each sampling plot was calculated as the absolute deviation of its mean  $T_e$  from the thermal range preferred by lizards (31.2–35.0 °C; Díaz, Iraeta & Monasterio, 2006). We used the deviation of the mean  $T_e$  rather than the mean deviation of  $T_e$  values (cf. Hertz, Huey & Stevenson, 1993) because, in cool environments, large psammodomus base thermoregulation on frequent switching between sunlit and shade locations, reaching mean body temperatures that are closer to the average of full sun and full shade patches than to the average equilibrium  $T_e$  within any of the two patch types (Díaz & Cabezas-Díaz, 2004). We considered spatio-temporal variation in the thermal quality of each sampling plot by recording  $T_e$  in four points evenly separated from one another, during six 2-h intervals evenly distributed between 8:00 and 20:00 h.

Food availability was estimated on the same sampling plots and time intervals, by counting all arthropods larger than 3 mm found during 1 min within a 20 × 20 cm frame

tossed twice on random locations in each sampling plot (see Díaz & Carrascal, 1991b for details).

### Lizard distribution

We searched for lizards from 2 to 6 days in each woodland fragment; in 40 out of 50 fragments lizards were searched for at least during three different days, and in 24 fragments at least during four days. Sampling effort (4.1 person-hours ha<sup>-1</sup> on average) was directly proportional to woodland size, roughly following a logarithmic scale. Given the detectability of this species, we assume that fragments in which we did not detect lizards lacked stable lizard populations, meaning that some isolated individuals might have been eventually detected in some woodlands scored as vacant, should we have applied impracticably more intensive sampling.

### Microhabitat selection

We studied microhabitat selection by lizards in six fragments (three Pyrenean oak fragments sized 3.2, 3.6 and

6.8 ha, and three Holm oak fragments sized 1.6, 4.0 and 6.5 ha), which were representative of all forest fragments in the study area (they were not significantly different from the 44 remaining woodlands in any component of vegetation structure, all  $P > 0.10$ ). We also studied microhabitat selection in two Pyrenean oak forests sized 227 and 317 ha, and in one Holm oak forest sized 567 ha, which was the only evergreen continent in the area. Every time a lizard was found, we estimated the cover of vegetation (variables described above) in a 5-m-radius circle around the spot where the lizard was first sighted. We recorded the structure of available microhabitats on 25-m-radius plots used to measure vegetation structure in the fragments, plus 108 plots sampled in the three large forests. While 5-m-radius circles realistically represent the average size of lizard territories (Díaz, 1993; Salvador & Veiga, 2001), using 25-m radius circles improved the balance between sampling effort and sample representativeness when scoring available habitat in each forest patch. Thus, our final sample consisted of 144 plots used by lizards (92 in continents and 52 in fragments) and 218 plots utilized to describe the availability of microhabitats (108 in continents and 110 in fragments).

## Data analyses

We used generalized linear models to analyse variation in habitat characteristics of woodlands, with log- or arcsin-transformed variables when it was necessary to meet the assumptions of parametric statistics. We used stepwise logistic regression, with the presence and absence of lizards in each fragment as the dependent binomial variable, to model the probability of lizard occurrence in relation to type of woodland, fragment size, fragment isolation and vegetation structure. Spatial autocorrelation could affect our results because two closely located sampling sites are likely to be more similar to each other than two distantly located sites (Dormann, 2007). We simultaneously tested for spatial effects (Legendre's polynomial; Borcard, Legendre & Drapeau, 1992) and habitat effects as determinants of lizard occurrence, and the analysis did not converge to a clear solution probably because spatial structure in our sample was primarily due to the distribution of deciduous and evergreen woods in the study area (Fig. 1). Thus, a logistic regression with only the geographic variables shows that fragments with lizards are mainly located in the northern part of the study area, a result that can be reasonably interpreted only in terms of the size and type (i.e. deciduous vs. evergreen) of the available forest patches (see Fig. 1). The existence of other, unknown geographical factors influencing the distribution of both lizards and trees is extremely unlikely at the scale of our study, and therefore we decided to remove spatial effects from our analyses.

Thermal quality, arthropod abundance and microhabitat selection data were analysed using ANOVA contrasts (planned comparisons; Hill & Lewicki, 2006). For thermal quality and arthropod abundance, we tested for differences between wood types computing the error term within habitat patches (two patches of each wood type). For

**Table 1** Planned comparisons (linear contrasts for both use and availability) within the two-way ANOVA of microhabitat characteristics, with woodland type and use versus availability as the factors

	Contrasts					
	S	F	W	S × F	S × W	S × F × W
Holm oak forest (1)						
Availability	-1	-2	-5	2	5	-10
Use	1	-2	-5	-2	-5	10
Pyrenean oak forests (2)						
Availability	-1	-2	4	2	-4	8
Use	1	-2	4	-2	4	-8
Holm oak fragments (3)						
Availability	-1	1	-5	-1	5	5
Use	1	1	-5	1	-5	-5
Pyrenean oak fragments (3)						
Availability	-1	1	4	-1	-4	-4
Use	1	1	4	1	4	4

The main effects are selection (S: use vs. availability), fragmentation (F: large forests vs. small fragments) and woodland type (W: evergreen Holm oaks vs. deciduous Pyrenean oaks). The number of woodlands within each category (i.e. cells for computing the error term) is shown in brackets.

microhabitat selection data, contrasts were specified within the two-way woodland (three large forests plus six small fragments) × selection (use vs. availability) design (Table 1). Therefore, our approach allowed us to calculate appropriate error terms and to avoid pseudoreplication by giving equal weight to all the woodlots represented in the pooled sample. Planned comparisons were used to test for lizard selection for each variable of habitat structure (difference between used and available plots), by simultaneously examining the effects of woodland type (Holm oak vs. Pyrenean oak), fragmentation (forests vs. fragments), and the interaction terms including microhabitat selection (Table 1). Except when otherwise stated, average values are reported as mean ± SD.

## Results

### Distribution of lizards in fragmented habitat

The size of the 50 studied forest fragments ranged between <0.1 ha (90 m<sup>2</sup>) and 6.8 ha (Supplementary Material Appendix S1). Lizards were found in 21 fragments (42%), which on average were larger, showed lower cover of trees and had higher ground-level vegetation cover than the fragments without lizards (Table 2). The smallest fragment with lizards was a 0.55 ha of deciduous woodland (Supplementary Material Appendix S1). Deciduous (Pyrenean oak) fragments were smaller, were located closer to the nearest continent, and had a higher cover of trees than evergreen (Holm oak) fragments (Fig. 1 and Table 3). Variation in tree cover between the two woodland types was explained by the fact that deciduous fragments were on average smaller, because (1) tree cover and fragment size were negatively correlated ( $R = -0.84$ ,  $n = 50$ ,  $P < 0.001$ ) and (2) differences

**Table 2** Results of ANOVA comparing structural features of fragments with lizards and fragments in which lizards were not found

	Fragments with lizards ( $n=21$ )	Fragments without lizards ( $n=29$ )	$F_{1,48}$	$P$
Surface area (ha)	2.3 ± 2.0	1.0 ± 1.6	19.43	<0.001
Distance to continent (m)	570.0 ± 623.9	406.3 ± 627.2	1.31	0.26
Distance to nearest fragment (m)	60.9 ± 56.5	62.3 ± 59.7	0.01	0.93
Cover of trees (%)	35.5 ± 13.3	64.3 ± 33.2	14.18	<0.001
Cover of shrubs (%)	45.0 ± 18.8	35.7 ± 22.8	2.35	0.13
Ground-level vegetation cover (%)	24.5 ± 12.1	18.5 ± 20.3	6.87	0.012
Cover of leaf litter (%)	49.8 ± 13.7	58.6 ± 32.0	1.38	0.25

Means, standard deviations and sample sizes are shown.

**Table 3** Results of ANOVA comparing structural features of Holm oak and Pyrenean oak fragments

	Holm oak fragments ( $n=19$ )	Pyrenean oak fragments ( $n=31$ )	$F_{1,48}$	$P$
Surface area (ha)	2.1 ± 1.9	1.2 ± 1.7	9.75	0.003
Distance to continent (m)	1029.4 ± 720.7	135.3 ± 109.6	43.93	<0.001
Distance to nearest fragment (m)	73.2 ± 61.5	54.6 ± 55.3	1.42	0.239
Cover of trees (%)	36.0 ± 14.3	62.2 ± 33.0	10.65	0.002
Cover of shrubs (%)	37.1 ± 12.2	41.1 ± 25.6	0.42	0.521
Ground-level vegetation cover (%)	17.0 ± 9.5	23.5 ± 20.6	0.003	0.955
Cover of leaf litter (%)	47.4 ± 15.8	59.5 ± 30.1	2.63	0.112

Means, standard deviations and sample sizes are shown.

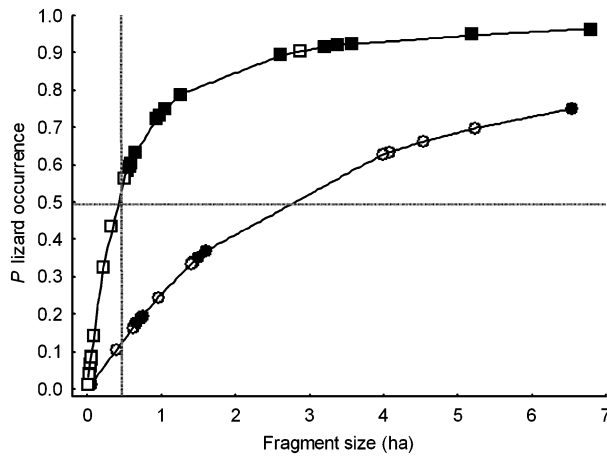
in tree cover between woodland types were not significant when fragment size was taken into account as a covariate in ANCOVA ( $F_{1,47} = 1.27$ ,  $P = 0.27$ ). In fact, 15 out of 17 fragments smaller than 0.5 ha were recently recovered deciduous woodlands in which tree cover exceeded 75% (Supplementary Material Appendix S1), due to both intense sprouting and lack of space for accommodating internal clearings.

A forward stepwise logistic regression model with lizard occurrence as the dependent variable, woodland type as a classification factor and all variables describing the characteristics of fragments as continuous predictors (size of the fragment, distance to nearest continent and fragment, and vegetation structure) acceptably predicted the probability of lizard occurrence (proportion of correct classifications = 0.78) based on size of the fragment and woodland type (goodness of fit of the model: deviance = 43.88, d.f. = 47,  $P = 0.603$ ). The interaction between habitat type and patch size was not significant (Wald's statistic = 2.9, d.f. = 1,  $P = 0.09$ ). We repeated the analysis using backward stepwise regression and found the same results. As expected, lizards were more likely to occur in larger fragments (Wald's statistic = 12.4, d.f. = 1,  $P = 0.0004$ ; Table 2). However, lizards were more often found in deciduous woodlands (14 out of 31 fragments had lizards) than in evergreen woodlands (seven out of 19 fragments had lizards; Wald's statistic = 5.8, d.f. = 1,  $P = 0.016$ ), despite the smaller average size of the former (Table 3). Given that holm oak woodlands are more isolated from continents than Pyrenean oak woodlands (Table 3), the question remains as to whether the effect of woodland type included in our model actually conceals a correlated effect of woodland isolation. However, if wood type is not added to the analysis, the only

variable entered in the model is fragment area: neither isolation (effect of distance to the continent:  $P = 0.82$ ) nor any other variable is selected as a significant predictor of lizard occurrence.

The logistic model revealed that, above a size of around 0.5 ha, woodland type was the sole predictor of lizard occurrence, with deciduous woodlands being more likely to house lizards (Fig. 2). Confirming the latter result, a logistic regression excluding fragments smaller than 0.5 ha included woodland type as the only significant predictor of lizard occurrence (Wald's statistic = 6.5, d.f. = 1,  $P = 0.011$ ; lizards were found in 14 out of 16 deciduous fragments larger than 0.5 ha, compared with seven out of 17 evergreen fragments larger than 0.5 ha; see Supplementary Material Appendix S1). In addition, among fragments larger than 0.5 ha, average fragment size was virtually identical for woodlands with lizards (mean = 2.27 ha, range = 0.55–6.8 ha,  $n = 21$ ) and woodlands without lizards (mean = 2.25, range = 0.51–5.2 ha,  $n = 12$ ;  $F_{1,31} < 0.001$ ,  $P > 0.99$ ). Remarkably, lizards were found in six out of the seven smallest deciduous woodlands above the 0.5 ha size limit (between 0.5 and 1 ha), while only two out of eight evergreen woodlands housed lizards within this range of fragment sizes (Supplementary Material Appendix S1). Below 0.5 ha, any isolation effect could be discarded because the mean distance to the nearest continent was shorter for fragments smaller than 0.5 ha ( $218.4 \pm 419.5$  m) than for fragments with lizards (Table 2;  $F_{1,36} = 5.1$ ,  $P = 0.031$ ). We are aware that small fragments were often less intensely sampled than large fragments, and consequently sampling effort and fragment size were somewhat confounded in our study. However, the possibility that sampling effort explained lizard occurrence

was very slim, because a logistic regression analysis in which sampling effort (measured as the time spent searching for lizards in each fragment) was included as an independent predictor of lizard occurrence produced the same result reported above for fragment size and habitat type (fragment size: Wald's statistic = 6.6, d.f. = 1,  $P = 0.010$ ; habitat type: Wald's statistic = 4.3, d.f. = 1,  $P = 0.039$ ), but failed to reveal any effect of sampling effort on the probability of finding lizards (Wald's statistic = 1.1, d.f. = 1,  $P = 0.290$ ).



**Figure 2** Probability of lizard occurrence in each fragment, in relation to fragment size and woodland type (squares: deciduous woodlands; circles: evergreen woodlands), as modelled by logistic regression analysis. The observed occurrence of lizards is indicated with filled symbols (occupied fragments) and open symbols (vacant fragments). The broken lines indicate 0.5 probability of occurrence (horizontal line), and the value of fragment size (0.5 ha) below which all fragments are predicted to lack lizards (vertical line).

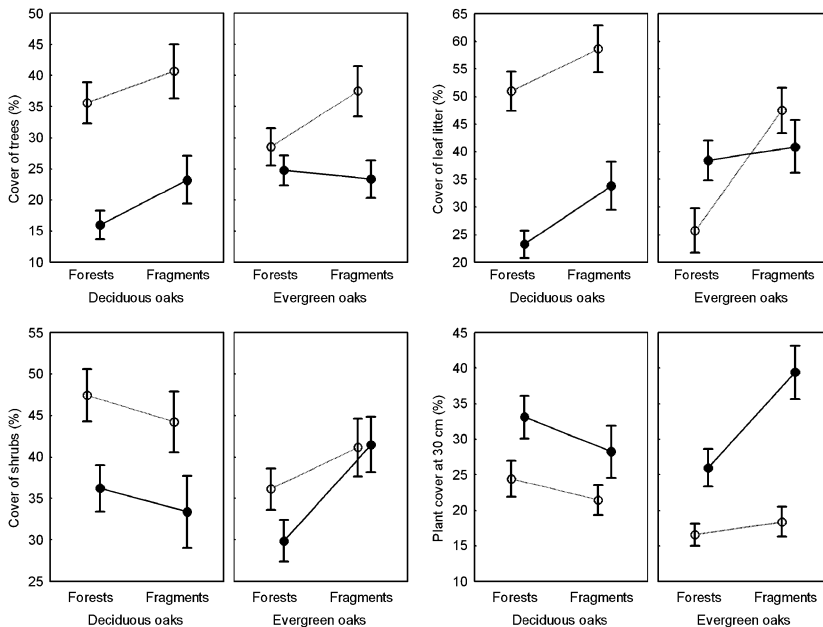
### Thermal quality and food availability in deciduous and evergreen woodlands

Mean daily  $T_e$  was higher in deciduous fragments ( $28.8 \pm 2.1^\circ\text{C}$ ) than in evergreen fragments ( $26.0 \pm 2.8^\circ\text{C}$ ; planned comparison  $F_{1,26} = 6.1$ ,  $P = 0.021$ ). Accordingly,  $T_e$  was closer to the lizards' preferred temperature range (i.e. overall thermal quality was higher) in deciduous fragments (mean deviation from preferred temperature range =  $1.6 \pm 1.5^\circ\text{C}$ ) than in evergreen fragments ( $4.0 \pm 2.7^\circ\text{C}$ ; planned comparison  $F_{1,26} = 5.6$ ,  $P = 0.026$ ).

Arthropods were nearly five times more abundant in deciduous fragments (mean number of arthropods per minute of search =  $1.17 \pm 0.62$ ) than in evergreen fragments ( $0.25 \pm 0.19$ ; planned comparison  $F_{1,26} = 23.8$ ,  $P < 0.001$ ).

### Microhabitat selection in forests and fragments

Lizards were selective in their patterns of microhabitat use, choosing locations with lower tree cover and, particularly, higher ground-level vegetation cover than available on average (Fig. 3, Table 4). Microhabitat selection remained unaffected by fragmentation, as the patterns of selection did not differ significantly between large forests and small fragments (see interaction terms in Table 4). Overall, lizards used similar microhabitats in all environments (Fig. 3), so that many significant interactions in Table 4 were attributable to differences in microhabitat availability (e.g. differences between continents and fragments were larger in evergreen than in deciduous woodlands, due to the lower cover of trees and leaf litter in the evergreen continent; see triple interactions in Table 4). However, selection by lizards of sites with abundant ground-level vegetation was especially intense in evergreen fragments. In deciduous



**Figure 3** Variation in structural features between sites used by lizards (filled dots and solid lines) and randomly selected sites (open circles and dashed lines), in relation to degree of fragmentation (large forests vs. small fragments) and woodland type (deciduous vs. evergreen forests).

**Table 4** Results of planned comparisons in an ANOVA testing for the effects of lizard habitat selection, habitat fragmentation, and woodland type on structural features of woodlands

	Trees		Shrubs		30-cm plants		Leaf litter	
	$F_{1,344}$	$P$	$F_{1,344}$	$P$	$F_{1,344}$	$P$	$F_{1,344}$	$P$
Selection	21.16	<0.001	2.06	0.152	45.63	<0.001	15.48	<0.001
Fragmentation	3.00	0.084	1.32	0.251	1.46	0.228	7.72	0.006
Woodland type	0.00	0.949	0.84	0.360	0.70	0.403	0.07	0.794
Selection × fragmentation	0.02	0.885	0.04	0.836	0.16	0.689	0.03	0.864
Selection × woodland type	0.76	0.384	0.16	0.691	1.72	0.191	7.79	0.006
Selection × fragmentation × woodland type	4.47	0.035	0.09	0.760	12.26	0.001	7.07	0.008

The cover of four different components of vegetation development are analysed.

woodlands (either continents or fragments), lizards were less selective with respect to ground-level vegetation cover, whereas in evergreen woodlands, and particularly in fragments, lizards selected sites with higher ground-level vegetation cover than available (Fig. 3).

## Discussion

Our results illustrate a common effect of habitat fragmentation on natural populations, with lizard populations seldom occurring in small habitat fragments. However, such an effect overlapped with the influence of variable habitat quality on lizard distribution, revealed by a different probability of occurrence between deciduous and evergreen woodlands. In addition, we found that microhabitat selection could interfere with the large-scale distribution related to fragmentation or overall quality of the habitat. For the sake of clarity, we will structure our discussion in four sections. Firstly, we will discuss pure effects of habitat fragmentation (size and isolation of habitat patches) on lizard distribution. Secondly, we will focus on differences between habitat types, using our detailed analysis of several deciduous and evergreen woodlands. Thirdly, we will discuss contrasting patterns of habitat selection emerging at different spatial scales, from microhabitat selection to regional distribution, by comparing our results with those obtained by Díaz *et al.* (2000). Finally, we will integrate all the above ideas drawing conclusions applicable to lizard conservation.

### Effects of habitat fragmentation

Many studies have reported negative effects of habitat fragmentation on lizards (e.g. Kitchener *et al.*, 1980; Smith *et al.*, 1996; Mac Nally & Brown, 2001; Fischer *et al.*, 2005; Scott *et al.*, 2006), usually suggesting that lizard populations are more affected by reduced habitat size than by fragment isolation (but see Fischer *et al.*, 2005). Exceptions are often generalist species, which thrive in disturbed habitats and suffer less from restricted dispersal in fragmented landscapes, where they persist as metapopulations (Sarre, Smith & Meyers, 1995; Smith *et al.*, 1996). Although our study area lacks corridors with suitable habitat connecting forest fragments, we failed to identify any effect of fragment isolation on lizard distribution. Therefore, the large psammmodromus

seems not to be a strict hard-edge species. That is, populations do not appear to be fully isolated from one another in different fragments. This finding is also supported by observations of marked lizards that moved nearly 100 m between forest fragments in our study area (T. Santos, J. A. Díaz, J. Pérez-Tris, R. Carbonell & J. L. Tellería, unpubl. data).

In our system, fragments below 0.5 ha were unlikely to maintain stable lizard populations. This could not be explained by increasing woodland isolation due to habitat fragmentation, because the fragments sized <0.5 ha were located closer to other woodlands than the fragments with lizards. Therefore, the inability of the smallest fragments to house lizard populations is probably due to other processes that start to operate when habitat becomes too small. One of such factors may be space limitation for the establishment of territories. In a Holm oak forest located in central Spain, the large psammmodromus had home ranges ranging 222–333 m<sup>2</sup> for males and 49–141 m<sup>2</sup> for females (Díaz, 1993). In a nearby Pyrenean oak forest, home-range size reached 312 m<sup>2</sup> for males and 74 m<sup>2</sup> for females (Salvador & Veiga, 2001). Therefore, some fragments below 0.5 ha might be simply too small to house a single male (Supplementary Material Appendix S1) or may contain only a very few males. As a consequence, many fragments sized <0.5 ha probably cannot sustain stable populations, but are at best sporadically colonized by small founder populations that recurrently go extinct.

Another possible, non-alternative explanation is that the probability of the smallest patches meeting all the necessary habitat requirements (Willis, 1979; Henle *et al.*, 2004b) becomes critically low for the large psammmodromus below 0.5 ha. In fact, the smallest fragments were significantly different from the fragments with lizards in microhabitat features that are important for thermoregulation, foraging and predator avoidance (Díaz & Carrascal, 1991a; Díaz, 1992). Thus, compared with the 21 fragments with lizards (Table 2), the 17 fragments sized less than 0.5 ha had higher tree cover ( $88.0 \pm 17.4$ ;  $F_{1,36} = 113.7$ ,  $P < 0.001$ ), higher leaf litter cover ( $70.8 \pm 35.5$ ;  $F_{1,36} = 6.23$ ,  $P = 0.017$ ) and lower ground-level vegetation cover ( $19.4 \pm 25.4$ ;  $F_{1,36} = 8.26$ ,  $P = 0.007$ ). Vegetation structure in the smallest fragments clearly diverged from what lizards used in our study area (Fig. 3, Table 4), suggesting that the smallest fragments were particularly unsuitable microhabitats. In particular,

excessive cover of trees (above 90% in 12 out of 17 such fragments) eliminates any mosaic of sunlit and shaded patches, probably making thermoregulation incompatible with foraging or predator avoidance, and forcing sun-seeking lizards to expose themselves to increased predation risk at the edge of the fragments.

### Habitat suitability

An interesting finding in our study was that above 0.5 ha, lizard occurrence was no longer dependent on fragment size, being primarily dependent on woodland type, with 88% of deciduous fragments and 41% of evergreen fragments maintaining lizard populations. A detailed analysis of several fragments showed that both thermal quality and food availability were higher in deciduous than in evergreen woodlands, supporting the idea that the former were more often occupied because they offered better habitat quality. Previous studies have suggested that habitat quality for the large psammophilus primarily depends on microhabitat structure and food availability (Díaz & Carrascal, 1991a; Díaz, 1997). In fact, Díaz (1997) found higher lizard density in a montane Pyrenean oak forest than in a lowland Holm oak forest located in central Spain, although the former had lower thermal quality. However, such a pattern might change in our study area, which is close to the northern edge of the species' range. During lizards' emergence from hibernation, environmental operative temperatures in the shade are still far from the temperature range preferred by lizards, which therefore require sunlit patches within short reach for efficient thermoregulation. Sunlit patches are more readily available in deciduous than in evergreen woodlands, because Pyrenean oak trees are not yet in leaf by the end of lizards' hibernation (Santos & Tellería, 1991). In fact, lizards avoided sites with high tree cover even in summer (Fig. 3), which was probably related to the selection of sunlit patches.

Food availability was much higher in deciduous than in evergreen fragments, further supporting the idea that Pyrenean oak woodlands make better habitats for lizards. It was obvious from our sampling that invertebrate prey of lizards could find abundant shelter underneath the abundant leaf litter in deciduous woodlands, although the unavoidable confusion between woodland type and cover of leaf litter made it impossible to test for the correlation between cover of leaf litter and food abundance. Other studies have reported energy-related benefits accrued by lizards in deciduous woodlands, compared with lizards in evergreen woodlands. For example, a reciprocal transplant experiment in unfragmented forests from central Spain showed that juveniles grew up faster in a Pyrenean than in a Holm oak woodland presumably because the former had more food available (Iraeta *et al.*, 2006).

### Lizard responses from patch to regional scales

In our study area, fragmentation seemed to affect lizard populations only when fragment size dropped below 0.5 ha,

imposing a limit to fragment occupancy that was independent of woodland type. However, above this patch size fragmentation effects vanished, and lizard occurrence depended more on structural features of woodlands that, through their association with woodland type (evergreen or deciduous), had a large effect on habitat suitability. Remarkably, ground-level vegetation cover, a structural trait that positively influences survivorship in other areas (Civantos & Forsman, 2000), was actively selected by lizards in our study area, and it was higher in fragments with lizards than in fragments without lizards, thus maintaining its effect from microhabitat to landscape scales, and possibly also at regional scales as shown previously (Díaz & Carrascal, 1991a,b).

However, other effects of fragmentation emerge in this area if the scale is increased up to include 20 nearby Holm oak woodlands studied by Díaz *et al.* (2000). The connectivity between both study areas is dramatically reduced by the existence of a motorway (the State road A1), which keeps 18 woodlands studied by Díaz *et al.* (2000) isolated from the forest remnants studied here. No lizards were found in any of these 18 sites, although 12 of them were larger than 0.5 ha, four of which ranged between 7 and 27 ha. No habitat factor was identified that could explain this result. In fact, a discriminant model based on microhabitat structure predicted the presence of lizards in most of these woodlands (Díaz *et al.*, 2000). Therefore, habitat fragmentation was the only factor determining the distribution of lizards west of the motorway, which seems difficult to reconcile with the results of this study. We suggest that the absence of lizards from the western zone of the study region may be due to historical effects of fragmentation (Díaz *et al.*, 2000) combined with severe isolation caused by the motorway, which would have prevented the recolonization of the western fragments by lizards dispersing from eastern woodlands. Although we could not test the impact of such man-made barriers on lizard populations, the two studies conducted in this area suggest that the effects of habitat quality and fragmentation on lizard distribution can be overridden by other factors operating at the regional scale.

### Conservation implications

The observed effects of forest fragmentation (see also Díaz *et al.*, 2000) call for actions for managing lizard populations at a regional scale. Lizard populations on the western side of the N-I motorway seem not recuperable by natural dispersal, so that conservation planning should carefully consider introducing lizards from nearby areas. In fact, we have successfully introduced in this area lab-born large psammophilus, whose mothers had been captured while gravid at nearby sites (Díaz *et al.*, 2005a).

Fragmentation usually reduces both the size and the quality of remaining habitat, which causes negative effects on populations (Saunders, Hobbs & Margules, 1991; Harrison & Bruna, 1999). However, changes in land use over the course of time can have shaped such effects wherever habitat fragmentation has been continuous



practice for centuries. By examining physiognomic changes of our study area over the last 50 years, we could identify increased fragmentation in some sectors, contrasting with land abandonment favouring re-growth of trees and coalescence of small woodlands in others (Díaz *et al.*, 2000). Interestingly, many of our Pyrenean oak woodlands smaller than 0.5 ha were recently created by tree sprouting. The absence of lizards from densely forested fragments recommends forest management to help in maintaining habitat quality for lizards; uses such as sheep grazing or selective tree extraction could improve lizards' thermoregulation opportunities, predator avoidance and foraging success (Vitt *et al.*, 1998). However, such human uses can negatively affect other species that require pristine forests, such as many birds (Santos *et al.*, 2002). Therefore, devising conservation plans that are equally effective for protecting all Mediterranean forest vertebrates may be difficult, if not impossible. This suggests that forest management actions should favour a mosaic of interconnected habitats with different degrees of vegetation development.

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## Supplementary material

The following material is available for this article online:

**Appendix S1.** List of fragments and continents (forests larger than 200 ha) arranged according to size and woodland type (Pyrenean oak or Holm oak). The occurrence of lizards is also indicated.

This material is available as part of the online article from <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-1795.2007.00146.x> (This link will take you to the article abstract).

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