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Effects of forest fragmentation on the distribution of the lizard *Psammodromus algirus*

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Abstract

This study reports the population responses of the lizard *Psammodromus algirus* to forest fragmentation by comparing its distribution in two contrasting situations of habitat conservation: a well connected mosaic landscape (forest patches larger than 2000 ha and/or connected by corridors that prevent their isolation), and an archipelago of forest remnants embedded within a matrix of cereal fields. The frequency of occurrence of *P. algirus* was larger in the unfragmented habitats (14 out of 19 censused plots) than in the fragments (two out of of 21 wood-lots). Vegetation structure was a good predictor of lizard occurrence under conditions of no fragmentation, but not in the fragments, where high plant cover seemed a necessary, but insufficient, condition for the survival of lizard populations, and where remnant size was the only variable that differed significantly between wood-lots with and without lizards. Historical fragmentation of the habitat is also crucial for understanding the current distribution of lizards, as shown by their absence from a large forest that was highly fragmented in the past but which has been regenerating for decades. It is hypothesized that the combined effects of fragmentation and predation in small remnants have led to the extinction of *P. algirus* in fragments smaller than c. 90 ha, recolonization being prevented by the very limited dispersal abilities of these forest lizards.

INTRODUCTION

Habitat fragmentation is the commonest and most serious conservation problem for forest organisms in the temperate zone (Burgess & Sharpe, 1981; Wilcove, Mclellan & Dobson, 1986; Bender, Contreras & Fahrig, 1998), and it has a pervasive influence on the distribution of terrestrial vertebrates. The reduction of suitable habitat has threatened the survival of species with large and/or very specific requirements, for example large endotherms (Wilcox & Murphy, 1985; Bright, 1993), or forest specialists (Wilcove, 1985; Verboom *et al*., 1991; Bright, Mitchell & Morris, 1994; Tellería & Santos, 1995). Furthermore, the increased distance among wood-lots has precluded their recolonization by ‘hard edge’ species (*sensu* Stamps, Buechner & Krishman, 1987) that are unable to cross the matrix of unsuitable habitats interspersed among forest remnants (Matthysen & Currie, 1996; Henein, Wegner & Merriam, 1998). In the southern European peninsulas, fragmentation has mainly affected lowland forests (e.g. Santos & Tellería, 1998), by reducing the availability of suitable habitat and by increasing the distance among habitat remnants.

Lizards have received little attention with respect to the effects of fragmentation on their distribution and abundance (although see Sarré, 1995; Smith *et al*., 1996). These terrestrial ectotherms, which form a conspicuous part of the vertebrate faunas in southern Europe, show a combination of traits that may have different effects on their ability to cope with habitat fragmentation. Their limited dispersal abilities, for instance, make them highly sensitive to the hard-edge effect mentioned above (Santos & Tellería, 1989; Sarré, 1995), especially if they are tightly linked to forest or shrub environments. However, this low recolonization ability contrasts with their ability to survive and even reach high population densities under conditions of limited food supply (Pough, 1980), which might favour the persistence of isolated populations in small forest fragments. In any case, it is a common observation that many of the most widely distributed lizard species in Europe are comparatively rare in areas where they might be expected to be abundant, although the reasons for this scarcity (or even absence) remain unexplained.

In this study, we compared the distribution of *Psammodromus algirus* (L.) 1758, in two contrasting situations of habitat fragmentation: a well connected mosaic of forest or shrub habitats in Madrid (central Spain), and an archipelago of forest remnants embedded

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within a matrix of cereal fields near Lerma (central-northern Spain). *Psammodeomus algirus* is one of the commonest lacertids in Mediterranean Iberia (Pleguezuelos, 1997). However, it is a lizard species that is closely associated with densely vegetated shrub or forest habitats (Arnold, 1987; Díaz & Carrascal, 1991), and it has been dramatically affected by the expansion of deforested agricultural habitats, which has restricted its survival to a few isolated riparian forests (Santos & Tellería, 1989). Here, we analyze the effects of fragmentation on the frequency of occurrence of *P. algirus* at a regional scale. We examine the habitat variables that might determine its presence or absence in the fragments (e.g. remnant size or structural quality of the habitat), and we discuss the historical and current factors that might explain the observed distribution pattern. In particular, we emphasize the importance of the past history of fragmentation for understanding the current patterns of organismal distribution. This issue has seldom been considered in fragmentation studies, except for the fact that the continued reduction of forests negatively affects the composition and structure of their animal communities (Wilcove *et al*., 1986; Soulé *et al*., 1988). However, many forest archipelagos, especially those in temperate countries, may be undergoing a process of regeneration. In that case, if the destruction of microhabitats has been larger in the past than today, then past metapopulation processes may be critical for explaining the absence of lizards from fragments whose size and present habitat structure would have been adequate for their maintenance.

METHODS

In Madrid, the abundance of *P. algirus* was estimated in July 1989 at 19 census plots forming a sample of relatively homogeneous sites (deciduous and perennial shrublands and forests) that were representative of the gradient of habitats found in central Spain. Data were taken within an area of 7000 km^2, between approximately 40 and 41ºN and between 3º20′ and 4º W, expanding from the Tajo Basin (500 m a.s.l.) to the northern slope of the Guadarrama Range (1900 m a.s.l.). Abundance was measured using 1 km transects in which all lizards seen within a 5 m wide belt were counted. The analysis of these data has been reported elsewhere (Díaz & Carrascal, 1991). Here, it should be noted that the Madrid census plots were part of large (> 2000 ha) patches of continuous habitat, or there were at least corridors, such as riparian forests, preventing the isolation of sampled areas. This situation contrasts sharply with the one found in our second study area, an agricultural landscape located around Lerma, in central-northern Spain (42º5′N, 3º45′W; 850 m a.s.l.). In this area, forest covers less than 10% of its former surface, occupying the landscape in the form of small wood-lots dominated by holm oaks, *Quercus ilex*, and interspersed among cereal fields.

We visited 21 fragments searching for lizards in July 1996. Whenever we found them (always in remnants ≥ 90 ha), we estimated their abundance by the same procedure employed in Madrid (Table 1). For each fragment, we also measured total surface area using 1:18 000 aerial photographs, and we recorded mean plant cover at the low shrub layer (height ≈ 30 cm: C30) and mean cover of leaf litter (CL), estimated visually on 25 m radius circular sample areas (Prodon & Lebreton, 1981; for further details on the sampling procedure, see Santos & Tellería, 1998). These two structural variables, indicative of the degree of vegetation development in the low shrub layer, were chosen because of their ability to predict the abundance of *P. algirus* under conditions of no fragmentation, since previous analyses had shown that the combined effects of C30 and CL explained 82.1% ($F_{2,16} = 36.7$, $P < 0.001$) of the variance in lizard densities in the unfragmented habitats from central Spain:

$$\text{number of lizards/ha} = -14.54 + 0.67 \times \text{C30} + 0.18 \times \text{CL}, \quad (1)$$

data taken from Díaz & Carrascal (1991). Thus, we regarded the values predicted by eqn (1), either in central Spain or in the archipelago, as a synthetic measure of structural habitat quality for *P. algirus*.

The effect of the past history of the fragments on the distribution of lizards was examined by comparing the current extent of fragments with aerial photographs taken in 1946 and in 1978, which was the latest date at which there were images available for all fragments. The situation in 1978 was quite similar to the present, with little change in the size, structure or spatial configuration of the fragments (Santos & Tellería, 1998). Each remnant woodland was assigned to one of the following categories: (1) sites whose conservation status was similar in 1946 and 1978, with equivalent values of tree and shrub cover; (2) sites that by 1946 maintained well conserved patches (similar to previous category), but with some of their surface covered by grasslands or even cultivated fields; (3) a large forest (Ruyales del Agua) that in 1946 was much more fragmented than today, with most of its surface covered by ploughed fields, so that its quality for lizards must have been worse in the past than today.

RESULTS

The frequency of occurrence of *P. algirus* was much larger in the unfragmented sample from central Spain (*P. algirus* was recorded in 14 out of 19 censused plots) than in the archipelago of forest fragments (only two out of 21 wood-lots with *P. algirus*; $\chi^2 = 17.1$, d.f. = 1, $P<0.001$), even if the structural quality of the habitat did not differ markedly between both data sets (Table 2). We used stepwise discriminant function analysis, with C30 and CL as the independent variables, to predict the presence or absence of *P. algirus* in the Madrid (unfragmented) area, after having checked the homogeneity of variances assumption (Sen & Puri's test: $\chi^2 = 1.52$, d.f. = 3, $P > 0.65$). The resulting model selected C30 as the

Table 1. Detailed description of the 21 fragments considered in this study

Fragment	lizards/ha	S (ha)	C30 (%)	CL (%)	P1	P2	1946 status
sc-11	0	12.0	54.4	36.0	0.995	0.071	++
sc-12	0	16.0	40.2	33.0	0.972	0.089	++
sc-13	0	7.0	30.5	37.0	0.917	0.046	++
sc-14	0	0.8	20.0	37.0	0.763	0.007	++
sc-15	0	0.5	15.0	60.0	0.641	0.005	++
sc-16	0	0.3	20.0	30.0	0.763	0.003	++
sc-17	0	0.3	20.0	50.0	0.763	0.003	++
sc-18	0	0.1	10.0	10.0	0.498	0.001	++
sc-19	0	0.3	10.0	20.0	0.498	0.003	++
sc-20	0	0.7	25.0	40.0	0.853	0.007	++
sc-21	0	2.0	16.4	50.0	0.678	0.016	+
sc-22	0	1.2	6.3	38.0	0.391	0.010	+
sc-23	0	27.0	15.7	51.0	0.660	0.134	++
sc-24	0	0.3	2.0	90.0	0.279	0.003	++
sc-25	0	0.2	25.0	40.0	0.853	0.002	++
sc-26	0	0.6	6.0	28.0	0.383	0.006	++
sc-27	0	1.3	25.0	43.0	0.853	0.011	++
Ruyales	0	350.0	25.1	34.0	0.854	0.586	+++
Quintanilla	20	280.0	29.7	38.0	0.910	0.539	++
Tordueles	0	170.0	15.3	41.0	0.649	0.431	++
Torrecilla	16	90.0	45.0	59.0	0.984	0.304	++

Description includes: relative abundance of *P. algirus* (lizards/ha); total surface area (S); mean plant cover 30 cm in height (C30); leaf litter cover (CL); posterior probability of supporting a lizard population according to (1) a discriminant function based on habitat structure (P1: conditions of no fragmentation), and (2) a discriminant function based on fragment size (P2); classification according to its conservation status in 1946 (+, no degradation; ++, partial degradation; +++, high degradation; see Methods for details).

only relevant variable (mean (± SE) at the sites where lizards were found = 27.4 (± 3.6) % versus 10.2 (± 2.3) % at the sites without lizards; $F_{1,17} = 7.5$, $P = 0.014$). This model correctly classified 15 out of 19 unfragmented study sites, 12 with and three without *P. algirus*. However, the model failed to predict the occurrence of *P. algirus* in the Lerma fragments (Table 1), since it incorrectly classified 14 out of 21 wood-lots using the *a priori* probabilities from the unfragmented zone, which is justified by the fact that if fragmentation had no added effects over those attributable to habitat structure, we should expect similar frequencies in both study areas (see Table 2). All these incorrect classifications were fragments where no lizards could be found, even when their C30 values indicated a relatively high structural quality (Table 1). Nevertheless, the two fragments with populations of *P. algirus* had values of C30 (mean (± 1 SE) = 37.4 (± 7.6) %) that were higher than those at the fragments free of lizards (20.1 (± 2.9) %), although the difference was marginally non-significant ($F_{1,19} = 3.5$, $P = 0.076$). Thus, high plant cover near the ground was a necessary, but insufficient, condition for the survival of lizard populations in the fragments.

The only variable that was selected by a discriminant function analysis as predicting the presence of *P. algirus* in the fragments was its surface area (log-transformed to meet the requirements of statistical tests; Sen & Puri's $\chi^2 = 6.51$, d.f. = 6, $P > 0.35$), which was significantly higher in the fragments with lizards (mean (± 1 SE) = 185 (± 94) ha) than in those without lizards (mean (± 1 SE) = 31 (± 20) ha; $F_{1,19} = 6.9$, $P = 0.016$). This second model correctly classified 19 out of the 21 fragments (Table 1). It failed to predict the absence of *P. algirus* in the largest fragment (Ruyales del Agua: 350 ha), and its presence in a 90 ha wood-lot (Torrecilla) covered by a mixed forest of *Quercus ilex* and *Quercus faginea* that was of high structural quality according to eqn (1) (predicted number of lizards = 26.4 lizards/ha). It should also be noted that the structural quality of the fragments (number of lizards predicted by eqn (1)) increased with their total surface area ($r = 0.502$, $n = 21$, $P = 0.02$; surface area log-transformed).

Table 2. Mean values (± 1 SE) of plant cover 30 cm in height (C30), leaf litter cover (CL), and predicted number of lizards (lizards/ha) according to eqn (1) for the unfragmented area (Madrid) and the archipelago of fragments (Lerma).

	Madrid (n = 19)	Lerma (n = 21)	t_{38}	P
C30 (%)	22.9 (± 3.2)	21.7 (± 2.9)	0.27	0.790
CL (%)	47.1 (± 5.9)	41.2 (± 3.5)	0.88	0.386
Lizards/ha	9.3 (± 2.4)	7.4 (± 2.0)	0.58	0.562

Data for the unfragmented area from Díaz & Carrascal (1991); see the text for details. The results of *t*-tests are also shown.

The two fragments with lizards were classified as intermediate according to their conservation status in 1946, whereas Ruyales (the largest fragment, in which no lizards were found, contrary to expectations based on size or habitat quality; see Table 1) was the only remnant that in 1946 was much more fragmented than today, with most of its surface covered by ploughed fields (Fig. 1).

DISCUSSION

Our results show that fragmentation had a dramatic impact on the distribution of *P. algirus*, whose populations were lacking from most of the fragments examined. This result might in part be due to a decrease in habitat quality (a smaller development of the shrub and leaf litter layers) as forest fragmentation proceeds. Such

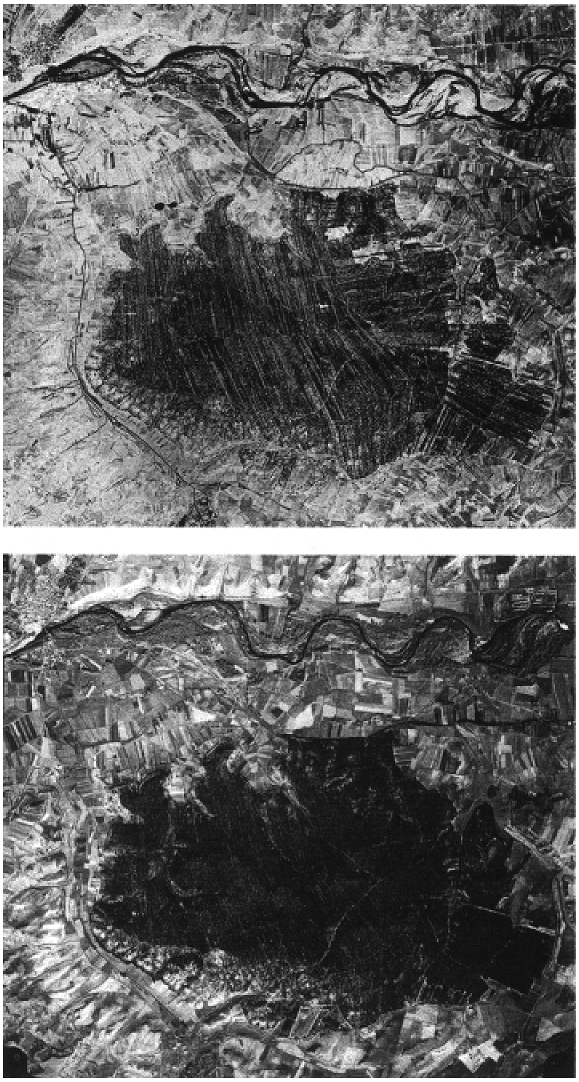

Fig. 1. Aerial photographs taken in (a) 1946 and (b) 1978 at Ruyales del Agua, a 350 ha 'continent-like' remnant that, unexpectedly, was free of lizards. The photographs show that this forest has been regenerating for the last decades, and that most of its surface was cultivated in 1946.

a decrease, however, could not explain the absence of *P. algirus* from some of the medium-sized remnants that were of high structural quality (for instance fragments sc-11 and sc-12, with CL and C30 values leading to predicted densities of 28.4 and 18.4 lizards/ha, respectively). In fact, habitat structure seemed to play a secondary role in determining the carrying capacity of fragments. Instead, the best predictor of lizard occurrence was fragment size, since lizard populations occurred only in forest remnants $\geq$ 90 ha. This result can be generalized to a wider spatial scale, as deduced from the data on 313 wood-lots that were investigated in an extensive study of fragmentation effects on the vertebrate fauna of the Iberian plateaux (Santos & Tellería, 1998, and unpublished data). In these forests, *P. algirus* was always absent except in the largest, 'continent-like' remnants (of 6775, 7500 and 605 ha).

A possible criticism of our sampling design is that our two study areas differed not only with respect to fragmentation but also in geographical location (latitude), and hence presumably in climate. This could produce differences in the population responses of *P. algirus* that might be more related to climatic or biogeographic factors (e.g. a loss of thermal quality 150 km further north) than to the process of fragmentation *per se*. However, three lines of evidence support the rejection of this alternative hypothesis. First, the abundance of *P. algirus* was unrelated to climate in the transects from the unfragmented zone, despite covering an altitudinal climatic gradient (500–1900 m a.s.l.) which was much more pronounced than the one reported here (Díaz & Carrascal, 1991). Second, differences in thermal quality are likely to be more contrasted between seasons (Christian & Bedford, 1995) or microhabitats (e.g. sun–shade patches: Bauwens, Hertz & Castilla, 1996; Díaz, 1997) than between fragments, and it has been shown that lizards can easily compensate for such differences by behavioural means. In addition, there is no apparent reason why mean thermal quality should be correlated with fragment size, whereas fragment size is the crucial variable if the disappearance of lizards can be attributed to fragmentation. Finally, it should be noted that in the two fragments where lizards were found, their abundance was within the 95% confidence interval for individual predictions derived from the Madrid regression. Thus, lizard populations can reach their usual numbers if given the chance to persist.

We conclude that neither changes in the structure nor in the thermal quality of the habitat provide an adequate explanation for the effects of fragmentation on lizard distribution. We suggest that the prevalent factor leading to the extinction of lizards in the agricultural landscape could be a combination of predation and historical fragmentation of the forest habitat. If populations are to persist over time, natality must balance mortality. Even a moderate excess of mortality over natality can lead to a precipitous decline in population numbers that, in small fragments, could rapidly fall to the minimum viable population size (Pimm, Jones & Diamond, 1988). Several sources of evidence suggest that predation pressure is indeed heavy in the fragments. Thus, predation on quail eggs increased with forest fragmentation in the study area (Tellería & Santos, 1992), the abundance of corvids increased as fragment size decreased (J. L. T. & T. S., unpublished data), and wild boars, that may consume not only active lizards but also clutches, were present (as shown by recent rootings) in 93% of the fragments smaller than 2 ha (Santos & Tellería, 1998). It should also be noted that *P. algirus* is a favoured prey in Mediterranean forest environments, as deduced from the variety of predators that feed on this lizard species (Martín & López, 1990).

Once populations become extinct, recolonization of the fragments would be precluded by the inability of lizards to cross the cereal fields interspersed among them. In cultivated areas from central Spain, *P. algirus*, originally the commonest lizard species in vegetated habitats, became the scarcest one in a landscape dominated by extensive agricultural practices (Santos & Tellería, 1989). The hard-edge status of *P. algirus* (Stamps *et al.*, 1987), together with historical factors, could also shed light on its absence from Ruyales, the largest forest sampled in the Lerma archipelago. A comparison of aerial photographs taken in 1946 and 1978 (Fig. 1) shows that this 350 ha forest remnant was actually a small archipelago of fragments in 1946, and that it has been regenerating for the last decades; by 1946, its limited offer of suitable habitat probably hindered the survival of *P. algirus*. If, by that time, lizards had become extinct, their present absence should be attributed to their inability to recolonize the previously lost patches of adequate habitat. This situation contrasts with the one found in Quintanilla del Agua, the 280 ha forest where lizards were found in higher densities (Table 1): aerial photographs show that this forest has maintained large-enough patches in a good conservation status at least since 1946. Thus, we might predict that deliberate reintroductions of lizards should be successful in large fragments that have recovered from destruction (e.g. Ruyales), but not in small remnants resulting from fragmentation of formerly intact, high quality habitat (e.g. sc-11 and sc-12). The role of history in lizard conservation is also interesting from the more theoretical viewpoint of the different time lags required by different organisms to react to forest fragmentation (Landres, 1992). The regeneration of the holm oak shrub layer, which is crucial to the survival of *P. algirus* at the Lerma site, takes place almost entirely by asexual means in fragmented landscapes (Santos & Tellería, 1997), and is therefore immediate after the cessation of agricultural practices and livestock grazing. Nevertheless, lizards are unable to benefit from such regeneration, due to their low regional density and extremely poor dispersal capacity.

In summary, forest fragmentation, after producing fragment sizes smaller than a minimum located somewhere below 90 ha, causes the irreversible extinction of *P. algirus*. This result should be taken into account when diagnosing the conservation status of these (and other similar) small terrestrial ectotherms, whose populations may appear to be healthy or at least unthreatened, despite being condemned to disappear in a short time if continued fragmentation of their habitat is not prevented.

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