ECOGRAPHY 22: 13–19. Copenhagen 1999

Distribution of birds in fragments of Mediterranean forests: the role of ecological densities

J. L. Tellería and T. Santos

Tellería, J. L. and Santos, T. 1999. Distribution of birds in fragments of Mediterranean forests: the role of ecological densities. – Ecography 22: 13–19.

This paper evaluates the role of ecological densities (densities in a given habitat) in predicting the ability of forest passerines to occupy fragments of eight oak *Quercus* spp. forest archipelagos of the Iberian Plateaux. Ecological density of individual species was the main predictor of their occurrence in fragments, whereas other biological traits (nesting site) and some potentially important landscape features (local cover of forests or distance to possible sources of individuals) were not correlated to fragment occupation. Feeding substrata of birds was also related to their comparative ability to occupy fragments since, after controlling for the effects of abundance and nesting site, foliage exploiters were more frequent in fragments. These results, that support the empirical usefulness of the random sampling hypothesis in predicting the ability of species to persist in fragments, may be affected by some particular features of the study area. Oak forests of the Iberian Peninsula have been heavily affected by human disturbance for a long time so that interior forest birds are now scarce or extinct and species adapted to shrubby forests form the bulk of these bird communities. It is possible that these species will not perceive differences in the habitat suitability of fragments, increasing the likelihood that stochastic sampling processes dictate their patch occupancy.

J. L. Tellería (telleria@eucmax.sim.ucm.es) and T. Santos, Dept of Animal Biology (Vertebrate Zoology), Univ. Complutense, E-28040 Madrid, Spain.

The density of individual species in a given habitat (ecological density; see Robinson and Redford 1986) is the basis of the random sampling hypothesis, an approach to study the effects of fragmentation which claims that species with high density are more likely to be included in fragments than scarce ones as a consequence of their abundance (Preston 1948, 1960, Connor and McCoy 1979, Haila 1983). As species tend to show geographical and inter-habitat differences in ecological density, this variable may be a useful guideline to predict the effects of habitat fragmentation according to the circumstances of each locality or habitat (Lawton 1993). However, although ecological density seems a good predictor of the comparative ability of species to occur in forest fragments (e.g. Soulé et al. 1988, Bolger et al. 1991, Tellería and Santos 1995, 1997), we know of no specific tests of its value as a predictor of the ability of individual species to occupy fragments of different habitats or sectors of a large region.

In this paper, we study the role of ecological density in predicting the occupation by birds of eight oak *Quercus* spp. forest archipelagoes of the Iberian Peninsula, an area located in the south-western edge of the Palearctic Region where the abundance of many forest birds decreases along a north-west/mesic to south-east/xeric gradient (Tellería and Santos 1993, 1994). We have followed two different, complementary approaches: A) Individual-species approach. We predict that the decrease in ecological density of many forest birds along the mesic-xeric gradient of the Iberian Plateaux will produce a concomitant fall in their rates of fragment occupation. As a consequence, species with decreasing ecological densities along the study gradient will show decreasing likelihood to occur in forest frag-

Accepted 13 July 1998

ISSN 0906-7590

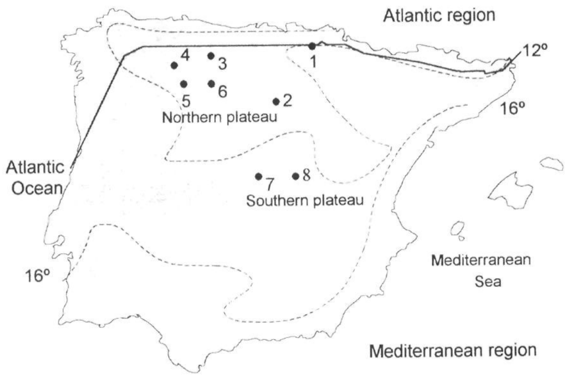

Fig. 1. Distribution of the archipelagoes studied in the Iberian Plateaux (1: Alava, 2: Lerma, 3: Sahagún, 4: Jamuz, 5: Páramo, 6: Valderas, 7: Villatobas, 8: Mota). Isotherms (broken lines) of 12°C and 16°C are shown along with annual rainfall over 600 mm (shaded). Shaded area includes the moist north-western Atlantic sectors of Iberia (Atlantic region and Portuguese coasts) and the inland mountains of the Mediterranean region. The continuous line shows the boundary between the Atlantic and Mediterranean regions.

ments (Santos and Tellería 1995, 1997). We have included in this analysis the effects of forest cover, mean fragment size and mean distance to other fragments since the occurrence of individual species in fragments may be affected by the landscape configuration of the habitat "archipelago" (see Andrén 1994 for review). B) Multi-species approach. We predict that mean ecological densities of bird species occupying oak forests of the Iberian Plateaux will determine their relative incidence in fragments. This has been observed at a local scale in other habitat archipelagoes (see references above), and positive relationships between regional abundances and distributions of species seems a rather common pattern in both birds and other taxonomic groups (Gaston 1994 for review). However, we have enlarged this comparative approach to test the role of other biological traits of species in predicting fragment occupation at the scale of the Iberian Plateaux. We have considered the effects of nest site and feeding substrata of species since they are two potential determinants of species abilities to occur in forest fragments (e.g. Tellería and Santos 1997).

Methods

Study area

We have studied forest fragments in central Iberian Peninsula (Fig. 1). This is an area of ca 200 000 km^2, separated in two plateaux by the Sistema Central Mountains. The northern plateau (ca 800 m a.s.l.), colder and rainier than its southern counterpart (600 m), is a transitional climatic area between the mesic, north-western Atlantic belt and the xeric, south-eastern Mediterranean sectors of the Iberian Peninsula (Font 1983). In these plateaux, oak forest fragments of different size are dispersed in a landscape used for cereal farming in which shelterbelts are absent. We looked for discrete groups of fragments on LANDSAT (1:100 000) images. We selected eight forest archipelagoes covered by three Mediterranean oak species *Quercus faginea* Lamk., *Quercus pyrenaica* Wildl. and *Quercus ilex* L. adapted to increasing degrees of environmental xericity (e.g. Salleo and LoGallo 1990; Table 1). The selected archipelagoes were fragmented several decades ago, as reflected in the first available aerial photographs dating 40 years ago. In each archipelago, we selected a number of fragments and two large control forests (> 100 ha in area) with similar tree cover and development (Carbonell et al. 1995 for details). As these forests have traditionally been used for collecting firewood and charcoal, hunting and cattle raising, they show a shrubby aspect, with a mean canopy of ca 5 m. We used aerial photographs (scale 1:18 000) to estimate the following variables: a) proportion of forest cover in each archipelago (cover), estimated as the mean cover of forest in an area lying within a line distributed 2 km

Table 1. Main climatic and landscape features (x ± SE) of the study archipelagoes. Cover: mean cover of forest within 2 km from the border of fragments, size: mean size of fragments, dist1: distance to the nearest fragment, dist2: distance to control forests (see text for details).

	Mean annual rainfall (mm)	No of study fragments	cover (%)	size (ha)	dist1 (m)	dist2 (km)
Alava[1]	853	24	10.9 ± 1.4	8.4 ± 2.2	248.2 ± 37.8	3.2 ± 0.5
Lerma[2]	431	27	7.9 ± 0.7	8.8 ± 3.0	62.9 ± 6.5	1.0 ± 0.2
Sahagún[3]	548	38	16.9 ± 1.8	8.7 ± 2.9	131.1 ± 17.4	2.7 ± 0.4
Jamuz[2]	410	43	11.5 ± 1.4	6.5 ± 2.1	204.2 ± 54.2	5.8 ± 0.6
Páramo[2]	498	32	5.0 ± 1.0	16.6 ± 4.0	248.8 ± 157.9	2.7 ± 0.3
Valderas[2]	440	27	5.9 ± 1.2	3.9 ± 1.3	123.2 ± 17.2	6.5 ± 0.3
Villatobas[2]	459	45	4.7 ± 2.0	8.7 ± 2.9	155.5 ± 25.9	5.5 ± 0.3
Mota[2]	393	36	9.7 ± 1.1	10.5 ± 2.8	114.4 ± 22.0	1.3 ± 0.2
Kruskall-Wallis test	–	–	H = 79.3 $p<0.001$	H = 9.9 $p = 0.191$	H = 28.4 $p<0.001$	H = 128.6 $p<0$ $p<0.001$

Dominant tree species: 1: *Quercus faginea*, 2: *Quercus ilex*, 3: *Quercus pyrenaica* from the border of each fragment (see Askins et al. 1987). b) Mean distance from each fragment to the nearest neighbouring forestal habitat, estimated as the mean distance to the nearest neighbouring fragment (dist1) or control forest (dist2). c) Mean size of fragments in each archipelago (size), estimated from the area of the individual fragments. Archipelagoes differed in landscape configuration, excepting size (Table 1). Landscape variables were statistically independent (r-Spearman coefficient non-significant for all the combinations), excepting cover and dist2 ($r_s = -0.81$, $p = 0.06$, $n = 8$). To avoid statistical interdependence of the variables, we excluded size and dist2 from the analyses.

We analysed the effects of landscape structure and local density on local incidence of species by means of r-Spearman correlation analyses. We used the eight values of local density and incidence to calculated mean density (regional density) and incidence (regional incidence) of the species at the scale of the Iberian Plateaux. The factors affecting regional incidence of individual species were studied by an analysis of covariance (ANCOVA), in which nest site and feeding substrata were included as factors, and regional density as the covariant. In this analysis, proportions were arcsin-transformed and densities were log-transformed (Zar 1984).

Species selection and census work

We included in the study small passerines that depend on forests during the breeding period. We thus excluded large birds (crows) and species which feed in the surrounding open lands (e.g. shrikes, starlings, sparrows, buntings and finches). The resulting group included warblers, tits, forest thrushes and other small insectivorous forest passerines. Species were classified according to their nesting substrata as a) open nests or b) holes nest species. The availability of tree holes in fragments may be a critical resource when forest size diminishes (Helle and Järvinen 1986, Haila et al. 1987, Tellería and Santos 1997). Birds were classified according to their feeding substrata as a) feeding in the foliage or b) feeding on the ground and trunks or thick branches. Total area available for ground and trunk exploiters is smaller than the one available for foliage gleaners (Jackson 1979). In fact, trunk exploiters and ground-dwelling birds are susceptible to fragmentation (e.g. Karr 1982, Tellería and Santos 1997).

Censuses were carried out during the spring of 1994, except for Lerma which was censused in 1989 (see Tellería and Santos 1997). The birds were recorded in the fragments by means of intensive searching during two–six visits (April–June). Visits started at dawn and ended before mid-day, when bird activity declined. We included in the species list of a given fragment all species with individuals displaying persistent song, nests, baiting behaviour or continuous presence in the fragment. Species which did not meet these criteria were excluded. We evaluated the ability of species to occupy fragments in each archipelago as the proportion of fragments in which the species was present (hereafter local incidence). Local ecological density of individual species (local density) was estimated by censuses in the two large control forests of each archipelago. Birds were counted in a 25 m wide strip on both sides of the established transects (Seber 1982), and the mean results of the two censuses in each archipelago were expressed as number birds 10 ha^{-1}.

Results

Bird communities of the control forests tended to show higher local densities and number of species in the northern Plateau than in the southern one (Table 2). We recorded 21 species of forest passerines (Appendix), although only eight species were broadly distributed along the study gradient and occupied five or more archipelagos (Fig. 2). This is the case of some common Palearctic forest passerines (e.g. *Erithacus rubecula* (L.), *Turdus merula* L., *Parus major* L., *Parus caeruleus* L.) that decreased from the moist forests of Alava to the xeric forests of the southern plateau. Other Mediterranean species (e.g., *Phylloscopus bonelli* (Vieillot), *Sylvia cantillans* (Pallas); see also *Luscinia megarhynchos* (Brehm)) decreased in both the mesic and the xeric extreme of the study gradient (Fig. 2). These birds, that conformed the bulk of the bird communities (Table 2), tended to show higher local densities in the northern than in the southern plateau.

These patterns of local density were correlated to local incidence of individual species in forest fragments in six out of eight species (Fig. 3). However, the role of landscape structure in this pattern was not significant since dist1 and cover were not correlated to local incidence in any species.

Regional density was the best predictor of the comparative ability of individual species to occupy fragments at the scale of the Iberian Plateaux (ANCOVA $F_{1,16} = 77.56$, $p < 0.001$; Fig. 4). The feeding substrate was, after the effects of abundance and nest site were removed, significantly related to species incidence ($F_{1,16} = 6.33$, $p < 0.05$), foliage-exploiter species being more frequent in fragments than ground-feeding species. After the effects of abundance and feeding substrate were removed, the nest site of birds was not related to their interspecific ability to occur in fragments ($F_{1,16} = 0.0002$, NS; nest × feeding substrate interaction: $F_{1,16} = 6.64$ $p < 0.05$). Neither nesting site nor feeding substrate showed any systematic deviation from the overall correlation between regional incidence vs

Table 2. Main features of the bird communities in the control forests of the study archipelagoes. Selected species refers to the percentage (%) of the total density of each bird community accounted by the eight species in Figs 2 and 3 (see text for details).

	censused area (ha)	no species	no 10 ha^{-1}	selected species (%)	The four more abundant species (no 10 ha^{-1})
Alava	44.9	14	57.1	57.7	*Sylvia atricapilla* (13.7), *Parus caeruleus* (10.0), *Troglodytes troglodytes* (6.3), *Turdus merula* (5.8)
Lerma	50.0	14	23.5	92.2	*Sylvia cantillans* (8.0), *Phylloscopus bonelli* (4.1), *Turdus merula* (2.3), *Luscinia megarhynchos* (2.3)
Sahagún	42.0	15	24.0	84.8	*Phylloscopus bonelli* (9.3), *Turdus merula* (2.7), *Parus major* (2.7), *Erithacus rubecula* (2.3)
Jamuz	48.0	13	35.1	94.6	*Sylvia cantillans* (15.8), *Luscinia megarhynchos* (5.7), *Turdus merula* (4.4), *Erithacus rubecula* (2.4)
Páramo	20.0	12	42.9	99.1	*Sylvia cantillans* (17.5), *Luscinia megarhynchos* (15.0), *Parus major* (4.0), *Parus caeruleus* (2.5)
Valderas	23.0	7	26.5	98.4	*Sylvia cantillans* (14.8), *Luscinia megarhynchos* (6.5), *Phylloscopus bonelli* (3.0), *Turdus merula* (0.9)
Villatobas	51.6	9	5.2	89.9	*Sylvia cantillans* (1.54), *Parus caeruleus* (1.3), *Parus major* (1.0), *Sylvia melanocephala* (0.5)
Mota	44.0	7	5.1	54.7	*Sylvia cantillans* (2.3), *Sylvia melanocephala* (1.1), *Sylvia undata* (1.1), *Parus major* (0.5)

density (Fig. 4; test of parallelism: nest site, $F_{1,15} = 0.135$, p: 0.719; feeding substrata, $F_{1,15} = 0.004$, p: 0.953).

Discussion

The results of this paper support the random sampling hypothesis in predicting the effects of forest fragmentation on individual bird species in the Iberian Plateaux, since ecological density was the best predictor of their incidence in forest fragments (individual-species approach). It also supports the strength of this feature when comparing the ability of species to cope with habitat fragmentation (multi-species approach), although feeding habit had also significant effect. The main role of ecological density in the context of the Iberian plateaux may however be conditional upon historical factors that have shaped the regional bird fauna.

The pool of interior forest birds is poor in our study forests. For instance, some common birds adapted to exploit trunks or thick branches of developed trees (*Certhia brachydactyla* Brehm, *Sitta europea* L.) were scarce, whereas other Mediterranean birds, better adapted to shrubby vegetation, were abundant (e.g. *Sylvia cantillans*). It has been suggested that the bird communities of xeric forests of the Mediterranean basin are impoverished as a result of a process of forest deterioration by human disturbance (Blondel 1990, Santos and Tellería 1995 for review at the scale of the Iberian Peninsula). Iberian forests have become increasingly shrubby and adapted to xeric conditions since the Holocene by replacing formerly predominant deciduous mesic trees (e.g. *Quercus pyrenaica* and *Q. faginea*) with heliophytic tree species (e.g. *Quercus ilex*; Costa et al. 1990, Peñalba 1994). The negative effects of this antropogenic habitat deterioration have probably been increased by the peripheral situation of the Mediterranean region, where most forest birds show decreasing abundance in comparison to their core areas in central Europe (Blondel 1990). In these circumstances, forest deterioration has probably been a major cause for severe reductions in the number and range of many Iberian birds (Santos and Tellería 1995). Since birds residing in fragments are not independent units but rather parts of regional populations (Haila 1986, Hanski and Gilpin 1991), these historical restrictions could explain why many passerines common to the mesic sectors in the Western Palearctic (e.g. *Parus palustris* L., *Phylloscopus collybita* (Vieillot), *Regulus ignicapillus* (Temminck), *Sylvia atricapilla* (L.), *Sylvia borin* (Boddaert), *Prunella modularis* (L.), *Troglodytes troglodytes* (L.), *Ficedula hypoleuca* (Pallas), *Phoenicurus phoenicurus* (L.), *Turdus philomelos* Brehm, etc. see Appendix) were lacking or very scarce in the study forests and fragments. This scenario, in which forest passerines are occupying disturbed forests at the limits of their range, could explain the observed poor ability of many common Palaearctic species to persist in forest fragments of the Iberian Plateaux. Kattan et al. (1994) and Santos and Tellería (1997) have also reported empirical evidences that bird species at the edges of their geographical range are more sensitive to forest fragmentation than when occupying the core areas of their range.

Since the forests in our study areas have been disturbed and fragmented for a long time, species breeding in deteriorated forests tend to be abundant in the study areas. It is possible that these species, often pre-adapted to shrubby forests (e.g. by feeding on foliage invertebrates), will not perceive many differences in the habitat suitability of these forests under different fragmentation pressure. It is significant, however, that the incidence in fragments of the two species included in the individual-species approach that depend of tree holes to nest (*Parus caeruleus* and *Parus major*) was not related to ecological density. This suggests that the incidence of some forest birds in fragments may be restricted by an array of specific habitat requirements we have not considered in this study (e.g. Hinsley et al. 1995).

That ecological density is the main predictor of bird occurrence in small fragments in the Iberian Plateaux, where forest cover ranges from 4.7 to 16.9% (Table 1), does not agree with the suggestion by Andrén (1994, 1996) that, under a given threshold value in proportion of suitable habitat (ca 25–30%), the relationships between density and incidence should decrease. Our results suggest that, in circumstances of rather extreme habitat fragmentation and deterioration, ecological densities of abundant species predict successfully their colonization ability and stochastic sampling processes dictate the general patterns of patch occupancy.

Acknowledgements – We are grateful to R. Carbonell, F. J. García and M. López de Carrión for field assistance. Comments by Y. Haila and S. Hinsley considerably improved an early version of this paper. This study was supported by project PB92-0238 (Spanish Ministry of Education and Science) and ICONA (Spanish Ministry of Agriculture).

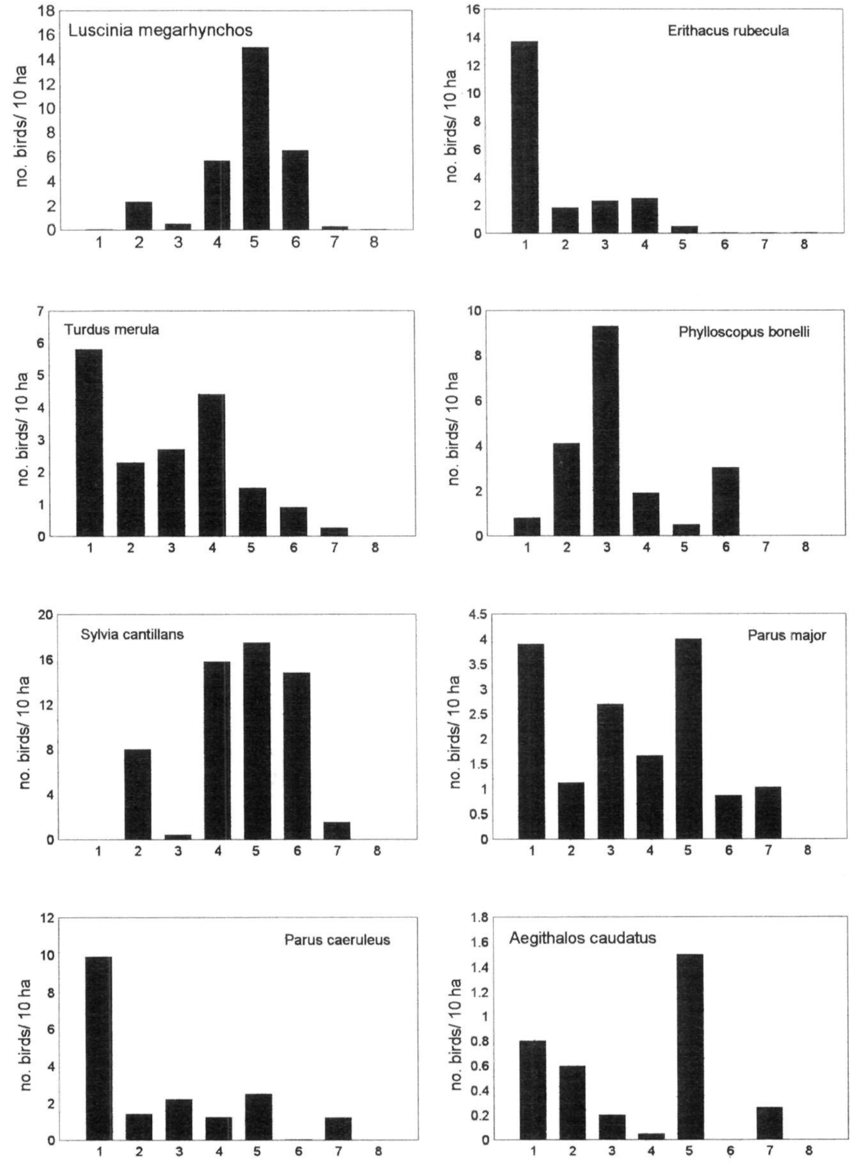

Fig. 2. Ecological densities of the eight selected species along the study archipelagoes. Code of archipelagoes as in Fig. 1.

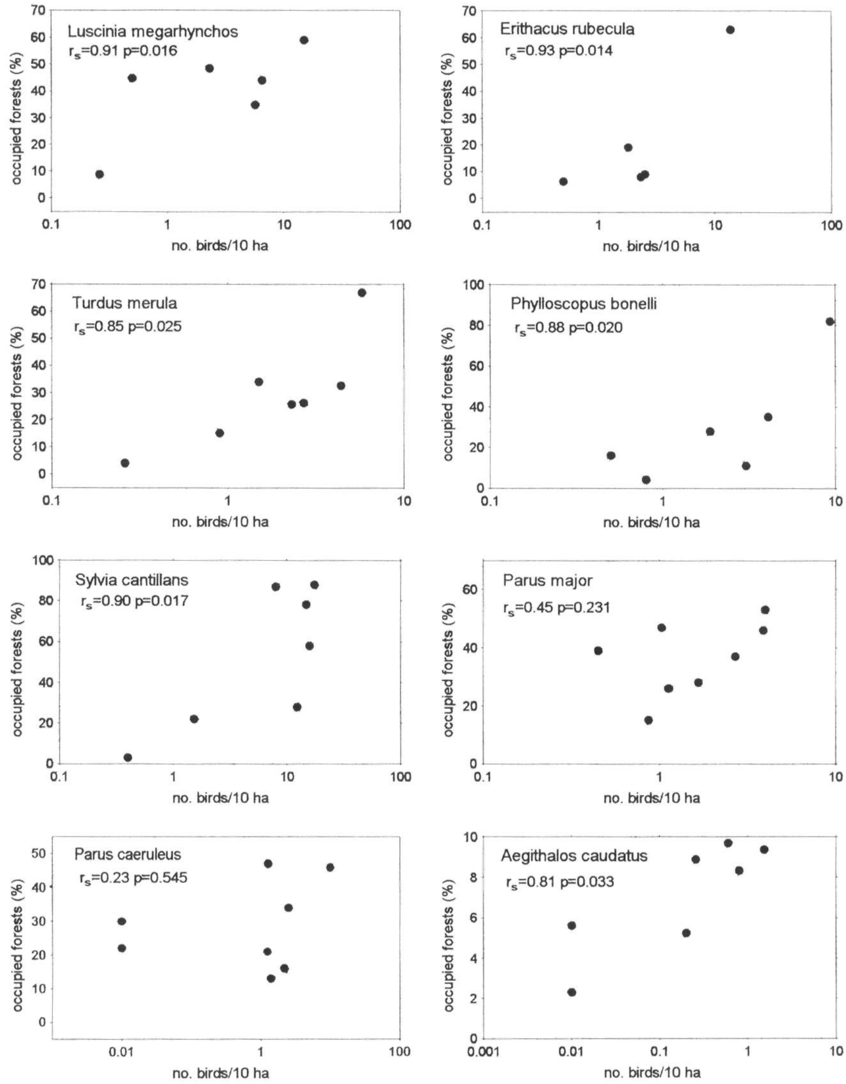

Fig. 3. Relationships between local densities and local incidences of the eight selected species.

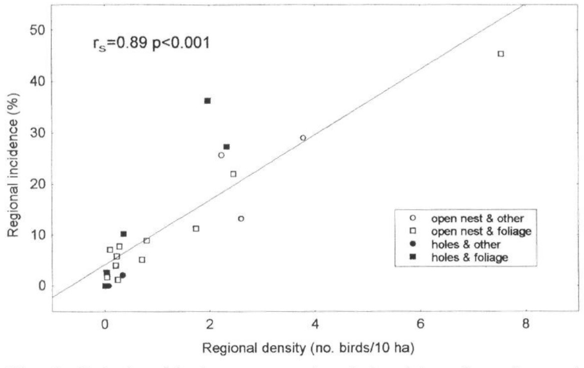

Fig. 4. Relationship between regional densities of species and their regional incidences in fragments of the study archipelagoes. The classification of birds according to their nesting sites and feeding substrata is also shown.

References

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. – Oikos 71: 355–366.

Andrén, H. 1996. Population responses to habitat fragmentation: statistical power and the random sample hypothesis. – Oikos 76: 235–242.

Askins, R. A., Philbrick, M. J. and Sugeno, D. S. 1987. Relationships between the regional abundance of forest and the composition of forest bird communities. – Biol. Conserv. 39: 129–152.

Blondel, J. 1990. Biogeography and history of forest bird fauna in the Mediterranean zone. – In: Keast, A. (ed.), Biogeography and ecology of forest bird communities. SPB Academic Publ., pp. 95–107.

Bolger, D. T., Alberts, A. C. and Soulé, M. E. 1991. Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. – Am. Nat. 137: 155–166.

Carbonell, R. et al. 1995. Efectos de la fragmentación sobre la estructura de los encinares. – In: Santos, T. and Tellería, J. L. (eds), Determinación de áreas mínimas para vertebrados forestales en bosques fragmentados, Report ICONA-UCM, Madrid, pp. 33–48.
Connor, E. F. and McCoy, E. D. 1979. The statistics and biology of the species-area relationships. – Am. Nat. 113: 791–833.
Costa, M. et al. 1990. La evolución de los bosques de la Península Ibérica: una interpretación basada en datos paleobriogeográficos. – Ecología 1: 31–58.
Font, I. 1983. Climatología de España y Portugal. – Instituto Nacional de Meteorología, Madrid.
Gaston, K. J. 1994. Rarity. – Chapman and Hall.
Haila, Y. 1983. Land birds on northern islands: a sampling metaphor for insular colonization. – Oikos 41: 334–351.
Haila, Y. 1986. North European land birds in forest fragments: evidence for area effects?. – In: Verner, J., Morrison, M. L. and Ralph, C. J. (eds), Wildlife 2000. Modeling habitat relationships of terrestrial vertebrates. The Univ. of Wisconsin Press, pp. 315–319.
Haila, Y., Hanski, I. K. and Raivio, S. 1987. Breeding bird distribution in fragmented coniferous taiga in southern Finland. – Ornis Fenn. 64: 90–106.
Hanski, I. and Gilpin, M. 1991. Metapopulation dynamics: brief history and conceptual domain. – Biol. J. Linn. Soc. 42: 3–16.
Helle, P. and Järvinen, O. 1986. Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. – Oikos 46: 107–115.
Hinsley, S. A. et al. 1995. Habitat and landscape factors influencing the presence of individual breeding bird species in woodland fragments. – J. Avian Biol. 26: 94–104.
Jackson, J. A. 1979. The surfaces as foraging substrates for insectivorous birds. – In: Dickson, J. C. et al. (eds), The role of insectivorous birds in forest ecosystems. Academic Press, pp. 69–93.
Karr, J. R. 1982. Avian extinction on Barro Colorado Island, Panama: a reassessment. – Am. Nat. 119: 220–239.
Kattan, G. H., Álvarez-López, H. and Giraldo, M. 1994. Forest fragmentation and bird extinctions: San Antonio eighty years later. – Conserv. Biol. 8: 138–146.
Lawton, J. H. 1993. Range, population abundance and conservation. – Trends Ecol. Evol. 8: 409–413.
Peñalba, M. C. 1994. The history of the Holocene vegetation in northern Spain from pollen analysis. – J. Ecol. 82: 815–832.
Preston, F. W. 1948. The commonness and rarity of species. – Ecology 29: 254–283.
Preston, F. W. 1960. Time and space and the variation of species. – Ecology 41: 611–627.
Robinson, J. G. and Redford, K. H. 1986. Body size, diet, and population density of Neotropical forest mammals. – Am. Nat. 128: 665–680.
Salleo, S. and LoGallo, M. A. 1990. Sclerophylly and plant water relations in three Mediterranean *Quercus* species. – Ann. Bot. 65: 259–270.
Santos, T. and Tellería, J. L. 1995. Global environmental change and the future to Mediterranean forest avifauna. – In: Moreno, J. M. and Oechel, W. C. (eds), Mediterranean-type ecosystems. Springer, pp. 457–470.
Santos, T. and Tellería, J. L. 1997. Effects of fragmentation on forest insectivorous passerines in two European woodlands. – Ardeola 44: 113–117.
Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. – Griffin, London.
Soulé, M. E. et al. 1988. Reconstructed dynamics of rapid extinction of chaparral-requiring birds in urban habitat islands. – Conserv. Biol. 2: 75–92.
Tellería, J. L. and Santos, T. 1993. Distributional pattern of insectivorous passerines in the Iberian forests: does abundance decrease near the border? – J. Biogeogr. 20: 235–240.
Tellería, J. L. and Santos, T. 1994. Factors involved in the distribution of forest birds in the Iberian Peninsula. – Bird Study 41: 161–169.
Tellería, J. L. and Santos, T. 1995. Effects of forest fragmentation on a guild of wintering passerines: the role of habitat selection. – Biol. Conserv. 71: 61–67.
Tellería, J. L. and Santos, T. 1997. Seasonal and interannual occupation of a forest archipelago by insectivorous passerines. – Oikos 78: 239–248.
Zar, J. H. 1984. Biostatistical analysis. – Prentice-Hall.

Appendix

Breeding forest passerines in the eight study archipelagoes. The numbers in parentheses (a,b,c) show a) the number of archipelagos in which the species was present; b) the nest site (1: ground and open tree nesters, 2: hole nesters) and c) the feeding substrate (1: ground and trunks, 2: foliage). *Troglodytes troglodytes* (2,1,2), *Prunella modularis* (4,1,2), *Luscinia megarhynchos* (6,1,1), *Erithacus rubecula* (5,1,1), *Turdus merula* (7,1,1), *Sylvia cantillans* (7,1,2), *Sylvia melanocephala* (2,1,2), *Sylvia hortensis* (4,1,2), *Sylvia undata* (4,1,2), *Sylvia atricapilla* (3,1,2), *Sylvia borin* (2,1,2), *Phylloscopus collybita* (3,1,2), *Phylloscopus bonelli* (6,1,2), *Regulus ignicapillus* (3,1,2), *Aegithalos caudatus* (7,2,2), *Parus major* (8,2,2), *Parus caeruleus* (8,2,2), *Parus cristatus* (1,2,2), *Parus palustris* (1,2,2), *Certhia brachydactyla* (3,2,1), *Sitta europaea* (2,2,1).