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Seasonal and interannual occupation of a forest archipelago by insectivorous passerines

J. L. Tellería and T. Santos

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The distribution of insectivorous passerines was studied in 31 fragments (0.1 to 350 ha) of a holm oak (*Quercus ilex*) Mediterranean forest archipelago in central Spain for two consecutive springs and winters (1988 to 1990). The study aimed to assess the role of forest size, abundance and other biological traits (nesting site and foraging substrata) of the species in their ability to occupy the fragments. The number of fragments occupied by the species (f_i) was correlated to their abundance (d_i) in spring and winter. Spring-to-winter changes of d_i correlated positively to changes of f_i due to the incidence of summer migrants but failed to show any significant pattern when restricted to species occurring in both seasons. The between-winter variations of d_i correlated positively with changes in f_i, while the between-spring changes of both parameters did not correlate, probably because of stronger effects of site fidelity on bird distribution in this period. Between-year persistence in the occupation of fragments was directly related to bird species abundance and, for a given abundance, persistence decreased in the smallest fragments. Hole-nesting species during the 1988 spring and the exploiters of scarce trees or foraging substrata during both winters showed an apparent restriction to colonize the smaller fragments due in part to changes in habitat structure related to fragmentation. These results support the hypothesis that abundance is a good predictor of the ability of species to occupy and persist in fragments. However, abundance alone does not fully explain the processes that determine these occupancy patterns, since other traits related to the spatial scale of analysis and the suitability of fragments for each bird species are also involved.

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Forest fragmentation leads to a loss of bird species in the fragments (Wiens 1989, Opdam 1991, Andrén 1994). This loss appears to depend on landscape structure (e.g., size and distance between fragments) and the species traits related to their ability to occupy fragments (dispersing ability, demographic stochasticity, abundance, etc.; MacArthur and Wilson 1967, Levins 1969, Leigh 1981, Goodman 1987, Wiens 1995). Alternatively, it has been proposed that the occupation of a given fragment by a species is only a direct function of its abundance (sampling hypothesis; Preston 1948, 1960). According to this view, the most abundant species are more likely to be included in the fragments than more scarce ones due to abundance alone.

It has been suggested that these alternative views should be a result of the scale of approach to the analysis of forest fragmentation (Howe 1984, Haila 1990). Andrén (1994) has indicated that although the sampling hypothesis probably is valid in early stages of forest fragmentation, there is a range of processes (e.g. regional habitat loss) that can lead to a subsequent selective loss of species at the final stages of the process (in very small patches). Haila et al. (1993) found that sampling explains year-to-year changes in the distribution of individual

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birds among small fragments in a given locality. These apparent contradictory views may be explained if we consider that, usually, populations are more stable and communities more constant on large space and time scales than on small scales, where more stochastic patterns are found (Wiens 1989, Landres 1992, Levin 1992). The random distribution of species on very small patches may therefore be interpreted as a result derived from the spatial and temporal scale in use. Thus, in spite of the important role of abundance (the basic premise of the sampling hypothesis), we think that the effect of other biological traits of the species in the structuring of the assemblages of each fragment should not be discarded in spite of the effect of the scale when working on very small fragments.

In this paper, we analyse the distribution of insectivorous passerines in a forest archipelago in central Spain (31 woodlots ranging from 0.1 to 350 ha) during two consecutive springs and winters (1988 to 1990) to evaluate the role of three hypothetical processes affecting the occupation of fragments by birds:

1) We test the effect of abundance on the colonizing ability of different bird species in spring and winter. We predict that the number of fragments occupied by each species will correlate positively with their abundance in the study habitat and that their interseasonal and interannual variations in abundance will be linked to concomitant changes in the number of occupied fragments.
2) We test whether, in addition to abundance, other factors influence the ability of species to occupy small forest patches. For this purpose, we use two biological traits of the birds: A) Species with more accessible nests seem to be more likely to disappear because nest predation increases in smaller fragments (Wilcove 1985, Martin 1988; see Tellería and Santos 1992 for evidences of this increasing pressure of predators in our study area). We predict that, on a given abundance, species with less accessible nests will be more frequent in smaller forest patches during the breeding period. B) We predict that, on a given abundance, species that depend on resources in short supply will reach thresholds that make their survival impossible in smaller fragments before those dependent on abundant resources (Wiens 1985, 1989, Tellería and Santos 1995).
3) Finally, we analyse the role of scale on the temporal patterns of occupation of the fragments by the birds. Lack of persistence in the occupation of small fragments may be due to the presence of one or very few individuals (McCoy 1982, Haila et al. 1993, Hinsley et al. 1995). It may be hypothesized that the time involved in the occupation or abandonment of a small fragment by a given species will therefore be much shorter than the time necessary to develop an identical process in a large fragment (see Wiens 1989, Landres 1992 and Levin 1992 for comments on space and time scale correlations). On our own space and time scale, we predict that species will be more persistent in the larger than in the smaller fragments. We also predict that abundance will be associated positively with persistence: at a given fragment size, the most abundant species should have larger populations and be less inclined to disappear than scarce species. For the same reason, those species with smaller interannual variations in their abundance will have a greater persistence in fragment occupation.

Material and methods

Study area

The study was done in a forest "archipelago" at Lerma (Central Spain, 42° 5′N, 3° 45′W). This is a plateau (altitude 800 m) at the western base of the Sistema Ibérico Septentrional mountains. The forests are fragmented and dispersed in a landscape used for cereal farming in which shelterbelts are absent. They cover around 5% of the area. Thirty-one forests were selected, their sizes ranging from 0.1 to 350 ha and their distance to the nearest woodlot ranging from 20 to 700 m (mean ± s.e., 197.1 ± 38.2 m). The dominant tree species is holm oak *Quercus ilex* L., followed by juniper *Juniperus thurifera* L. and Lusitanian oak *Quercus faginea* Lamk.

Several vegetation traits that are potentially relevant to the occurrence of forest birds were measured throughout the whole area in the small fragments (<1 ha) and in 25-m radius circular plots distributed at 30-m intervals along transects in the larger ones. The variables estimated were: tree cover, holm oak cover, Lusitanian oak cover, juniper cover, tree height, no. trunks >10 cm dbh, no. trunks >30 cm dbh and no. holes/trunk >30 cm dbh.

Species selection and census work

Because habitat fragmentation can have different effects on different groups of species, we chose to study those passerines that are strictly dependent on the forest all around the year because they are most affected by fragmentation. We thus excluded birds which depend on the surrounding croplands during a part of the seasonal cycle (e.g., finches, buntings, thrushes, crows, etc.). The resulting group of species was composed of insectivorous passerines such as warblers (e.g. *Sylvia*, *Phylloscopus*, *Regulus*), tits (*Parus*, *Aegithalos*), small thrushes (*Erithacus*, *Luscinia*) and other small insectivores (e.g. *Certhia*, *Sitta*, *Prunella*, *Troglodytes*).

Bird censuses were carried out during the spring of 1988 and 1989 and the winter of 1988–89 and 1989–90.

The birds were recorded in the smallest fragments (<7 ha) by means of intensive searchings on four to six visits each spring (April to June) and winter (December to February). The abundance of individual species in the larger forests was sampled by means of repeated strip transects (Seber 1982) in which birds were counted in two strips 25 m wide on both sides of the established transect. These results were expressed as individual species densities ($d_i =$ no. birds/10 ha). Breeding species in a given fragment were considered to be all those with individuals displaying territorial behaviour (persistent song), nests, baiting behaviour or persistence in the fragment throughout the spring. In winter, a period in which some species move among patches, we recorded all the species that were observed searching for food in each fragment. These data were used to calculate the number of fragments (f_i) occupied by each species in each season and year.

Species classification

Nesting site

Birds were classified as nesting on the ground, in open tree nests or in tree holes. These are three levels of accessibility to predators (Lack 1968, Ricklefs 1969) that can condition their ability to occupy the small fragments (Martin 1988).

Use of space

Forest physiognomic and floristic composition are two groups of variables that usually synthesize the set of environmental requisites of forest birds (e.g. Wiens 1989). On the basis of a previous study on the habitat selection of species in the study forests (Tellería and Santos 1995, unpubl.), they were classified according to whether their preferences coincided or not with the most abundant foraging sites. Species that exploit trunks or thick branches (*Sitta europaea* (L.) and *Certhia brachydactyla* Brehm.) were considered to depend on scarce foraging sites given that the total area occupied by these substrata is much smaller than the area available for the species that exploit the foliage (Wilson 1970, Jackson 1979). This group also includes birds that feed on the scarce junipers (*Parus ater* L. and *Parus cristatus* L., two conifer specialists; Cramp and Perrins 1993) and Lusitanian oaks (actively selected by *Aegithalos caudatus* (L.) during the study period; Tellería and Santos 1995, unpubl.). The rest of the species were considered as depending on abundant foraging sites.

Analyses

We used the individual species densities (d_i) in the largest forests (>100 ha) to test by regression analysis the role of abundance in determining the ability of birds to occupy fragments, measured by the number (f_i) of fragments occupied by each species (see Soulé et al. 1988 for a similar approach). We used the residuals of this regression analysis to detect whether, at a given regional abundance, a larger or smaller number of fragments was colonized according to the nesting site and use of substrata. Furthermore, we considered the qualitative traits as dummy variables (Zar 1984) in a multiple stepwise regression analysis (F to enter $= 4$) to evaluate their role (explained variance) in the species' ability to occupy fragments.

Results

Species composition

The insectivorous bird community of these fragments during the two study springs and winters included 19 species (Table 1). Five of them (*Sylvia cantillans* (Pall.), *Sylvia hortensis* (Gm.), *Phylloscopus bonelli* (Vieill.), *Muscicapa striata* (Pall.) and *Luscinia megarhynchos* Brehm.) were summer migrants and two (*Troglodytes troglodytes* (L.) and *Regulus regulus* (L.)) were wintering species. *Sitta europaea* arrived in winter 1988, bred in spring 1989 and disappeared after the winter 1989, while *Phylloscopus collybita* (Vieill.) bred in one fragment during 1988, but then disappeared until the winter 1989. *Regulus ignicapillus* (Temm.) received considerable inputs of individuals in both winters. Many of these wintering birds probably came from the nearby forested mountains which are snow-covered in winter and host large breeding populations of these species (De Juana 1980).

The number of species present in each fragment correlated positively with their area during both spring and winter, showing a similar pattern in both years (Fig. 1). The majority of the species present in a fragment were also found in the immediately larger fragments, reflecting an orderly pattern of species loss as the fragment sizes diminishes (nested pattern; Patterson and Atmar 1986). This pattern was evaluated for each species by means of the Mann-Whitney U-test between sizes of occupied and unoccupied forests (Simberloff and Martin 1991; Table 2).

Abundance and occupation ability

The number of fragments occupied by species f_i correlated positively with their abundance (d_i) during the two springs and winters (Fig. 2). The interseasonal changes in abundance, measured as $d_{si} - d_{wi}$, where d_{si} is the spring density and d_{wi} is the winter density of species i, appeared to be correlated during the two years (1988: $r_s = 0.45$, $p < 0.05$; 1989: $r_s = 0.53$, $p < 0.05$) with the changes in the number of occupied

Table 1. Spring and winter distribution of densities (*d*, no. ind/10 ha), number of occupied fragments (*f*), type of nests and a classification according to the feeding substrata of the studied species. *ds* and *dw* are the spring and winter densities and *fs* and *fw* the number of occupied fragments in spring and winter.

	1988				1989				
Species	*ds*	*fs*	*dw*	*fw*	*ds*	*fs*	*dw*	*fw*	nest/use
Troglodytes troglodytes	–	–	0.20	10	–	–	0.05	6	*/0
Prunella modularis	0.33	6	0.60	12	0.06	4	0.05	2	0/0
Sylvia hortensis	0.05	6	–	–	0.11	8	–	–	0/0
Sylvia cantillans	8.90	27	–	–	7.98	31	–	–	0/0
Sylvia undata	0.30	3	0.15	5	0.23	2	0.10	7	0/0
Phylloscopus collybita	0.01	1	–	–	–	–	0.05	7	–1/0
Phylloscopus bonelli	5.50	15	–	–	4.08	15	–	–	–1/0
Regulus regulus	–	–	0.15	2	–	–	0.35	6	*/1
Regulus ignicapillus	2.55	8	7.35	24	1.00	8	5.28	23	0/0
Muscicapa striata	0.08	1	–	–	0.01	1	–	–	0/0
Erithacus rubecula	3.13	12	1.60	19	1.77	10	2.43	18	–1/0
Luscinia megarhynchos	2.88	20	–	–	2.28	19	–	–	–1/0
Aegithalos caudatus	0.45	2	1.13	3	0.10	3	0.55	5	0/1
Parus cristatus	0.38	2	0.63	4	0.63	3	0.78	4	1/1
Parus ater	–	–	–	–	–	–	0.30	2	*/1
Parus caeruleus	4.20	6	3.3	23	3.05	8	2.43	18	1/0
Parus major	3.20	8	1.40	14	1.38	8	1.13	12	1/0
Sitta europaea	–	–	0.78	4	0.01	1	–	–	1/1
Certhia brachydactyla	0.28	3	0.30	3	0.01	3	0.28	4	1/1

nest: –1: ground nest, 0: arboreal open nest, 1: arboreal hole nest, *: not considered; use of substrata: 0: depending on abundant foraging sites, 1: depending on scarce foraging sites.

fragments, measured as $f_{si} - f_{wi}$, where f_{si} and f_{wi} are the number of fragments occupied by species *i* during spring and winter, respectively. However, this pattern was determined by the incidence of the most abundant summer migrants (*Sylvia cantillans*, *Phylloscopus bonelli* and *Luscinia megarhynchos*), and by the massive winter arrival of *Regulus ignicapillus*. The nine species occurring both seasons revealed no link between their small changes in abundance and the variations in the number of occupied fragments (1988: $r_s = -0.20$, n.s.; 1989: $r_s = 0.13$, n.s.). In fact, eight out of the nine species increased the number of occupied fragments during both winters despite that five (1988) and four (1989) of them decreased their densities in the large forests during this period (Table 1).

The interannual changes in spring and winter abundance, measured as $d_{1i} - d_{2i}$, where d_{1i} and d_{2i} are densities of species *i* for the two springs or winters, correlated positively during the winter but not during the spring (Fig. 3) with the changes in the species distribution between fragments (measured as $f_{1i} - f_{2i}$, where f_{1i} and f_{2i} are the number of fragments occupied by species *i* in the spring or winter of both years).

The role of species characteristics

Habitat structure

Small fragments tended to have few number of holes per tree and a lower cover of junipers than the large ones; they did not show any differences in the remaining variables (Table 3).

Nesting site

During spring, the nesting site contributed partially to an uneven distribution of species. Hole nesting birds occupied a significantly lower number of fragments than nesters on the ground (Mann-Whitney *U*-test for residuals in Fig. 2, 1988: $z = 2.17$, $p < 0.05$ and 1989: $z = 2.09$, $p < 0.05$). However, the differences between the residuals were not significant for the three types of nests neither in 1988 (Kruskall-Wallis test $H = 3.92$, $p = 0.07$) nor in 1989 (Kruskall-Wallis test $H = 2.01$, n.s.) and nest placement was not included as part of the model (stepwise multiple regression analysis) to predict the number of fragments occupied in spring.

Use of substrata

This was linked to a significant variation in fragment occupation during the 1988 spring (Mann-Whitney *U*-test for residuals in Fig. 2, $z = 1.81$, $p < 0.05$) but not in 1989 ($z = 0.59$, n.s.). In both winters, however, the species depending on more scarce substrata had significantly more negative residuals than the species depending on abundant foraging sites (Mann-Whitney *U*-test: winter 1988, $z = 2.76$, $p < 0.01$; winter 1988, $z = 2.42$, $p < 0.01$). The multiple stepwise regression analysis between the number of fragments occupied and the abundance and specialization in the use of substrata included this variable in both winters, increasing the explained variance with 20% and 32%, respectively (winter 1988: $\log(f_i) = 1.13 + 0.34 \log(d_i) - 0.53$ use, $F = 89.83$, $p < 0.001$, $R^2 = 0.95$; winter 1989: $\log(f_i) = 1.11 + 0.34 \log(d_i) - 0.38$ use, $F = 17.35$, $p < 0.001$, $R^2 = 0.78$).

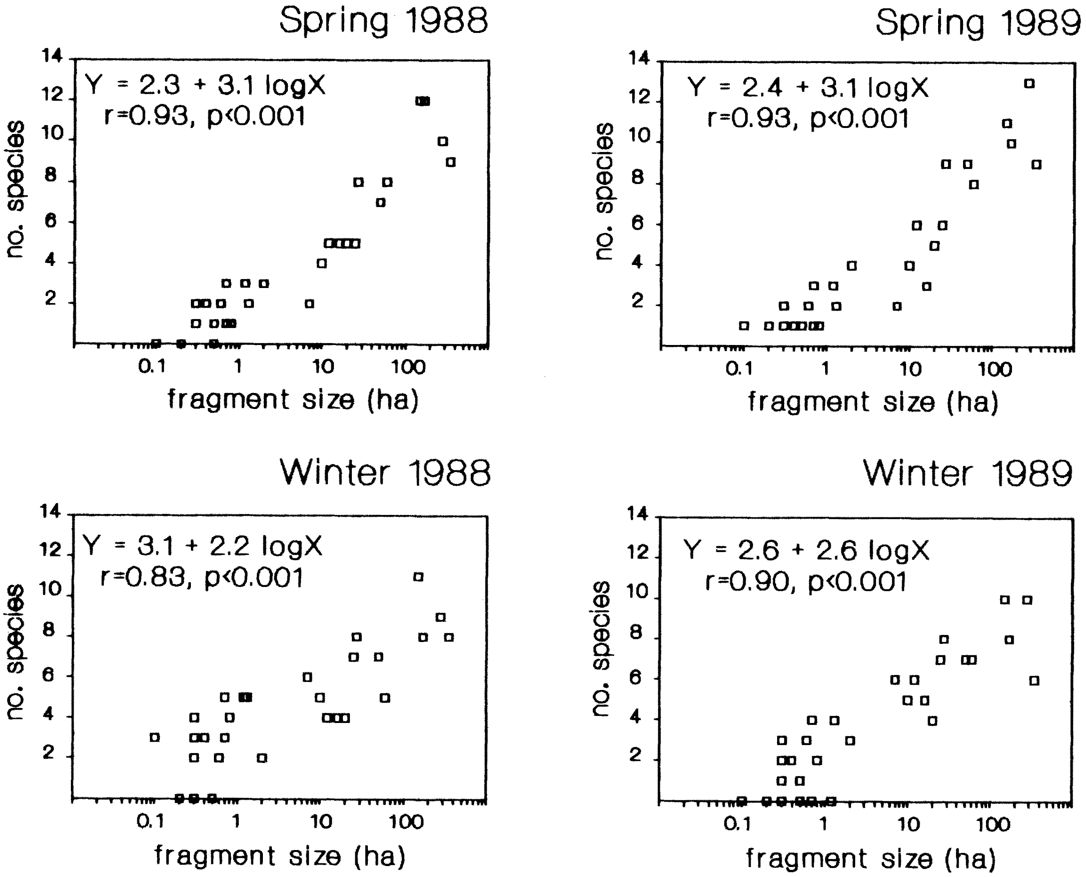

Fig. 1. Relationship between fragment size and number of species during the four study periods.

Forest size and persistence

The interannual persistence of each species in the occupation of fragments, measured as f'/f, where f' is the number of fragments occupied in both years and f is the total number of fragments occupied in either year, correlated positively with the mean interannual abundance of the species, measured as $(d_1 + d_2)/2$, and negatively with their interannual variation, measured as $(d_1 - d_2)/(d_1 + d_2)$, where d_1 and d_2 are species densities in each year (Fig. 4). To analyse the distribution of species persistence according to fragment size, we selected the seven most abundant species (>1 individual per 10 ha in each season) and which were thus relatively well represented along the whole size gradient. Grouping the fragments into intervals (<10, 10–100 and >100 ha), we found that the smallest fragments tended to have a smaller persistence in the interannual occupation by species (Table 4).

Discussion

The results of this paper corroborate the important role of abundance as a predictor of the ability of species to occupy fragments in spring and winter. The more abundant species occupied a wider range of sizes than the more scarce species, which tended to be relegated to the larger forests (as reflected by the observed nested pattern). We have also seen that the interannual variations in fragment occupation in winter correlated with variations in abundance. It is important to note, however, the lack of correlation between interannual changes in abundance and the variation in the number of fragments occupied in spring. This difference may be due to a greater fidelity of birds to the fragments in spring (see review in Willard et al. 1995). Site-fidelity may induce reluctance by individuals to abandon the fragments they occupied in previous years (Wiens 1995), regardless of the decline in their regional abundance. Although certain species appear to show site fidelity throughout the annual cycle (e.g. Cantos and Tellería 1994), the good fit between interannual variations of winter abundance and fragment occupation might be due to the increasing possibility of moving between fragments after the breeding period, when birds are freed from their link to the nesting site. This could facilitate a local redistribution of birds more dependent on the variation of their abundances.

Table 2. Mean size (means ± s.e.) of the fragments occupied for each species. Asterisks show the significance of a Mann-Whitney *U*-test between the size of occupied and non-occupied fragments (the size of unoccupied fragments was ever smaller).

	1988		1989	
Species	spring	winter	spring	winter
T. troglodytes	–	91.6 ± 40.0***	–	72.9 ± 42.3*
P. modularis	122.5 ± 39.4***	79.52 ± 34.3***	93.8 ± 63.0*	140.4 ± 139.0$^{\mathrm{ns}}$
S. hortensis	112.9 ± 71.1$^{\mathrm{ns}}$	–	112.0 ± 47.6***	–
S. cantillans	43.9 ± 17.2**	–	38.3 ± 15.2$^{\mathrm{nt}}$	–
S. undata	116.4 ± 63.4*	116.4 ± 63.4*	260.0 ± 90.0*	112.7 ± 46.3***
Ph. collybita	60$^{\mathrm{nt}}$	–	–	113.2 ± 53.1**
Ph. bonelli	78.3 ± 28.4***	–	73.4 ± 27.0***	–
R. regulus	–	75.4 ± 74.6$^{\mathrm{ns}}$	–	107.3 ± 45.3**
R. ignicapillus	135.3 ± 44.6***	59.1 ± 22.4**	88.0 ± 30.7***	51.5 ± 19.9**
M. striata	350.0$^{\mathrm{nt}}$	–	280.0$^{\mathrm{nt}}$	–
E. rubecula	97.5 ± 33.3***	57.3 ± 23.8**	112.6 ± 38.5***	65.2 ± 24.5**
L. megarhynchos	59.2 ± 22.4***	–	62.3 ± 23.4***	–
A. caudatus	225.0 ± 55.0*	156.8 ± 51.8**	156.8 ± 51.8**	139.2 ± 60.1**
P. cristatus	164.5 ± 5.5*	237.5 ± 47.1**	200.0 ± 40.4**	152.5 ± 55.4**
P. ater	–	–	–	225.0 ± 55.0**
P. caeruleus	171.2 ± 51.6***	49.4 ± 19.2**	137.9 ± 43.8***	53.0 ± 22.2***
P. major	133.1 ± 45.4***	82.6 ± 30.1***	137.4 ± 44.0***	96.4 ± 33.6***
S. europaea	–	156.8 ± 51.8**	150.0$^{\mathrm{nt}}$	–
C. brachydactyla	200.0 ± 40.4**	200.0 ± 40.4**	200.0 ± 40.4**	152.5 ± 55.4***

*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, ns: not significant, nt: no test because of the structure of data.

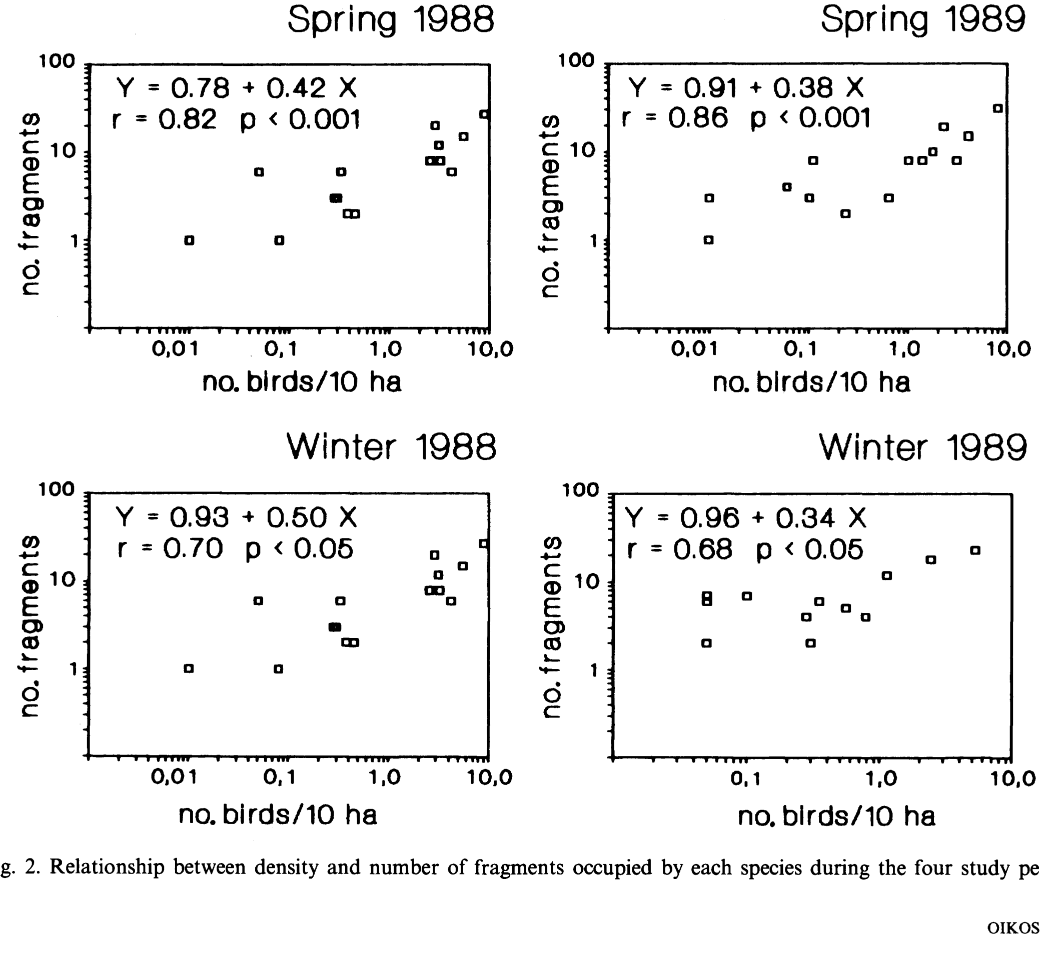

Fig. 2. Relationship between density and number of fragments occupied by each species during the four study periods.

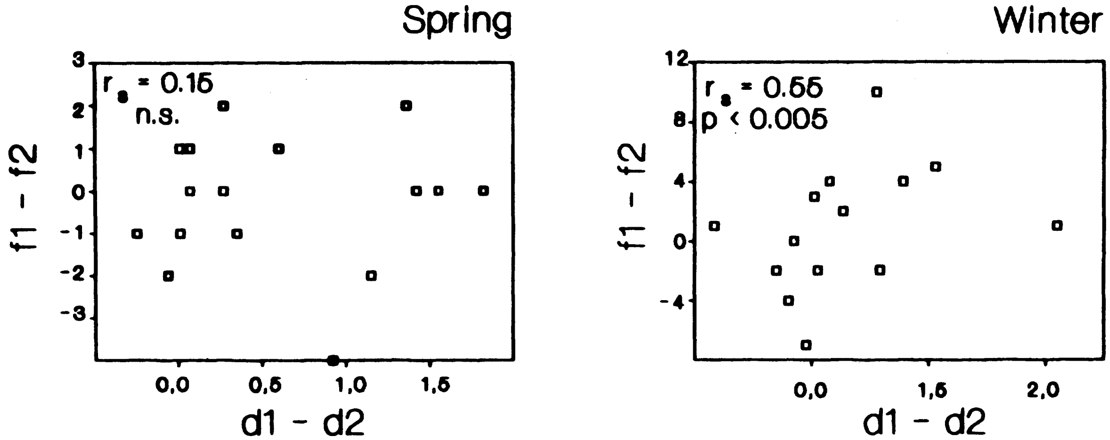

Fig. 3. Relationship between interannual change in density ($d_1 - d_2$) and interannual change in number of occupied fragments ($f_1 - f_2$) during spring and winter (1: 1988, 2: 1989).

Although abundant birds as a rule colonized successfully the smaller fragments, this pattern appeared to be conditioned by certain traits of the species. In the Lerma forest archipelago, birds that nest in tree holes were less able to colonize the smallest fragments than ground nesters with the same abundance. This apparently contradict Martin's (1988) suppositions, according to which the former species would be the least sensitive to predation in the smallest fragments and hence be best adapted to occupying the whole fragmentation gradient. This result, however, can be interpreted from the perspective of the decreasing habitat suitability of small fragments since holes can reach critical abundances when forest size diminishes (Haila et al. 1987) or, as it has been shown in our study area, may decrease hole density in small fragments. This increased scarcity of holes would produce a sharp decrease of hole nesters in small fragments and the contrasting seasonal distribution of some hole nesters (e.g. *Parus caeruleus* and *Parus major*). When reproduction and hole dependence concludes, a period of vagrancy begins so that part of the population moves from the large forests to exploit the smaller forest fragments. Given that these are the only hole nesting species which make use of the non-specialized substrata, they may develop this seasonal strategy of spatial usage in Lerma archipelago. These and other seasonal changes in habitat preferences of birds might explain the difficulties to track some correlation between the interseasonal changes in abundance and the ability of species to occupy the fragments.

A similar conclusion can be drawn from the patterns of fragment occupancy by species with more scarce foraging sites. This seems to be a relevant trait during winter, when the forest birds condition their behaviour to food searching (Gibb 1954, Suhonen et al. 1992). Furthermore, the abundance of winter food resources appears to be the most important conditioning factor in their distribution by influencing their survival ability (Jansson et al. 1981). This may be the reason why the species that depend on relatively scarce resources such as the trunks (*Sitta europaea*, *Certhia brachydactyla*) of Lusitanian oak (*Aegithalos caudatus*) only occupied the largest fragments of the archipelago (Tellería and Santos 1995), despite the fact that the density of trunks and the cover of oaks remained similar between forest size ranges. As in the case of hole nesters, the species depending of junipers (*Parus cristatus*, *P. ater*) were perhaps more intensively affected by the decreasing cover of this tree in small fragments (see Santos and Tellería 1994 for a discussion on the conservation problems of this tree in these fragments).

Abundance is also linked to the role of scale on the interannual persistence of bird species in fragments. According to prediction 3, those species with smaller interannual variations in abundance were the most persistent and the most rare species were the least persistent in the smaller fragments. This last result, also observed in a three-year study of Dutch forest fragments (Van Noorden 1986 in Opdam 1991), may be due to the birds' inability to immediately colonize all the potentially appropriate sectors of the regions where their populations are unsaturated (Opdam 1991), a probably common situation in many seasonal habitats (Wiens 1989).

All these processes (abundance, habitat suitability and scale-induced patterns of persistence) affecting the patterns of fragment occupation by birds may be integrated by models aiming to predict the distribution of populations among habitat patches of different quality at a local scale (see Ims 1995 for a review of the factors affecting the distribution of individuals at different scales). These models assume that increasing population size leads to the progressive occupation of sub-optimum habitat patches via processes of intraspecific interference (competition for exploitation, territorial

Table 3. Vegetation structure changes according to ranges of forest sizes. Means ± s.e. have been obtained from mean scores of each forest in which variables have been obtained from 25-m-radius circular plots. *F* shows the results of an ANOVA test between ranges of forest sizes. Covers have been arcsine-transformed. See text for further details.

Forest size No. of forests	<10 ha 19	10–100 ha 8	>100 ha 4	 *F*
% tree cover	39.4 ± 5.6	36.3 ± 1.7	31.7 ± 2.0	0.24 ns
% holm oak cover	36.8 ± 5.8	35.7 ± 3.1	30.1 ± 3.5	0.14 ns
% Lusitanian oak cover	2.4 ± 0.9	3.6 ± 1.6	1.4 ± 0.9	0.61 ns
% juniper cover	1.2 ± 0.5	0.3 ± 0.1	4.2 ± 0.9	7.25 **
Tree height (m)	4.6 ± 0.2	4.1 ± 0.2	4.5 ± 0.6	0.69 ns
No. trunks >10 cm dbh	48.4 ± 10.7	13.4 ± 2.4	16.6 ± 2.7	3.01 ns
No. trunks >30 cm dbh	5.5 ± 2.9	0.7 ± 0.3	2.0 ± 1.0	0.72 ns
No. holes/tree	0.15 ± 0.05	0.13 ± 0.03	0.80 ± 0.35	9.09 ***

**: $p < 0.01$, ***: $p < 0.001$, ns: not significant.

behaviour, etc.; Brown 1969, Fretwell and Lucas 1969). They also predict the influence of abundance on persistence in sub-optimum patches, as the density will always be much less variable in good habitats which are nearly always filled to capacity, than in poorer habitats, which may be occupied only during years of high population densities (Orians and Wittenberger 1991). However, this interpretation of bird distribution between fragments on a local scale must be supported by two previous assumptions: a) Birds can distribute easily among habitat fragments of the studied archipelago. This condition seems to be easily met by birds at a local scale, especially if they undergo periodical colonizations and abandonments associated with their seasonal

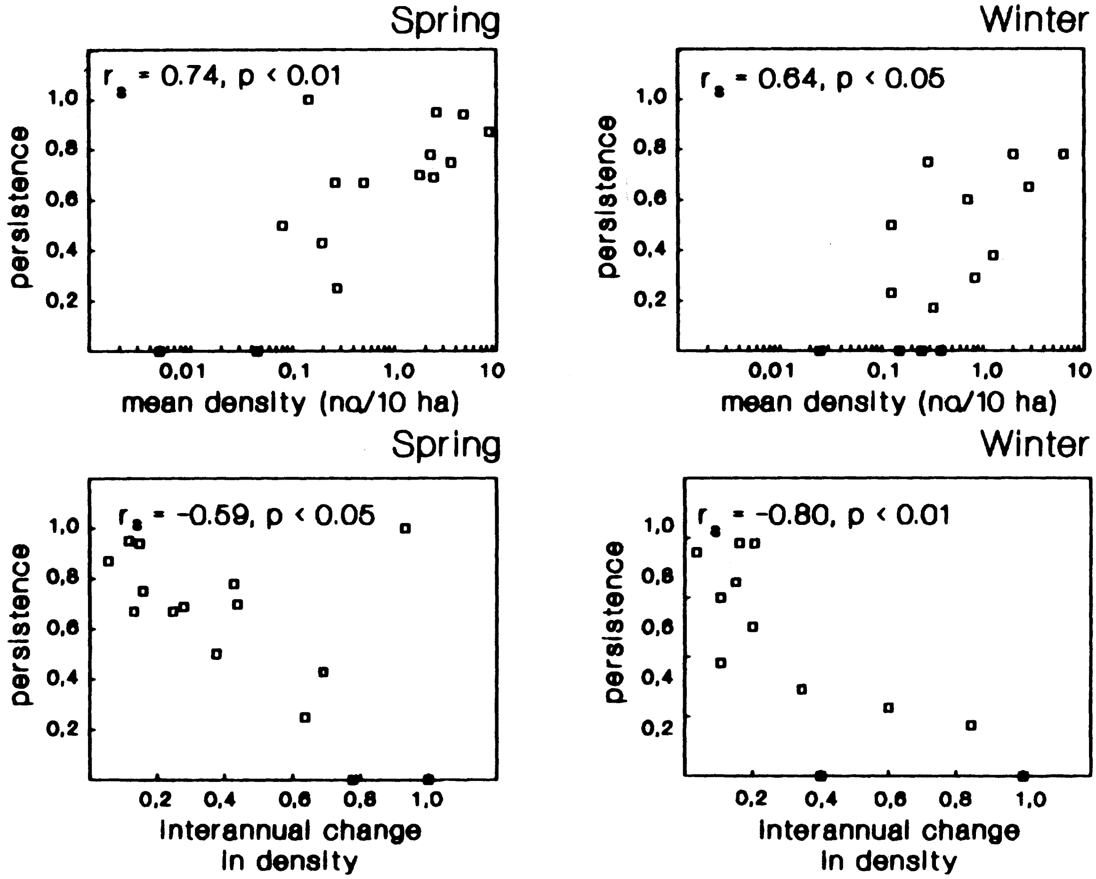

Fig. 4. Relationship between interannual mean density ($(d_1 + d_2)/2$), interannual change in density ($(d_1 - d_2)/(d_1 + d_2)$) and proportion of fragments occupied in both years (persistence).

Table 4. Proportion of forest fragments occupied both years according to ranges of forest sizes. In brackets, the no. of forests occupied at least one year. Results of a Kruskall-Wallis test is also shown.

Forest size No. of forests spring	<10 ha 19	1–100 ha 8	>100 ha 4
Sylvia cantillans	0.84 (19)	1 (8)	1 (4)
Phylloscopus bonelli	0.75 (4)	1 (8)	1 (4)
Regulus ignicapillus	– (0)	0.67 (6)	0.75 (4)
Erithacus rubecula	0 (1)	0.63 (8)	1 (4)
Luscinia megarhychos	0.86 (7)	1 (8)	1 (4)
Parus caeruleus	– (0)	0.50 (4)	1 (4)
Parus major	– (0)	0.60 (5)	1 (4)
	K-W test, $H = 5.76$, $p = 0.056$		
winter			
Regulus ignicapillus	0.57 (14)	1 (8)	1 (4)
Erithacus rubecula	0.60 (15)	1 (8)	1 (4)
Parus caeruleus	0.33 (12)	1 (8)	1 (4)
Parus major	0 (4)	0.75 (8)	1 (4)
	K-W test, $H = 9.37$, $p = 0.009$		

movements (Haila 1983, Howe 1984, Haila et al. 1993). b) Smaller fragments are suboptimal habitat patches for forest birds. This should produce the gradual occupation of small fragments by surplus individuals coming from larger, more suitable fragments giving place to nested patterns in the species distribution. The reduction in the area of woodlots has been associated with a progressive deterioration of their habitat suitability (Saunders et al. 1991, Murcia 1995 and this study for hole nesters and juniper exploiters) and of the body condition of birds (Møller 1995) so that there are some empirical evidences that support this hypothetical scenario.

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