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EFFECTS OF FOREST FRAGMENTATION ON A GUILD OF WINTERING PASSERINES: THE ROLE OF HABITAT SELECTION

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Abstract

*This study analyses the winter colonization of an archipelago of 31 forests (0·1–350 ha) in central Spain by the guild of pariforms (*Parus, Aegithalos, Regulus, Sitta *and* Certhia*). Two hypotheses are considered: (a) that birds with similar habitat preferences tend to disappear simultaneously with the reduction in forest size, leading to a 'nested' pattern of species distribution; or (b) that the species in the smallest forests are a random sample of those found in the larger ones. The results support hypothesis (a). The species that depend on relatively scarce resources, such as tree trunks and junipers* Juniperus thurifera *(*Sitta europaea, Certhia brachydactyla, Parus cristatus *and* P.ater*) only occupied the largest forests. On the other hand, species that exploit abundant, ubiquitous resources, such as holm oak* Quercus ilex *foliage (*Regulus ignicapillus *and* Parus caeruleus*), were distributed uniformly throughout all the fragments. These results emphasize the need for a better understanding of habitat selection by species when designing conservation strategies for fragmented populations.*

Keywords: forest fragmentation, habitat selection, Spain, wintering passerines.

INTRODUCTION

Several pariforms, a guild of insectivorous forest passerines (*Parus, Aegithalos, Regulus, Certhia* and *Sitta*; see Ulfstrand, 1977), fail to breed in the smallest woodlots which result from forest fragmentation (Opdam *et al.*, 1985; Helle & Järvinen, 1986; Ford, 1987; Haila *et al.*, 1987; Kuitunen & Helle, 1988). Little is known, however, about their ability to use these small woodlots in winter, when they tend to develop vagrant, irruptive or migratory movements (Cramp, 1992; Cramp & Perrins, 1993). This paper deals with the factors affecting the distribution of these species when over-wintering in forest fragments in Spain. Simberloff and Martin (1991) have recommended studying the response by individual species to the fragmentation process, rather than the analysis of whole communities. The latter is frequently very difficult to interpret (Wiens, 1989) and not useful for conservation purposes.

It has been shown empirically that the populations of the rarest species tend to be those that disappear first during the process of habitat fragmentation (Jones & Diamond, 1976; Diamond, 1984; Pimm *et al.*, 1988; Soulé *et al.*, 1988). This may be explained by two alternative hypotheses:

(a) The species that depend on resources in short supply soon reach thresholds in smaller fragments that make their survival impossible (Harrison *et al.*, 1988; Wiens, 1989). If this is the case, the relationship between habitat requirements and ability to occupy small forest fragments ought to lead to an orderly pattern of disappearance of species with similar habitat preferences. This pattern has been called 'nested' when all N species occupying a fragment are also present in the fragments with N+1 species (Patterson & Atmar, 1986; Blake, 1991; Bolger *et al.*, 1991).

(b) An alternative hypothesis assumes that the species recorded in different sized fragments are a random sample of the set of species present in an unfragmented habitat (Preston, 1948; Connor & McCoy, 1979; Haila *et al.*, 1993). In this instance, scarce species are less likely to be detected in the smaller fragments because a small number of individuals stays there (Preston, 1948).

This work examines both hypotheses in relation to the distribution of wintering pariforms in an archipelago of Mediterranean forests in central Spain. A difference in ability to disperse among fragments seems to be one of the main determinants of the interspecific patterns of fragment colonization of species (e.g. Wilcox, 1980; Opdam, 1990). However, these small birds form mobile multispecific flocks in winter so that it may be assumed that species of this guild have rather similar abilities to fly among forest patches during this season. They forage on similar resources, mainly tree insects (Betts, 1955), but have different foraging sites that can be easily quantified according to tree species, location in tree, etc. (Alatalo, 1982).

METHODS

Study area

The study was done in an archipelago of forests located in an area around Lerma (central Spain, 42°5'N,

Table 1. Distribution matrix for bird species in the fragmented forests during winter (27 fragments with at least one species; in four fragments of 0·2, 0·3, 0·5 and 0·5 ha no species was observed) and spring (10 fragments with at least one species)

Fragments are ranked by species richness and species are ranked by fragment occurrences (indicated by 'X'). Deviations from perfect nestedness are indicated by asterisks (*). MFS, Mean forest size for each species; *Rig, Regulus ignicapillus; Pca, Parus caeruleus; Pma, Parus major; Rre, Regulus regulus; Aca, Aegithalos caudatus; Pcr, Parus cristatus; Cbr, Certhia brachydactyla; Seu, Sitta europaea; Par, Parus ater.*

Fragment size (ha)	No. of species	*Rig*	*Pca*	*Pma*	*Rre*	*Aca*	*Pcr*	*Cbr*	*Seu*	*Pat*
Winter										
280	9	X	X	X	X	X	X	X	X	X
170	9	X	X	X	X	X	X	X	X	X
150	8	X	X	X	X	X	X	X	X	
350	5	X	X	X	*	X	*	*	X	
27	5	X	X	X	*	X	X	*		
12	5	X	X	X	X	X	*	*		
16	5	X	X	X	*	*	X	X		
25	4	X	X	X	*	X				
10	4	X	X	X	X					
7	4	X	X	X	X					
60	3	X	X	X						
50	3	X	X	X						
20	3	X	X	X						
1·3	3	X	X	X						
1·2	3	X	X	X						
0·3	3	X	X	X						
2	2	X	X							
0·8	2	X	X							
0·7	2	X	X							
0·7	2	X	X							
0·6	2	X	X							
0·5	2	X	X							
0·3	2	X	X							
0·3	2	X	X							
0·3	2	X	X							
0·2	1	X								
0·1	1	X								
MFS (ha)		43·9	47·4	73·7	104·8	144·9	128·6	154·0	237·5	225·0
Spring										
280	6	X	X	X		X	X	X		
170	6	X	X	X		X	X	X		
150	6	X	X	X		X	X	X		
27	4	X	X	X		X				
350	3	X	X	X						
60	3	X	X	X						
50	3	X	X	X						
25	1	X								
20	1	X								
16	1	X								
MFS (ha)		114·8	155·3	155·3		156·8	200·0	200·0		

3°45'W). This is a plateau at the western base of the Sistema Ibérico Septentrional mountains, with an altitude of 800 m. The forests are dispersed in a landscape used for cereal farming. Thirty-one forests with similar floristic composition and physiognomy were selected. They ranged in size from 0·1 ha to 350 ha (Table 1) and their distance to the nearest woodlot ranged from 20 m to 700 m (mean ± SE, 197·1 ± 38·2 m). The predominant tree species is holm oak *Quercus ilex*, with 30% cover, followed by juniper *Juniperus thurifera* with 4% and Lusitanean oak *Quercus faginea* with 1·4%. Holm oak and juniper are evergreens and Lusitanean oak is marcescent; they consequently all preserve their foliage throughout winter. The average tree height is 4·5 m. The shrub cover, predominantly *Cistus laurifolius*, is 25·6%.

Census

Bird censuses were carried out during the winters of 1988–89 and 1989–90 at least twice each winter in December and January–February. Intensive searches were made, in the smallest fragments (< 2 ha), attempting to avoid double contacts. The large forests were sampled by counting birds in two strips 25 m wide on both sides of established transects (Järvinen & Väisänen, 1977; Seber, 1982). The results were expressed in densities (no. of birds/10 ha) for each fragment. The mean forest size (MFS) occupied by each species was calculated from the suite of woodlands sampled. A study of the bird fauna was undertaken in these forests using the same procedure in spring 1988 and 1989 to compare the wintering with the breeding communities.

Habitat selection

The winter biology of pariforms is determined by the search for food (Gibb, 1954; Jansson *et al.*, 1981; Suhonen *et al.*, 1992). They are therefore associated with certain types of trees and substrata (trunks, branches, foliage) which can be used to typify the resource selection of each species. In the two winters, we recorded the use of the feeding substrata by all the species in the large forests (see Morrison, 1984). Each observation of an individual searching for food was attributed to one of six types of substrata (AIR, SHRUB, GROUND, HOLM OAK, JUNIPER and LUSITANEAN OAK). When feeding was recorded in a tree, the location was classified as TRUNK (trunks and branches >5 cm diameter) or FOLIAGE (branches <5 cm and leaves). A data matrix was thus produced to quantify the habitat preferences of each species according to the proportion of each substratum and tree species used. A principal components analysis (PCA; Capen, 1981) was performed on this matrix after standardizing its values with an arcsine transformation (Zar, 1984). The location of the species in each component (measured by their factor scores) was used to characterize their habitat preferences.

Nestedness

The RANDOM1 Monte Carlo simulation program (Patterson & Atmar, 1986) was used to test whether or not the species distribution by forests fitted the 'nested' pattern. This program produces random assortments of species within forest fragments, constrained to match the observed overall frequency of species and their relative numbers within fragments. It was used to generate 1000 archipelagoes to calculate the mean number (and standard deviation) of 'non-fulfilments' of the nested pattern. If the number of non-fulfilments obtained in our archipelago lay within the range of variation of the modelled results, the 'nested' hypothesis of species distribution would be rejected (see Simberloff & Martin, 1991, for a review of this methodology).

RESULTS

Species distribution

Six species (*Regulus ignicapillus, Parus caeruleus, Parus major, Aegithalos caudatus, Parus cristatus* and *Certhia brachydactyla*) bred in the largest forests during the two study springs (Fig. 1, Table 1). Three other species (*Parus ater, Regulus regulus* and *Sitta europaea*) arrived in winter, when a general increase in the number of forests colonized by the birds was also observed (Fig. 1, Table 1).

Winter data on bird densities were grouped into three categories of small (< 10 ha), medium (10–100 ha) and large (> 100 ha) forests to facilitate their interpretation and analysis. Due to the lack of significant between-winter variations in the structure of the wintering pariform communities (Table 2), the mean densities of both years were combined to produce a 2-year mean density for each species. There were, however, some differences in the density distributions in relation to forest size. Five species did not appear at all in the small or medium forests (Table 2). Only *Parus caeruleus, Regulus ignicapillus* and *R. regulus* did not show significant differences in distribution among the three size categories (Table 2). There was a clear negative relationship (Fig. 2) between mean forest size (MFS) occupied by each species and their density (D) in forests > 100 ha. This shows that density in the unfragmented habitat is an important predictor of the ability of these species to adapt to the smaller fragments.

Habitat selection

The PCA of the matrix of spatial usage from both winters (Table 3) generated three components with eigenvalues > 1 (Table 4). PC-1 could be interpreted as a physiognomical gradient by contrasting the use of trunks and large branches (TRUNK substratum) with a mixture of the rest of the feeding substrata. *Sitta europaea* and *Certhia brachydactyla* responded to this gradient (Table 5). PC-2 could be interpreted as a floristic gradient, because it contrasted the use of junipers and holm oaks (Table 4). *Parus ater, P. cristatus* and *Regulus regulus*, all specialists in conifer exploitation, and *P. caeruleus, P. major, Aegithalos caudatus*

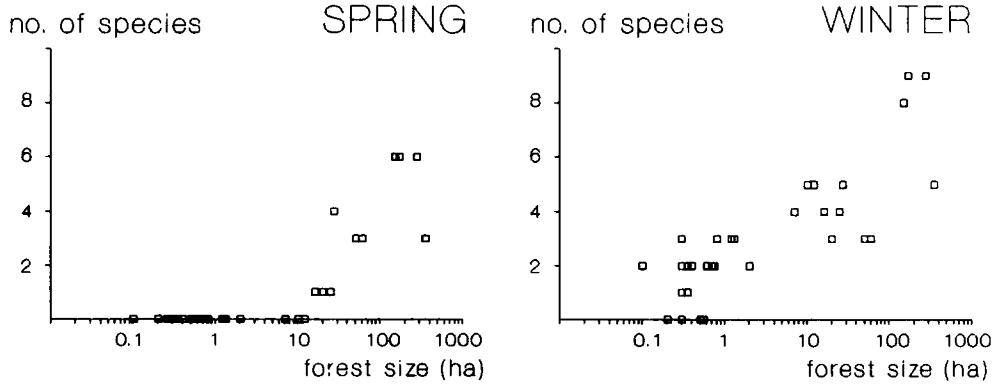

Fig. 1. Relationship between the number of species (S) and forest size (FS) in spring ($S = -2{\cdot}25 + 1{\cdot}36 \log(FS)$, $r = 0{\cdot}75$, $p < 0{\cdot}05$, $n = 31$) and winter ($S = 0{\cdot}13 + 2{\cdot}89 \log(FS)$, $r = 0{\cdot}81$, $p < 0{\cdot}001$, $n = 31$).

Table 2. Mean densities and standard error (no. birds/10 ha T) according to ranges of forest sizes

Mean densities reached in winters 1988–89 and 1989–90 indicated in brackets. Results are given for the ANOVA performed on the distribution of mean densities, transformed logarithmically, between ranges (F), and also for the Wilcoxon test (Z) used to compare the differences in the community structure between winters.

Forest size No. of forests	< 10 ha 19	10–100 ha 8	> 100 ha 4	 ANOVA
P. caeruleus	4·35±1·66 (3·68–5·48)	2·41 ± 0·55 (2·71–2·15)	2·80 ± 0·29 (3·12–2·43)	F = 0·08 NS
P. major	0·18 ± 0·10 (0·32–0·05)	1·39 ± 1·15 (1·09–1·68)	1·15 ± 0·49 (1·40–1·13)	F = 12·34***
P. cristatus	0	0·06 ± 0·006 (0–0·14)	0·70 ± 0·24 (0·63–0·78)	F = 23·89***
P. ater	0	0	0·15 ± 0·10 (0·00–0·30)	F = 10·36***
A. caudatus	0	0·80 ± 0·44 (0·66–0·94)	0·73 ± 0·31 (1·13–0·28)	F = 6·61***
R. ignicapillus	12·02 ± 3·25 (11·1–12·99)	7·21 ± 0·93 (7·69–7·95)	6·30 ± 1·6 (7·35–5·28)	F = 0·04 NS
R. regulus	0·29 ± 0·21 (0·22–0·37)	0·15 ± 0·10 (0–0·28)	0·18 ± 0·10 (0·15–0·35)	F = 0·02 NS
C. brachydactyla	0	0	0·30 ± 0·13 (0·30–0·28)	F=24·16***
S. europaea	0	0·09 ± 0·09 (0·16–0)	0·40 ± 0·20 (0·78–0)	F=9·18***
Wilcoxon	Z = 0·50 NS	Z = 0·76 NS	Z = 0·67 NS	

**$p < 0·01$, *** $p < 0·001$.

Table 3. Use distribution (percentages) of substrata and species of trees by birds

Species (*n*)	Substrata[a]					Tree species[b]		
	G	T	B	A	S	H	L	J
P. caeruleus (221)	33·7	9·4	40·0	0·4	16·5	91·1	0·7	8·2
P. major (86)	67·0	5·2	15·5	2·1	10·3	85·7	0·0	14·3
P. cristatus (205)	10·0	7·0	81·1	0·0	2·0	43·2	0·0	56·8
P. ater (80)	16·7	1·2	82·1	0·0	0·0	24·2	0·0	75·8
A. caudatus (103)	3·4	0·0	79·7	0·9	16·1	52·5	37·4	10·1
R. ignicapillus (400)	8·3	1·4	81·0	5·0	1·4	83·6	0·0	16·4
R. regulus (144)	19·7	0·8	75·6	1·6	2·4	32·8	0·0	67·2
C. brachydactyla (118)	1·8	92·1	6·1	0·0	0·0	54·3	2·6	43·1
S. europaea (47)	0·0	84·8	15·2	0·0	0·0	83·0	10·6	6·4

[a] G, ground; T, trunks; B, branches; A, air; S, shrubs.

[b] H, holm oak; L, Lusitanean oak; J, juniper.

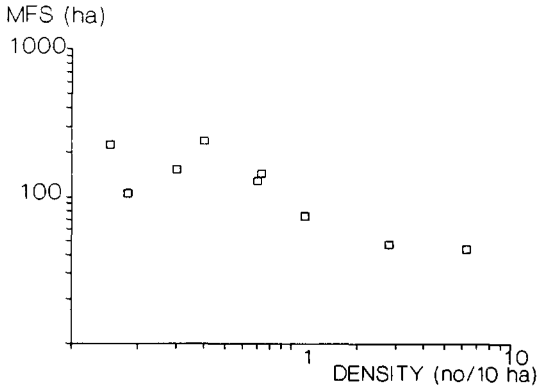

Fig. 2. Relationship between mean size of forests (MFS) occupied by the nine species and their mean density (D) in the four largest forests (log(MFS) = 1·97–0·42 log(D), r:–0·84, $p < 0·01$).

Table 4. Principal components analysis with the data in Table 3

Correlations among variables and components are shown (asterisks show significant correlations).

	PC-1	PC-2	PC-3
Ground	0·77031**	–0·17471	–0·45773
Trunks	–0·95575***	–0·08328	–0·16871
Branches	0·59340	0·36931	0·63037
Air	0·70115*	–0·42654	0·05727
Shrubs	0·47516	–0·65996	0·26466
Holm oaks	–0·09025	–0·90255***	–0·29358
Lusitanean oaks	–0·49958	–0·40290	0·71242*
Junipers	0·17362	0·95475***	–0·11067
Eigenvalue	2·8642	2·6798	1·3147
Variance	35·8	33·5	16·4
ac. variance	35·8	69·3	85·7

*$p < 0·05$, **$p < 0·01$, ***$p < 0·001$.

Table 5. Scores of species in the three components obtained in Table 4

Species	PC-1	PC-2	PC-3
P. caeruleus	0·3750	−1·1042	−0·4078
P. major	0·9090	−1·0517	−1·3642
P. cristatus	−0·0589	0·9325	0·0467
P. ater	0·3518	1·6520	0·0813
A. caudatus	−0·1162	−0·7842	2·2773
R. ignicapillus	0·8681	−0·4334	0·1498
R. regulus	0·9195	0·9138	0·1201
C. brachydactyla	−1·5316	0·4016	−0·8596
S. europaea	−1·7168	−0·5264	−0·0436

and *Regulus ignicapillus*, specialists of broad-leaved forests (Snow, 1954; Lack, 1971), segregated well along this gradient (Table 5). Finally, PC-3 generated a floristic gradient (use of Lusitanean oaks, Table 4) to which *Aegithalos caudatus* responded (Table 5).

These gradients allowed us to assess the suitability of the study habitat for each species, and to predict their abundances in large forests (> 100 ha). Given that the area of branches is higher than the area of trunks (Wilson, 1970; Jackson, 1979), foliage exploiters will have a greater availability of substrata to search for food. PC-1 thus permits a typification of the species according to this gradient of trophic resource abundance (foliage vs. trunk exploiters). Similarly, the densities of the juniper-exploiting species are limited in the study forests by the lower cover of this tree in comparison with holm oak. This gradient is described by the location of the birds along PC-2 and, with a lower explanatory value, by the use of Lusitanean oak in PC-3.

The combination of the first two components (physiognomic and floristic) in a multiple regression analysis explains a considerable proportion of the variance in the density (D) of species in the large forests: $\log(D) = 0{\cdot}18 + 0{\cdot}21\,(\text{PC-1}) - 0{\cdot}39\,(\text{PC-2})$ ($F = 5{\cdot}36$, $p = 0{\cdot}0463$ and $R^2 = 0{\cdot}64$, $n = 9$). The two components also explain a large proportion of the variance in the size of forests colonized by pariforms: $\log(\text{MFS}) = 2{\cdot}036 - 0{\cdot}139\,(\text{PC-1}) + 0{\cdot}164\,(\text{PC-2})$ ($F = 6{\cdot}50$, $p = 0{\cdot}0315$, $R^2 = 0{\cdot}68$, $n = 9$). This relationship supports hypothesis (a) by indicating that pariforms exploiting trunks and/or junipers will experience resource thresholds in the smaller fragments much sooner than the foliage and holm oak exploiters.

Nestedness

The distribution of the nine overwintering species had an apparently 'nested' structure, although four species did not fit the pattern perfectly (10 'non-fulfilments; Table 1). The 1000 Monte Carlo random simulations gave a mean + SD of 64 ± 9·4 non-fulfilments, which is significantly greater than that observed ($t = 5{\cdot}74$, d.f. = 999, $p < 0{\cdot}001$; t-test for comparison between one single value and a sample; Sokal & Rohlf, 1981). The null hypothesis that the observed pattern could occur by chance is therefore rejected.

DISCUSSION

Habitat selection plays an important role in structuring bird communities (Cody, 1985; Wiens, 1989) and our results support the hypothesis that it is also important in determining species distribution in fragmented forests (Harrison *et al.*, 1988). The floristic and physiognomic composition of the forests are two groups of variables that usually synthesize the set of environmental requisites of forest birds (Holmes & Robinson, 1981; Robinson & Holmes, 1984). They are good predictors of pariform abundance and the species' ability to occupy forest fragments during winter. During the breeding period, these relationships are likely to be accentuated by the need to select nesting sites and the rising food demand during breeding. They are, indeed, demonstrated in the 'nested' pattern observed for the species distribution in spring (Table 1).

The case of wintering pariforms in Mediterranean forests in central Spain shows that the parallel increase in species numbers and forest size is the result of a gradual increase in the amount of resources available for those species with more selective habitat requirements. These were the trunk exploiters — Blake (1977) and Fremark and Merriam (1986) have shown similar patterns for forest birds in North American woodlots — and the specialists in the exploitation of a scarce tree species (juniper). This relationship between the habitat selection and distribution patterns of species among habitat patches of different size explains the existence of nested groups of species with similar feeding or breeding behaviour. This does not lead to random combinations of species in the fragments, but rather to an orderly grouping (Bolger *et al.*, 1991).

Human management may further accentuate the paucity of resources naturally scarce in habitat patches. In central Spain, many holm oak forests have changed their physiognomy and floristic composition through human pressure (Costa *et al.*, 1990). Fire, logging and firewood extraction have replaced the original forests by a predominantly shrubby vegetation, dominated by holm oak, and in which juniper has become increasingly rare due to its traditional usage for furniture and building construction in rural areas (Ceballos & Ruiz, 1979). These forests are thus suboptimal habitats for species adapted to exploit old trees or junipers. This is the reason why pariforms have low abundance in the larger woodlots and fail to use the small fragments in which these resources are under some critical threshold.

These results emphasize the need to intensify the study of habitat suitability when investigating the distribution of species in fragmented habitats or deciding on management strategies for conservation. Much work has been done on the role of 'stepping-stone' fragments and corridors for increasing the dispersal ability of isolated populations, with a view to reducing the risk of extinction (the 'rescue effect' of Brown & Kodric-Brown, 1977; see also Wiens, 1989; Opdam, 1990; Shafer, 1990). However, little attention has been explicitly paid to ways of reducing the known environmental deterioration of fragments (Wilcox, 1980) through habitat manipulation, a common method for species management (Morrison *et al.*, 1992). This may open the possibility of increasing the densities of fragmented populations under a special recovery plan, an alternative form of guaranteeing their survival when the area cannot be increased or the protected fragments cannot be connected. As discussed by Robbins *et al.* (1989) and Simberloff and Martin (1991), the applied conclusions of fragmentation studies have focused almost exclusively on the design of reserves aimed at hosting the largest possible number of species linked to the protected habitat, without considering other possible strategies. The real needs in many countries, however, tend to require steps to safeguard individual endangered species (Simberloff, 1988) that could benefit from habitat manipulation in the protected fragments.

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