

Nested patterns of species distribution and winter flock occurrence of insectivorous birds in a fragmented landscape¹

Esteban FERNÁNDEZ-JURICIC, Department of Ecology, Evolution & Behavior, University of Minnesota, 100 Ecology Building, 1987 Upper Buford Circle, St. Paul, Minnesota 55108-6097, U.S.A., e-mail: estebanfj@yahoo.com

Abstract: The goal of this paper is to evaluate whether the probabilities of aggregating in flocks are dependent on the patterns of species distribution across the landscape. I analyzed winter species distribution and flock occurrence (flock formation in a given fragment) at the community and individual species levels of a guild of small insectivorous birds in a fragmented landscape. Species distributed following a nested pattern, which was mainly affected by fragment size. Flock occurrence (single- plus mixed-species flocks) followed a nested pattern, such that the probability of joining flocks was affected by the distribution of species across the landscape. However, when analyzed separately, single-species flock occurrence showed a nested pattern, but mixed-species flock occurrence followed a random pattern. Fragment size and total bird density (as an indicator of the availability of individuals to join flocks) accounted for nestedness. At the individual species level, conspecific and heterospecific densities were the foremost factors increasing flock occurrence probabilities, suggesting that species tended to aggregate when there was an increase in the local availability of individuals. Fragment size and habitat structure (coniferous cover and number of thick trees) also increased flock occurrence, likely because of higher resource availability, which allowed the colonization of more species and individuals. Greater isolation reduced flock occurrence, maybe as a result of lower availability of individuals in distant fragments. Overall, fragmentation conditions can disrupt flocking behaviour of small insectivorous species, which could decrease survival and increase predation risk during winter.

Keywords: nestedness, flock occurrence, fragmentation, insectivorous birds, winter flocks.

Résumé : Cet article a pour but d'évaluer si les probabilités d'agrégation d'une volée d'oiseaux dépendent des patrons de répartition de l'espèce dans le paysage. J'ai étudié la répartition hivernale et la présence de volées (dans un fragment donné) de petits oiseaux insectivores se déplaçant dans un paysage fragmenté. Les données ont été analysées pour l'ensemble de la communauté aviaire et pour chaque espèce. Les espèces se répartissaient selon un patron emboîté qui était principalement affecté par la taille du fragment. La présence des volées (formées d'une seule ou de plusieurs espèces) suivait un patron emboîté, de telle façon que la probabilité pour un individu de se joindre à une volée était affectée par la répartition des espèces dans le paysage. Néanmoins, j'ai remarqué dans des analyses séparées que les volées composées d'une seule espèce suivaient un patron emboîté, alors que celles composées de plusieurs espèces présentaient un patron aléatoire. La taille du fragment et la densité totale d'oiseaux (indicateur de la possibilité pour les individus de se joindre à une volée) pouvaient expliquer l'emboîtement. Pour une espèce donnée, la densité des congénères et celle des oiseaux toutes espèces confondues étaient les principaux facteurs d'accroissement des probabilités de formation de volées. Cela suggère que les espèces étaient plus susceptibles de se réunir lorsqu'il y avait une augmentation du nombre d'individus. Il y avait davantage de volées qui se formaient lorsque les fragments étaient de grande taille et lorsqu'il y avait un couvert forestier coniférien constitué de gros arbres, probablement parce qu'il y avait davantage de ressources. Une plus grande disponibilité des ressources permettrait la venue de plusieurs espèces et individus au sein du fragment. Par ailleurs, l'isolement du fragment nuisait à la formation de volées, probablement en raison d'une plus faible disponibilité des individus dans les fragments éloignés. Dans l'ensemble, on peut dire que les caractéristiques de la fragmentation peuvent désorganiser le comportement des volées des petits oiseaux insectivores, ce qui peut entraîner une diminution de la survie et une augmentation des risques de prédation pendant l'hiver.

Mots-clés : emboîtement, formation de volées, fragmentation, oiseaux insectivores, volées hivernales.

Introduction

Habitat fragmentation affects community structure in such a way as to form subsets of species with respect to communities in unfragmented habitats (reviewed in Boecklen, 1997; Wright *et al.*, 1998). Such nested structure is also visible within fragments, where communities in small remnants are often subsets of communities in large remnant forests (Worthen, 1996; Boecklen, 1997; Wright *et al.*, 1998). Insectivorous birds are particularly sensitive to fragmentation conditions, probably due to their high habitat specificity (Canaday, 1996; Tellería & Santos, 1997; Ford *et al.*, 2001), low vagility (Belisle, Desrochers & Fortin, 2001; Sekercioglu *et al.*, 2002), and preference for interior

areas of forest fragments (Fernández-Juricic, 2001a; Rodewald & Yahner, 2001). Recent evidence shows that variation in fragment size and resource availability may bring about nested patterns in the distribution of insectivorous species across fragmented landscapes (Tellería & Santos, 1995; Miller & Cale, 2000).

Fragmentation conditions can also modify the behaviour of individuals (Lima & Zollner, 1996; Yahner & Mahan, 1997). For instance, as species disappear from increasingly smaller forest fragments, insectivorous species modify their foraging behaviour by switching prey targets (Miller & Cale, 2000) and their scanning behaviour by increasing the time spent vigilant in winter flocks with lower abundance of flock-mates (Tellería *et al.*, 2001).

Since the probabilities that individuals aggregate in flocks are dependent upon the presence of conspecifics and heterospecifics within fragments (Tellería & Santos, 1995), I hypothesize that flock occurrence (defined as the formation of flocks in a given fragment) is affected by the pattern of species distribution across a fragmented landscape. If species distribution follows a nested pattern, then flock occurrence is expected to be nested as well; that is, the probability that species aggregate in flocks would be related to their distributional patterns across the landscape. Moreover, the factors that modify species distribution (fragment size, isolation, habitat structure, etc.) could also affect flock occurrence. For instance, as the density of conspecifics and heterospecifics (as an indicator of the availability of individuals to join flocks in fragments) increases, the probabilities of single- and mixed-species flock occurrence are expected to increase (Latta & Wunderle, 1996; Yaukey, 1996; Maldonado-Coelho & Marini, 2000; Tellería *et al.*, 2001). An increase in fragment size would raise species occurrence probabilities of species with particular habitat requirements (Tellería & Santos, 1995), which could enhance their involvement in single- and mixed-species flocks (Maldonado-Coelho & Marini, 2000; Tellería *et al.*, 2001). Conversely, isolation and habitat structure may modify flock occurrence because distant and low quality fragments have lower probabilities of being occupied (Tellería & Santos, 1995; 1997; Develey & Stouffer, 2001; Sekercioglu *et al.*, 2002) and fewer species and individuals are expected to join flocks (Fernández-Juricic, 2000a).

This paper studies winter flock occurrence of a guild of insectivorous birds in a fragmented landscape and examines how the distribution of species may influence flock formation. A previous study (Fernández-Juricic, 2000a) examined the effect of area and habitat structure upon flocking behaviour. In the present study, I am interested in analyzing whether the output of this behavioural process is affected by the pattern of species occurrence (and the associated factors). Firstly, I determined the degree of nestedness in species distribution and its explanatory factors. Secondly, I measured how nestedness affected flock occurrence and which factors accounted for such patterns for the entire set of species, considering first single- plus mixed-species flocks and then the two flock types separately. Such an approach is designed to detect differences in aggregation patterns at different levels of social organization, taking into account conspecifics as well as heterospecifics. I considered social (conspecific and heterospecific density), landscape (fragment size and degree of isolation), and habitat structure factors. Thirdly, I determined the relative contribution of these factors on the probabilities of flock occurrence for individual species.

Methods

STUDY AREA, BIRD, AND FLOCK SURVEYS

The study was conducted in the city of Madrid (Spain) in 23 wooded parks ranging from 0.23 ha to 118 ha during the 1998 winter. These parks were distributed throughout the whole city and were considered forest fragments imbedded in an urban matrix (Fernández-Juricic, 2000b). All parks had areas of watered grass, shrub cover, and a mix of deciduous and coniferous trees (for a complete description

of the parks, see Fernández-Juricic, 2000b). Many authors have employed urban fragments as natural laboratories for ecological research (Crooks & Soulé, 1999), mainly because ecological patterns and processes in urbanized areas are similar to those of other natural habitats (McDonnell & Pickett, 1990; Fernández-Juricic & Jokimäki, 2001). In Madrid, for instance, bird species in wooded parks are affected by factors (area, habitat structure, etc.) similar to those of other fragmented landscapes (Fernández-Juricic, 2000b,d).

I sampled the number and density of small insectivorous passerines that gather in flocks during the winter, including species of the following genera: *Parus*, *Aegithalos*, *Certhia*, *Regulus*, *Phylloscopus* (Ulfstrand, 1977). Each park was surveyed from 0700 to 1030, over a total of 6 visits (January-February). The following seven species were the only small insectivorous birds present in the wooded parks sampled: great tit (*Parus major* L.), blue tit (*Parus caeruleus* L.), coal tit (*Parus ater* L.), long-tailed tit (*Aegithalos caudatus* L.), chiffchaff (*Phylloscopus collybita* Vieillot), firecrest (*Regulus ignicapillus* Temminck), and treecreeper (*Certhia brachydactyla* Brehm). I recorded the number of individuals seen and displaying vocal behaviours, along with the occurrence of single- and mixed-species flocks, in 100 m × 50 m fixed-line transects (details in Fernández-Juricic, 2000a). Individuals within 25 m at each side of the observer were recorded separately from individuals beyond the main belt. To calculate densities, I used 0.5 ha as the unit measurement and averaged the number of birds in each transect throughout all visits. Final figures were, however, expressed as number of individuals in 10 ha to facilitate comparisons with other studies. The number of transects per park was established in relation to a logarithmic scale of its size. The mean number of transects per park size category was as follows: parks > 30 ha: 76.09 ± 6.34 transects ($n = 2$); parks 10-29 ha: 27.77 ± 8.79 transects ($n = 5$); parks 2-9 ha: 7.12 ± 2.67 transects ($n = 6$); parks < 2 ha: 1.49 ± 0.32 transects ($n = 5$). In five parks (Plaza de Toros, Peñuelas, Joan Miro, Pa. Sanchez Camara, and Tirso Molina), I sampled the whole park employing an amount of time proportional to that used in line transects (for similar survey procedures, see Tellería & Santos, 1995), because their spatial configuration and size did not allow the use of line transects. In these cases, the calculation of density was based on the total area of the fragment, which could have the effect of inflating density estimates (Haila, 1988). However, I deemed the potential effects on the dependent variables negligible, as only two out of the five parks were occupied by these species, and their densities were within the range of values usually encountered in this landscape. A similar criterion was also followed in previous studies in the same habitat (Fernández-Juricic, 2000a,b,c,d). For the analyses of flock occurrence at the individual species level, I calculated for each species the density of conspecifics (number of individuals of the focal species per 10 ha) and the density of heterospecifics (number of individuals of the other six species per 10 ha) in each fragment.

I considered flocks of at least two individuals. Birds were regarded as being members of flocks when they were recorded foraging with one or more individuals of the same or different species during the time I moved across the tran-

sect. When birds were detected flying among trees, I slowed down until I determined whether individuals kept moving together or perched in a tree to forage. The time spent checking the membership of an individual in a flock varied from 30 seconds to 120 seconds. The criterion used to determine flocks followed that of previous studies conducted in fragmented habitats with similar ranges of fragment size (Fernández-Juricic, 2000a; Tellería *et al.*, 2001).

LANDSCAPE AND HABITAT FACTORS

In the present study, I did not examine predation risk as a causal factor. A study conducted in the same landscape showed that the density of small insectivorous birds during winter is mainly determined by the local availability of resources rather than by predation (Fernández-Juricic *et al.*, unpubl. data). I therefore deemed predation effects to be negligible at the scale at which this study was conducted. It has been previously shown that flock size in this habitat was affected by fragment size, isolation from regional source areas, and habitat structure (Fernández-Juricic, 2000a). Even though that study was focussed on the local behaviour of flocks, those factors were also considered in the present study to assess their influence on the probabilities of flock occurrence. Fragment size was taken from the last edition of the official catalogue of the Municipality of Madrid. Casa de Campo, a 1,722-ha forest fragment immediately north-west of the city of Madrid, was regarded as a source area, since it was representative of the regional pool of species (Fernández-Juricic, 2000b). The city of Madrid has three structurally and functionally different elements: urban matrix, wooded streets, and wooded parks. Wooded streets appear to function as corridors increasing the general connectivity of the landscape (Fernández-Juricic, 2000c). I determined the degree of regional isolation on a 1:20,000 map by means of two measures of isolation aimed at reflecting not only structural, but also functional properties of the landscape (Tischendorf & Farig, 2000). The first was the straight-line distance between a focal park and Casa de Campo (Distance to Source Area 1, DSA1). This measure assumed that all landscape elements (urban matrix, other parks, and corridors) between the focal park and Casa de Campo were of lower quality (Figure 1a). The second measure was the distance between a focal park and Casa de Campo considering only the urban matrix (Distance to Source Area 2, DSA2, Figure 1b). This latter measure assumed that other parks and corridors were elements that could facilitate the movement of individuals through the landscape by being used as stepping-stones; consequently, they were not included in the estimation of distance between the focal points (Figure 1b).

Habitat structure variables were measured in 25-m radius circular plots located in the same areas in which bird surveys were conducted (Tellería & Santos, 1997). The mean number of plots per park size category was as follows: parks > 30 ha: 59.76 ± 10.01 plots ($n = 2$); parks 10-29 ha: 22.43 ± 5.33 plots ($n = 5$); parks 2-9 ha: 6.90 ± 1.87 plots ($n = 6$); parks < 2 ha: 1.39 ± 0.41 plots ($n = 10$). Cover variables were visually estimated (Prodon & Lebreton, 1981). Vegetation traits included shrub cover, shrub height, number of shrub species, coniferous cover, deciduous cover, number of tree species, tree height, and number of

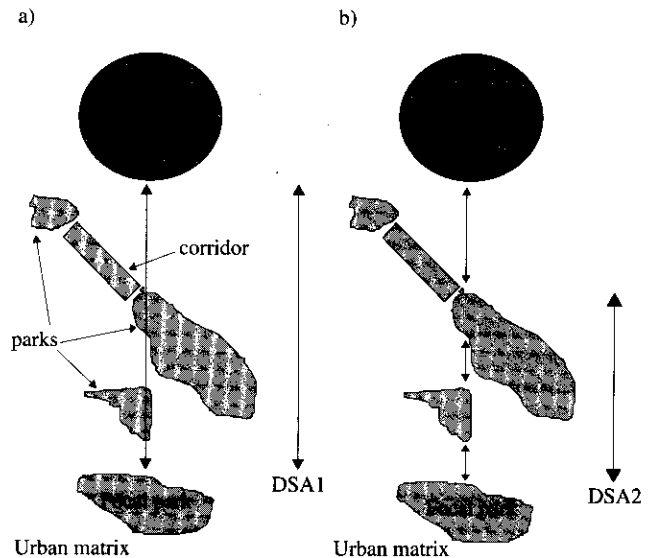


FIGURE 1. Measures of isolation used in the present study. a) Distance from a focal park to source area 1 (DSA1) considers all landscape elements in-between (urban matrix, other parks, and corridors) as similar and having lower quality than the focal park. b) Distance from a focal park to source area 2 (DSA2) takes into account only those landscape elements of putatively lower quality (urban matrix), as other parks and corridors could be used as stepping-stones to ease movements through the landscape.

stems < 10 cm, 10-30 cm, 30-50 cm, and > 50 cm diameter at breast height (d.b.h.). All cover variables corresponded to different vegetation substrates. To reduce the number of vegetation structure variables to a few factors, I performed a principal component analysis (PCA). Since the number of sample plots per park category differed (see number of bird survey transects per fragment size above), I included in the analysis the averaged values of every vegetation trait in each park. A correlation matrix was employed because variables were on different measurement scales. Only those PCA factors with eigenvalues > 1 were selected (Kaiser criteria), and the factor loadings were rotated with a varimax raw transformation. The PCA generated four significant components (Table I). PC1 referred to shrub cover and height. PC2 correlated negatively with number of stems < 10 cm d.b.h. and positively with tree height and number of stems > 50 cm d.b.h., *i.e.*, tall, large trees. PC3 correlated negatively to coniferous cover, whereas PC4, positively to number of stems 10-30 cm d.b.h. These four factors were included as explanatory variables in the analysis of flock occurrence.

STATISTICAL ANALYSES

Before determining the relationships between species distribution and flock occurrence, I explored possible correlations between explanatory variables. I also related species richness to the explanatory factors to find out which accounted for the accumulation of species in this landscape. All these relationships were determined using Pearson product moment correlations. Since the sampling effort varied somewhat between large and small parks, I estimated species richness across fragments using rarefaction procedures by standardizing for equal sampling effort (Rathbun, 1981).

To assess whether species distribution affected flock occurrence, I conducted analyses of nestedness, which are

TABLE I. Factor loadings of the individual variables obtained by a principal component analysis on the vegetation structure of 23 wooded parks in the city of Madrid. Significant correlations between variables and factors are marked with *. d.b.h., diameter at breast height.

	Factor 1	Factor 2	Factor 3	Factor 4
Shrub cover	0.872*	0.079	-0.158	-0.154
Number of shrub species	0.698	-0.217	0.370	0.207
Shrub height	0.746*	0.275	-0.137	0.120
Coniferous cover	0.218	0.131	-0.882*	0.260
Deciduous cover	0.364	0.317	0.653	0.488
Number of tree species	0.574	0.166	0.067	0.125
Tree height	0.237	0.839*	0.093	0.216
Number of stems < 10 cm d.b.h.	0.198	-0.796*	0.328	-0.057
Number of stems 10-30 cm d.b.h.	-0.022	0.010	-0.116	0.951*
Number of stems 30-50 cm d.b.h.	-0.026	0.562	0.308	-0.299
Number of stems > 50 cm d.b.h.	0.285	0.703*	0.052	-0.238
Eigenvalues	3.124	1.965	1.613	1.330
Variance (% total explained)	28.399	17.865	14.660	12.088
Cumulative Variance (%)	28.399	46.265	60.925	73.013

aimed at determining a) whether the distribution of a set of species across a landscape follows a random or hierarchical order and b) the factors that may account for nested distributions. Generally, in assessing nestedness, different methods calculate the statistical significance of metrics based only on presence/absence data (reviewed in Wright *et al.*, 1998; but see also Lomolino, 1996; Brualdi & Sanderson, 1999). A recent paper (Sfenthourakis, Giokas & Mylonas, 1999) evaluated two of the most used procedures: the “temperature” method of Atmar and Patterson (Atmar & Patterson, 1993; 1995) and the “departures” method of Lomolino (Lomolino, 1996), concluding that the former is more suitable for evaluating nestedness. Therefore, I first analyzed nestedness with the “temperature” method, which compares the observed distribution of species to that expected under maximum nestedness. This procedure identifies unexpected presences and absences, which are regarded as sources of disorder or entropy in the species assemblage. The Nestedness Calculator software (Atmar & Patterson, 1995) yields the temperature of the matrix (response variable), which is a thermodynamic-like metric reflecting the degree to which a species assemblage deviates from perfect nestedness. A perfectly nested assemblage would have 0°, whereas one that deviates from nestedness (more unexpected presences and absences) would increase its temperature, up to 100°, which would reflect an assemblage of species distributed randomly (see calculation details in Atmar & Patterson, 1995; Patterson & Atmar, 2000). The significance of nestedness was assessed with Monte-Carlo-derived probability (Atmar & Patterson, 1995). The observed temperature was compared to that of 1,000 random matrices in order to obtain a Z score that would indicate the probability that the observed temperature falls outside the range of simulated scores (Patterson & Atmar, 2000). In analyzing nestedness in species distribution (objective 1) and flock occurrence (objective 2), I set up presence/absence matrices that included the species present in each fragment and those species recorded in flocks (single-species and mixed-species, data available from author upon request). Individual species, arranged in columns, were ranked by decreasing occurrence proceeding right, whereas fragments were ordered by decreasing occurrence from top to bottom.

The second part of the nestedness analysis included the assessment of explanatory factors that accounted for the

hierarchical order in species distribution. I analyzed the role of the following factors in determining nestedness of species distribution (objective 1) and flock occurrence (objective 2): fragment size, DSA1, DSA2, PC1, PC2, PC3, and PC4. Total bird density was included as an explanatory factor in the analyses of flock occurrence. To validate results the temperature and departures procedures were performed, as they are computed differently (Lomolino, 1996; Patterson & Atmar, 2000). With the temperature procedure, I correlated, with a Spearman rank correlation, the ranking order of fragments in the observed matrix (arranged to maximize nestedness; Patterson & Atmar, 2000) with the order of fragments after re-arranging the matrix in relation to the aforementioned explanatory factors. A significant correlation would suggest that species are packed in a predictable order owing to the influence of a given factor (Patterson & Atmar, 2000). The departures method is not correlational; it measures nestedness of matrices ordered by different explanatory variables and then compares these scores to those generated for randomly ordered matrices (Lomolino, 1996). I sorted species distribution and flock occurrence matrices according to the explanatory factors and then determined the unexpected presences of species (or departures). Statistical significance was expressed as the proportion of 1,000 simulations with departure values less than or equal to that of the observed matrices (Lomolino, 1996). It is noteworthy that the departures procedure also enables determination of the relative importance of factors in nestedness by analyzing the effect of one factor after controlling for the effect of the other (Lomolino, 1996). Consequently, those factors that were found to significantly account for nestedness were analyzed in combinations to assess their relative contribution. To that end, for each departure in the matrix ordered by one variable, I counted the number of departures that can be accounted for by the relative change in the second variable (Lomolino, 1996). For instance, when analyzing fragment size and total bird density, I determined the number of departures not explained by area that could be affected by density: absent to present due to increasing density. The significance of the departures combining two factors was evaluated with a binomial test (Lomolino, 1996).

To determine the influence of independent factors on flock occurrence of individual species (objective 3), I per-

formed multiple stepwise logistic regressions, which estimated the dependency of a dichotomous variable (presence/absence of flocks) from a set of independent traits (Hosmer & Lemeshow, 1989). Fragment size, DSA1, DSA2, PC1, PC2, PC3, PC4, and conspecific density were included in the analyses of single-species flocks, whereas heterospecific density was incorporated when analyzing mixed-species flock occurrence.

Because of the high number of probability estimations, I conducted a correction to circumvent the effect of increasing the probability of Type I error. Several types of corrections have been suggested (Wright, 1992); however, many of them are so stringent that they risk increasing Type II errors (decreasing the power of individual tests) (Chandler, 1995). To overcome this problem, I followed a two-tiered approach. I first identified groups of related tests (following Chandler, 1995), and then I performed a less conservative correction (Sidák correction; Wright, 1992) of each of them. Within each group, p -values (p_i) were first ordered so that $p_1 < p_2 < \dots < p_n$, and then each p_i was sequentially adjusted to $p_{i(Sidák)} = 1 - (1 - p_i)^{(n-i+1)}$, where n is the number of p -values in each group of tests (Wright, 1992).

Results

CORRELATION BETWEEN INDEPENDENT FACTORS

Some independent variables were correlated significantly: fragment size ($\log x_{+1}$) and total bird density ($r = 0.57, P < 0.01$), and DSA1 and DSA2 ($r = 0.96, P < 0.001$). The other correlations were not significant (r varied from -0.22 to 0.41, $P > 0.05$).

SPECIES RICHNESS AND DISTRIBUTION

Species richness (total number of species within fragments) correlated positively with fragment size ($r = 0.49, P < 0.05$). The other independent factors (DSA1, DSA2, PC1, PC2, PC3, and PC4) did not affect species richness (r varied from -0.37 to 0.34, $P > 0.05$). The distribution of species was highly nested ($T^{\circ}_{obs} = 9.00, T^{\circ}_{rand} = 42.57, SD = 9.04, P < 0.001$). This pattern was only affected by fragment size (Table II), such that species sequentially accumulated in increasingly larger fragments.

FLOCK OCCURRENCE AT THE COMMUNITY LEVEL

As for single- plus mixed-species flocks, I found that flock occurrence was nested ($T^{\circ}_{obs} = 9.3, T^{\circ}_{rand} = 44.17, SD = 8.46, P < 0.001$), such that the probabilities of occurrence of flocks were dependent on the distribution of species across the landscape. According to the temperature method, two factors accounted for nestedness: fragment size and total bird density (Table III). The same results were obtained with the departures method (Table III). When fragment size effects were factored out, total bird density still explained nestedness (proportion of departures explained by total bird density = 0.93, $P < 0.01$). However, separate analyses of single- and mixed-species flocks yielded different results.

Flock occurrence showed a higher degree of nestedness in single-species flocks ($T^{\circ}_{obs} = 4.72, T^{\circ}_{rand} = 45.74, SD = 8.29, P < 0.001$). The temperature and the departure methods identified the same explanatory factors: fragment size and total bird density (Table III). When analyzed simultaneously, I found that after controlling for the effects

TABLE II. Explanatory factors for species distribution. In the temperature procedure, Spearman r and its associated probability (in parenthesis) are shown, indicating the correlation of the observed nested matrix with each independent factor. In the departures procedure, number of departures in the ordered matrix and the proportion of random runs with fewer departures (P in parenthesis) for 1000 permutations are shown. P -levels were adjusted with a Sidák correction. Abbreviations: DSA1, distance to source area considering urban matrix, wooded streets, and urban parks; DSA2, distance to source area considering only the urban matrix; PC1-4 as in table I (see text).

	Temperature method	Departures method
Area	0.89 (<0.001)	15 (<0.001)
DSA1	0.32 (0.358)	31 (0.805)
DSA2	0.38 (0.142)	33 (0.883)
PC1	-0.30 (0.507)	34 (0.977)
PC2	0.27 (0.715)	36 (0.999)
PC3	0.31 (0.394)	32 (0.943)
PC4	0.15 (0.976)	36 (0.999)

TABLE III. Explanatory factors for single- plus mixed-species flock occurrence (S&M-species flocks) and for single-species flock occurrence (S-species flocks). In the temperature procedure, Spearman r and its associated probability (in parenthesis) are shown, indicating the correlation of the observed nested matrix with each independent factor. In the departures procedure, number of departures in the ordered matrix and the proportion of random runs with fewer departures (P in parenthesis) for 1,000 permutations are shown. P -levels were adjusted with a Sidák correction. Abbreviations: DSA1, distance to source area considering urban matrix, wooded streets, and urban parks; DSA2, distance to source area considering only the urban matrix; PC1-4 as in table I (see text).

	Temperature method	Departures method
S&M-SPECIES FLOCKS		
Fragment size	0.87 (<0.001)	13 (<0.001)
DSA1	-0.30 (0.714)	33 (0.109)
DSA2	-0.36 (0.382)	35 (0.841)
PC1	0.33 (0.537)	38 (0.983)
PC2	0.38 (0.283)	40 (0.999)
PC3	-0.41 (0.153)	31 (0.999)
PC4	0.21 (0.961)	36 (0.998)
Total bird density	0.84 (<0.001)	19 (<0.001)
S-SPECIES FLOCKS		
Area	0.85 (<0.001)	12 (<0.001)
DSA1	-0.33 (0.385)	24 (0.109)
DSA2	-0.31 (0.565)	30 (0.841)
PC1	0.38 (0.198)	32 (0.983)
PC2	0.24 (0.899)	36 (0.999)
PC3	-0.11 (0.999)	34 (0.999)
PC4	0.29 (0.665)	33 (0.998)
Total density	0.89 (<0.001)	15 (<0.001)

of fragment size, departures were significantly accounted for by total bird density (proportion of departures explained by total bird density = 0.92, $P < 0.01$).

Flock occurrence of mixed-species flocks turned out to be random instead of nested ($T^{\circ}_{obs} = 27.02, T^{\circ}_{rand} = 39.77, SD = 9.97, P = 0.101$): the probabilities of mixed-species flock occurrence were not related to the distribution of species in the landscape.

FLOCK OCCURRENCE AT THE SPECIES LEVEL

Since the nested patterns of flock occurrence of single- and mixed-species flocks differed, I performed analyses for

both flock types separately at the species level. Flock occurrence of only one (treecreeper) of the seven species could not be modelled, owing to the low number of fragments in which flocks were recorded. Conspecific density was the main factor accounting for the probabilities of single-species flock occurrence of chiffchaffs, coal tits, long-tailed tits, blue tits, great tits, and firecrests (Table IV). In the case of coal tits and great tits, DSA2 negatively affected flock occurrence. Fragment size increased flock occurrence probabilities of two species (blue tit and great tit); coniferous cover (PC3, coal tit) and number of stems 10-30 cm d.b.h. (PC4, chiffchaff) also increased flock occurrence probabilities (Table IV).

Regarding mixed-species flocks, conspecific density increased flock occurrence probabilities of three species: long-tailed tit, blue tit, and firecrest (Table IV). Heterospecific density positively affected flock occurrence of chiffchaff, coal tit, and great tit (Table IV). Fragment size was another important factor, influencing mixed-species flock occurrence of coal tit, long-tailed tit, and great tit (Table IV). DSA1 decreased flock occurrence probabilities of great tits, whereas tree height and the number of stems > 50 cm d.b.h. (PC2) and coniferous cover (PC3) increased flock occurrence of firecrests and chiffchaffs, respectively.

Discussion

Small insectivorous species followed a nested distributional pattern in this landscape mainly determined by fragment size, whereby species present in small fragments were subsets of those in larger fragments. Flock occurrence also followed a nested pattern, suggesting that the loss of species due to fragmentation affected the probabilities of species joining flocks within fragments. This pattern was related to both the area of fragments and the density of individuals, indicating that the probabilities of flock occurrence increased with fragment size and with the availability of conspecifics and heterospecifics. When analyzed separately, single-species flock occurrence showed a nested pattern as well; however, mixed-species flocks followed a random pattern. Hence, the probabilities of aggregating in mixed-species flocks were independent of the distribution of

species across the landscape. A possible interpretation is that mixed-species aggregations are related to the occurrence of environmental features that are commonly required by different species and that are distributed irrespective of the size of fragments. Species may then switch their foraging needs when joining mixed-specific flocks regardless of flock composition.

Conspecific density was by far the foremost factor increasing single-species flock occurrence probabilities. When density increases within a given fragment, two possible outcomes are that individuals tend to separate due to intra-specific competition (moving to other fragments [Fernández-Juricic, 2001b], increasing territorial segregation [Newton, 1998]) or that they aggregate in foraging groups, which would decrease or increase, respectively, flock occurrence probabilities (Tellería *et al.*, 2001). In this system, the availability of conspecifics raised the probabilities of aggregation in foraging flocks in six of the seven species studied. Likewise, for chiffchaffs, coal tits, and great tits, more individuals from other species increased the chances of aggregation in mixed-species flocks. A previous study in Madrid showed that individuals preferred to associate with the most abundant species within fragments (Fernández-Juricic, 2000a), suggesting that social facilitation mechanisms may account for flock occurrence patterns (Yaukey, 1996; Maldonado-Coelho & Marini, 2000). Actually, local enhancement can play an important role in increasing the probabilities of fragment occupation (Smith & Peacock, 1990; Pöysä, 1992), as the presence of conspecifics and heterospecifics may affect habitat selection processes (Mönkkönen, Forsman & Helle, 1996; Mönkkönen *et al.*, 1997; Forsman *et al.*, 1998). For instance, experimentally increased densities of resident species in boreal forests were related to an increase in the density of migrants, such that the latter might be using residents as indicators of environmental conditions (Mönkkönen, Helle & Soppela, 1990).

Fragment size could affect the aggregation in flocks by virtue of a higher availability of resources (Suhonen *et al.*, 1992; Burke & Nol, 1998; Zanette, Doyle & Trémont, 2000) and greater habitat diversity (Martin, Gaston &

TABLE IV. Logistic regression models considering flock occurrence of single- and mixed-species flocks. The table depicts the factors and their *b*-coefficients, the Chi² statistic, its probability, degrees of freedom (df), and the percentage of fragments correctly classified as occupied or unoccupied (%CC). *P*-levels were adjusted with a Sidák correction. Abbreviations: Const, constant; F size, fragment size; C Den, conspecific density; H Den, heterospecific density; DSA1, distance to source area considering urban matrix, wooded streets, and urban parks; DSA2, distance to source area considering only the urban matrix; PC1-4 as in table I (see text).

Species	Chi ²	df	<i>P</i>	%CC	Const	F Size	C Den	H Den	DSA1	DSA2	PC2	PC3	PC4
SINGLE-SPECIES FLOCKS													
Chiffchaff	18.94	2	<0.001	95.7	-3.47		0.67						0.43
Coal tit	12.53	3	0.028	82.6	0.32		0.52			-0.81		-0.09	
Long-tailed tit	19.47	1	<0.001	91.3	-4.3		1.16						
Blue tit	9.91	2	0.041	82.6	-2.67	0.25	0.46						
Great tit	23.34	3	<0.001	95.6	-2.58	0.97	1.28			-1.06			
Firecrest	10.69	1	0.004	78.3	-2.33		0.61						
MIXED-SPECIES FLOCKS													
Chiffchaff	17.19	2	<0.001	82.6	-3.41			0.2				-1.71	
Coal tit	9.86	2	0.04	73.91	-2.34	0.05		0.09					
Long-tailed tit	10.46	2	0.03	82.61	-1.83	0.49	0.54						
Blue tit	9.09	1	0.01	60.87	-1.94		0.49						
Great tit	24.99	3	<0.001	95.6	-5.28	0.27		0.35	-3.05				
Firecrest	19.36	2	<0.001	91.3	-4.1		0.95				3.58		

Hitier, 1995). Species with specific habitat requirements, like most of these small insectivores, would be able to colonise mainly large fragments (Tellería & Santos, 1997), which would increase the number of species and individuals available to join single- and mixed-species flocks (Fernández-Juricic, 2000a). Interestingly, the patterns of nest-ness in flock occurrence were not linear from large to small fragments. Flock occurrence patterns of six of the seven species began disrupting in wooded parks less than 5 ha, suggesting the existence of a threshold in the response of birds to fragmentation. Another study on the same guild of species found changes in flock size and composition in fragments less than 3 ha (Tellería *et al.*, 2001). Insectivorous species with particular habitat requirements may be the first to disappear from fragments below a critical size, due to the lack of specific resources (Tellería & Santos, 1995; Miller & Cale, 2000; Ford *et al.*, 2001; Major, Christie & Gowing, 2001), thereby affecting the pool of species that can persist and join flocks in small fragments (Fernández-Juricic, 2000a; Tellería *et al.*, 2001). Therefore, further reductions in fragment size could trigger more negative effects in terms of flocking aggregations in large fragments than in small fragments.

The degree of isolation affected two species, coal tits and great tits, decreasing flock occurrence probabilities. Recent evidence suggests that birds moving in foraging flocks do not tend to cross forest gaps (Develey & Stouffer, 2001), that movements of forest species are limited when travelling through deforested and fragmented landscapes (Belisle, Desrochers & Fortin, 2001), and that, consequently, forest boundaries act as habitat barriers, modifying flock movements (Desrochers & Fortin, 2000). In our system, moving through the urban matrix to reach more isolated fragments could have been associated to higher risk of predation or human disturbance (Fernández-Juricic, 2000c). Distant fragments could have a lower availability of individuals and species to aggregate in flocks (Fernández-Juricic, 2000a), reducing flock occurrence as a result.

Certain habitat features (coniferous cover, number of thick trees) raised the chances of flock occurrence of chifchaffs, coal tits, and firecrests, likely because of higher prey abundance during winter (Fernández-Juricic *et al.*, unpubl. data). Consequently, individuals and flocks would tend to spend more time foraging in these kinds of substrates (Fernández-Juricic, 2000a). Scarcity of foraging substrates and food resources has been found to decrease the chances of fragment occupation (Burke & Nol, 1998; Zanette, Doyle & Trémont, 2000; Ford *et al.*, 2001). For insectivorous species, food shortage in patchy habitats can have important effects on winter populations (*e.g.*, decrease in survival; McNamara, Houston & Lima, 1994) due to their habitat specificity. Such effects could become worse if different factors interact synergistically (Laurance & Cochrane, 2001), *i.e.*, food scarcity in small and isolated fragments.

What would be the ecological consequences of the disruption of flocking behaviour in fragmented landscapes? Flock formation encompasses benefits and costs associated to predation risk, variability in food resources, and availability of conspecifics and heterospecifics (Pulliam & Millikan, 1982; Pulliam & Caraco, 1984; Suhonen, Halonen & Mappes, 1993; Mönkkönen, Forsman & Helle, 1996; Dolby & Grubb, 2000; Jullien & Clobert, 2000). An

increase in the severity of fragmentation conditions can modify these aggregation trade-offs through different mechanisms (Dolby & Grubb, 1999; 2000; Fernández-Juricic, 2000a, Tellería *et al.*, 2001). For instance, insectivorous birds could perceive higher predation risk and increase their scanning behaviour in response to a scarcity of individuals to form large mixed-species flocks (Dolby & Grubb, 1998) and the absence of dominant species that fail to colonize small fragments (Tellería *et al.*, 2001). Variations in time budgets (more time being vigilant, less time foraging) in small fragments and the increasing spacing of forest patches may augment energetic demands (Dolby & Grubb, 1998; Hinsley, 2000). If such demands are not met, species inhabiting fragmented habitats could decline in body condition and survival probabilities, particularly during winter (Dolby & Grubb, 1998). Therefore, fragmented landscapes can be considered risky habitats that may imperil the local persistence of species during the non-breeding season through disruption of flocking behaviours.

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