FOREST FRAGMENTATION AFFECTS WINTER FLOCK FORMATION OF AN INSECTIVOROUS GUILD

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The purpose of this paper was to assess the effects of forest fragmentation on winter flock formation in a guild of insectivorous birds in 23 parks (0.23-118 ha) in the Madrid area, Spain. Flock size was positively affected by fragment size, the amount of coniferous cover, and the mean number of trees > 50 cm diameter at breast height; and negatively by the distance to the nearest large forest track (1722 ha). Flock richness was not affected by any landscape and habitat factor. Coefficients of associations in multi-species flocks were higher for the most abundant species. That the probabilities of flock formation decreased in small fragments is probably a result of the reduction of habitat quantity and quality. Flock formation appears greatly affected by the abundance of individual species (Chiffchaff *Phylloscopus collybita* and Coal Tit *Parus ater*), as they attract less abundant species and form the core of the winterflocks.

Key words: fragmentation - winter - flock size - flock richness - insectivorous guild

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INTRODUCTION

Flock formation is a trade-off process that encompasses benefits and costs of mono- and multi-species aggregation (Caraco & Pulliam 1980; Swenson *et al.* 1995). Feeding efficiency, predator avoidance, and heterospecific attraction have been put forward as explanations for foraging aggregations (Pulliam & Millikan 1982; Alatalo *et al.* 1985; Suhonen *et al.* 1993; Mönkkönen *et al.* 1996). Other factors can also play a role, among which are air temperature, wind speed, social status, and body condition (Hogstad 1989; Ekman 1990; Gosler 1996; Lens 1996). Yet, the modification of flocking patterns in fragmented landscapes has received little empirical consideration, even though social processes could be affected in patchy environments (Clemmons & Buchholz 1997). Flocking patterns can be studied in different ways. For example, one can consider the number of individuals in flocks irrespective of the species being present (flock size, FS), but also the number of species present within a flock (flock richness, FR). These factors are expected to vary in fragmented landscapes due to the decrease in habitat quantity and quality associated with fragmentation (Tellería & Santos 1995). The density of individual species could also influence flocking patterns (Alonso *et al.* 1987; Latta & Wunderle 1996; Jullien & Thiollay 1998), particularly in fragmented landscapes, as widespread and abundant species are bound to be the core of flocks upon which less abundant species aggregate (Hutto 1994). This paper focuses on the effects of forest fragmentation upon winter flock formation of a guild of insectivorous birds by analysing (1) the influence of landscape (area and isolation) and habitat (vegetation structure) features upon FS and FR, and (2) the association patterns of multi-species flocks. The approach of this study was not to com-

pare fragmented vs. continuous forests, but to assess how flocking patterns changed within a fragmented landscape with a large variability in fragment size, isolation, and habitat quality.

METHODS

Study area and bird surveys

The study was conducted in the city of Madrid. Scattered across an area of 95 km^2, 23 urban parks ranging from 0.23 ha to 118 ha were sampled during two consecutive winters (1997-98). All parks had both evergreen and deciduous cover, with areas of watered grasses. Each park was weekly surveyed from 0700 to 1030H, during December-February, so that a total of 6-7 visits were accumulated to determine the number and abundance of the following insectivorous species: Great Tit *Parus major,* Blue Tit *Parus caeruleus,* Coal Tit *Parus ater,* Long-tailed Tit *Aegithalos caudatus,* Chiffchaff *Phylloscopus collybita,* Firecrest *Regulus ignicapillus,* and Short-toed Treecreeper *Certhia brachydactyla.* I recorded the number of individuals seen and displaying vocal behaviours, along with the occurrence of mono- and multi-species flocks, in 100 x 50 m fixed line transects in large parks (Tellería & Santos 1995). In small fragments, birds were detected by thorough searches (Tellería & Santos 1997). In estimating density, each transect was considered a sample unit; densities were averaged considering all the visits undertaken in 1997 and 1998 at each park. I lumped the information of both winter periods, and expressed final figures as number of birds 10 ha^{-1}. Density estimations only included data from urban parks in which a particular species was present.

Landscape and habitat factors

Three types of landscape and habitat factors were considered: fragment size, isolation, and habitat structure. Fragment size was taken from the last edition of the official catalogue of the Municipality of Madrid (Anonymous 1997). Isolation was measured on a 1:10000 scale map as the following distances (km) between parks: distance to the nearest park, distance to the nearest park harbouring at least n_{+1} species, and distance to the 'mainland' (Casa de Campo), a 1722 ha forest stand located NW of Madrid. This forest fragment was considered representative of the regional pool of species in the province of Madrid (Fernández-Juricic unpubl. data), and thus a possible source of species to colonise urban parks. Habitat structure traits were measured in 25-m radius circular plots distributed at 30-m intervals along transects in large parks, and randomly in small ones (Tellería & Santos 1997). Cover variables were estimated visually (Prodon & Lebreton 1981). Vegetation traits included: shrub cover, shrub height, coniferous cover, deciduous cover, number of tree species, tree height, and number of stems < 10, 10-30, 30-50, and > 50 cm diameter at breast height. All cover variables corresponded to different vegetation substrates.

Statistical analysis

The sampling unit was each urban park, so I assessed mean flock size and mean flock richness for each of the 23 parks. In every visit, mean flock size and richness were calculated, and then averaged after the completion of all visits. Birds were considered members of flocks when they were recorded foraging with one or more individuals of the same or different species during at least 10 min (Hutto 1994). In analysing landscape and habitat factors, I first controlled for the effect of FS and FR on each other due to their correlation. For a given FS, I assessed how much of FR variability could be explained, and vice versa. Since the effect of landscape and habitat factors may have been confounded by their lack of independence (e.g. isolated parks tend to be smaller), I assessed independently their influence on FS and FR (for a similar approach see Wiggins & Møller 1997). Hence, a linear regression was performed for fragment size, and stepwise multiple regressions for factors with several levels (isolation and habitat structure). To meet normality and homogeneity of variance requirements, some independent factors were log$_{10}$-transformed (fragment size and

shrub height). In this analysis, I included isolated foragers in FS and FR since the probability that individuals joined flocks could be affected by the occurrence of any number of individuals in fragments (Tellería & Santos 1995).

Flock association patterns in multi-species flocks were analysed with a half-weight index to determine a coefficient of association (COA). This COA indicated the preference for certain species during flock aggregation, and was calculated as:

$$COA = \frac{X}{X + 1/2 \, (Ya + Yb)}$$

where X was the number of encounters that included species A and B, Ya was the number of encounters of species A without B, and Yb was the number of encounters of species B without A (Cairns & Schwager 1987). The index may range from 0 (species never seen together) to 1 (species always associated).

RESULTS

In 1997 and 1998, there was a significantly positive correlation between range size and the density of individual species (for 1997: $r = 0.82$, $P < 0.05$; for 1998: $r = 0.78$, $P < 0.05$). Densities differed among species, with Chiffchaff, Coal Tit, and Long-tailed Tit being the most abundant species (ANOVA, $F_{6, 79} = 10.13$, $P < 0.001$, Chiffchaff = 16.94 ± 10.21, Coal Tit = 6.41 ± 4.48, Long-tailed Tit = 6.23 ± 3.88, Blue Tit = 5.51 ± 3.17, Great Tit = 5.48 ± 2.64, Firecrest = 5.39 ± 3.11, Treecreeper = 1.79 ± 1.34).

FS and FR were significantly correlate ($r = 0.57$, $P < 0.01$). After partialling out the effects of FS and FR on each other, only FS variability could be explained, independently, by three factors (Table 1). Flock richness (FR) could not be modelled by any of the landscape and habitat factors considered (Table 1). Flock size, FS, (controlling for the number of species within flocks) increased with the area of the fragment (Fig. 1a), the amount of coniferous cover and the mean

Table 1. The independent effect of patch area, isolation and habitat structure upon flock size and richness of insectivorous species recorded during two consecutive winters (1997-98) in urban parks of Madrid, Spain. Parks without flocks were excluded from the regression analyses. Shown are the factors selected by the forward-stepwise regression models. (+) Since flock size and richness are highly correlated, they were previously weighted for the effect of each other. Bold: significant factors.

Flock size (+)	df	F	r^2	P
Fragment size	1,18	5.701	0.198	**0.028**
Isolation				
– Distance to the mainland	1,18	6.448	0.223	**0.021**
Habitat Structure				
– Trees > 50 cm diameter at breast height				
– Coniferous tree cover	2,17	3.692	0.223	**0.046**

Flock richness (+)	df	F	r^2	P
Patch Area	1,18	0.629	0.01	0.438
Isolation				
– Distance to nearest park				
(with n+1 species)	1, 18	0.041	0.001	0.841
Habitat Structure				
– Coniferous tree cover	1, 18	1.31	0.02	0.266

Table 2. Number of times a given individual was recorded foraging with any other individual of the same or other species, and the median of coefficients of associations (COA) of multi-species flocks.

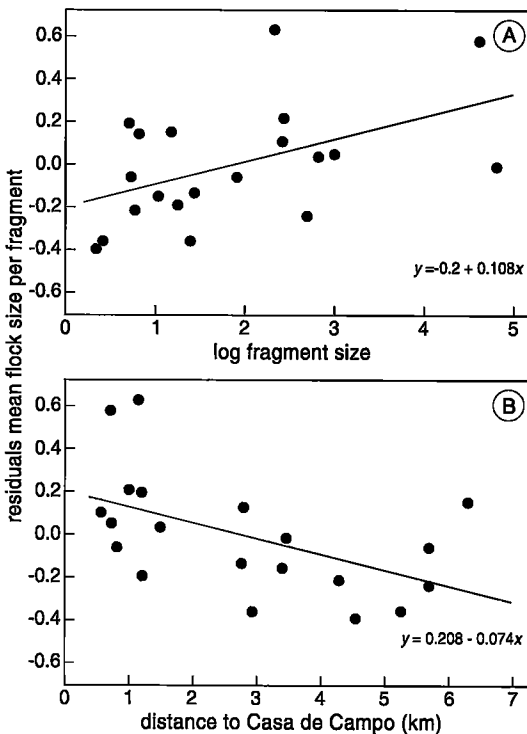|	Chiffchaff	Coal Tit	Blue Tit	Great Tit	Firecrest	Long-tailed Tit	Treecreeper
Chiffchaff	73	7	5	1	8	5	0
Coal Tit	-	22	6	2	6	4	0
Blue Tit	-	-	13	1	3	3	1
Great Tit	-	-	-	17	0	0	0
Firecrest	-	-	-	-	7	2	0
Long-tailed Tit	-	-	-	-	-	13	1
Treecreeper	-	-	-	-	-	-	1
COA median	0.23	0.23	0.17	0.04	0.14	0.15	0

Fig. 1. Fragmentation effects upon flock size. Residuals of mean flock size per fragment (after correcting for the effect of flock richness) in relation to area (A) and distance to the 'mainland', Casa de Campo (B).

number of trees > 50 cm diameter at breast height, and decreased with the distance to the 'mainland' (Casa de Campo) (Fig. 1b). 146 individuals were recorded in flocks of the same species, and 110 individuals in mixed-species flocks (Table 2). Coefficients of associations in multi-species flocks differed significantly among species (Kruskal-Wallis test, $H_5 = 11.17$, $P < 0.05$), being higher those of the most abundant species (Chiffchaff and Coal Tit) (Table 2).

DISCUSSION

Flock formation is modified by the reduction in habitat quantity associated with fragmentation conditions. Fragment size affected FS patterns probably as a result of a higher availability of resources and habitat diversity in large fragments (Alonso et al. 1987; Suhonen et al. 1992; Burke & Nol 1998). Such an increase in the amount of resources is expected to be of benefit to individuals joining flocks, because they may reduce the variability in food intake and augment the profitability of group foraging (Pulliam & Milikan 1982; Pulliam & Caraco 1984; Ruxton et al. 1995). Isolation (distance to the 'mainland') influenced flock size by reducing the number of individuals in flocks. The lower availability of species/individuals in distant fragments could have reduced the probability of encountering individuals for

aggregation (Ruxton et al. 1995; Mönkkönen et al. 1996; Wiggins & Møller 1997).

FS was also influenced by habitat quality, particularly by the availability of thick trees (> 50 cm diameter at breast height) and the amount of coniferous cover, both being suitable substrates for food items during winter (Suhonen et al. 1992; Swenson et al. 1995). Such substrates may enhance arthropod productivity, and hence, increase the probabilities of flock formation (Pulliam & Milikan 1982; Pulliam & Caraco 1984). Furthermore, an increase in habitat complexity (and associated food resources) could also reduce home ranges of individual species leading to an increase in density and FS, as has been found in tropical species (Latta & Wunderle 1996; Jullien & Thiollay 1998).

FS rather than FR appears to be the main determinant of flocking patterns in this fragmented urban landscape, which means that generally species occur singly or in mono-specific flocks rather than in multi-specific flocks. These flocking patterns may reflect the behaviour of certain species (Chiffchaff and Coal Tit) in response to specific habitat requirements (Hutto 1994; Jullien & Thiollay 1998), rather than the aggregation of individual species in response to inter-specific social influences (competition, predation avoidance, heterospecific attraction). By no means does this conclusion undermine the role of social factors in flocking patterns. Rather it supports the suggestion that social relationships could be disrupted in patchy landscapes (Pöysä 1992). The results of this study indicate that there is a preference for individuals to join flocks with abundant species (Table 2). These abundant species might increase the likelihood of flock formation, since they arise as the core of flocks upon which other less abundant (satellite) species get together (Hutto 1994). Core species might serve as cues for other satellite species in this fragmented landscape; a kind of social facilitators that may be reflecting levels of food availability, local predator abundance, etc. (Hutto 1994; Forsman et al. 1998).

Fragmentation effects act at intraspecific (e.g. dispersal, reproductive success) and interspecific (e.g. predation, parasitism) levels (see review in Faaborg et al. 1995). In the case of interspecific interactions during winter, the evidence of the adverse effects of fragmentation is contradictory. Some studies indicate that neither foraging niches nor relationships between dominant and subordinate species are significantly affected by forest fragmentation (Nour et al. 1997a, b). My results nevertheless suggest that patterns of flock formation are greatly influenced by fragmentation conditions, as habitat quantity (area and isolation) and quality (habitat structure) modify the number of individuals within flocks (regardless of the number of species).

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SAMENVATTING

De mogelijke effecten van biotoopgrootte en -isolatie op de grootte en de soortenrijkdom van groepjes rondtrekkende zangvogels werd onderzocht door de vogels 's winters te tellen langs lijntransecten in 23 parken in Madrid, Spanje. De grootte van de parken liep uiteen van 0,24 tot 118 ha; ook de afstand tot een 1722 ha groot bosgebied ten noordwesten van Madrid was heel variabel. De rondtrekkende groepjes konden bestaan uit Koolmees *Parus major*, Pimpelmees *P. caeruleus*, Zwarte Mees *P. ater*, Staartmees *Aegithalos caudatus*, Tjiftjaf *Phylloscopus collybita*, Vuurgoudhaantje *Regulus ignicapillus* en Boomkruiper *Certhia brachydactyla*. Hoe groter het park, hoe meer coniferen er in

dat park aanwezig waren en hoe groter en ouder de bomen waren, des te groter de groepsgrootte van de aanwezige zangvogels was. De totale groepsgrootte was negatief gecorreleerd met de afstand tot het grote bos. De soortenrijkdom van de groepjes vertoonde echter geen enkel verband met de grootte van het park of de afstand tot het grote bos. De talrijkste soorten kwamen het meeste samen voor. Dat de kans dat er groepjes werden gevormd afnam met de grootte van het park is vermoedelijk een gevolg van de afnemende biotoop-kwaliteit bij verdergaande fragmentatie. Het ziet ernaar uit dat het al of niet voorkomen van rondtrekkende groepjes afhangt van de aanwezigheid van Tjiftjaffen en Zwarte Mezen. Deze vogels trekken andere aan en vormen zo de kern van de rondtrekkende groepjes. (TP)