

## Behavioural responses to changing landscapes: flock structure and anti-predator strategies of tits wintering in fragmented forests

José Luis Tellería, Emilio Virgós, Roberto Carbonell, Javier Pérez-Tris and Tomás Santos

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We analysed the effects of forest fragmentation on the flock structure of insectivorous forest passerines (*Parus*, *Aegithalos*, *Certhia*, *Regulus*, etc.), and on the anti-predator behaviour and energy management of blue tits in these flocks. We surveyed flocks in Central Spain during two winters. Flocks in fragments comprised fewer individuals and species than flocks in unfragmented forests. The most abundant species in forest flocks (blue tit, *Parus caeruleus*, and firecrest, *Regulus ignicapillus*) were also the most abundant in fragments, while the rarest species in the area never occurred in small woodlots. We investigated how fragmentation and related changes in flock structure affect anti-predator behaviour of blue tits, a widely distributed species in the area. In fragments but not in forests, blue tits increased scanning rates with decreasing flock size. Vigilance was relaxed when great tits, *Parus major*, were abundant as flock mates, suggesting that the absence of this dominant species in fragments could intensify anti-predator behaviour of blue tits. Blue tits enhanced anti-predator behaviour in the second winter parallel to an increase in the abundance of raptors. This behavioural change was stronger in fragments, where blue tits foraged deeper in the canopy and increased scanning and hopping rates. Under increased predation risk, birds are expected to reduce body mass to improve predator avoidance. On average, blue tits weighed similar in fragments and forests the second winter. However, they accumulated fat along the day in fragments only, and adjusted body mass to body size more closely in that habitat type. This suggests that blue tits perceived fragments as unpredictable habitats where fattening would help avoid starvation, but also as dangerous sites where overweight would further increase the risk of predation. In summary, our results support that fragmentation affects individual behaviour of blue tits, and show the potential of behavioural approaches to unravel how different species face the advancing fragmentation of their habitats.

J. L. Tellería, E. Virgós, R. Carbonell, J. Pérez-Tris and T. Santos, Departamento de Biología Animal I (Zoología de Vertebrados), Facultad de Biología, Universidad Complutense, E-28040 Madrid, Spain (telleria@eucmax.sim.ucm.es).

A large body of primary research has been devoted to disentangle how habitat fragmentation affects survival, dispersal potential, demography and other determinants of the ability of different species to persist in fragmented habitats. However, little attention has been paid to the effects of fragmentation on the social organisation and behaviour of individuals (see, however, Villard et al. 1993, Noor et al. 1997, 1998, Hobson and Villard 1998), despite the current claims for an increasing commitment between behavioural ecology and con-

servation biology (Lima and Zollner 1996, Sutherland 1998, Reed 1999). Indeed, it has been explicitly suggested that behavioural studies of individuals living under different landscape configurations could help us understand how animals face habitat fragmentation and other human-induced environmental changes (Lima and Zollner 1996, Caro 1999).

This paper studies the effects of forest fragmentation on the winter behaviour of small insectivorous passerines that gather in mixed-species flocks outside the

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breeding season (*Parus*, *Aegithalos*, *Certhia*, *Regulus*, *Phylloscopus* and other less common genera; Ulfs-trand 1977). Benefits accrued to the birds by joining these flocks (such as gaining protection against predators and increasing foraging efficiency) take place at the expense of increasing competition for resources, raising aggressive interactions and accentuating dominance hierarchies (Matthysen 1990, Lahti 1998). This trade-off between the costs and benefits of flocking behaviour may be affected by the interaction between habitat characteristics (like food availability or predator abundance) and the pool of species or individuals being susceptible to gather in flocks. Given that forest fragmentation dramatically changes the availability of suitable habitat, the pool of birds available for flocking and the abundance of predators (Saunders et al. 1991, McCollin 1998), we have investigated how these changes affect the behaviour of wintering passerines. We pose the following predictions:

1) *Flock structure*. Flock size is limited by the number of individuals each fragment can support throughout the winter. Unless fragments are large enough to satiate all flock mates, individuals will encounter additional difficulties to secure themselves enough resources when sharing fragments with others. In this situation flock size is expected to be adjusted so as to fit the available resources in the occupied habitats (Pulliam and Millikan 1982, Ekman 1984). On the other hand, the species composition of flocks in forest fragments could be also restricted by the particular habitat requirements of each species. Because fragmentation causes a differential loss of resources depending on their availability in prime habitat, the species adapted to the use of originally scarcer resources should be less capable to endure in fragmented landscapes (Tellería and Santos 1995). Therefore, we predict that flocks will be composed of fewer individuals and species in small fragments, thereby adjusting to the lower resource availability with decreasing fragment size.

2) *Anti-predator behaviour*. Small forest passerines may improve predator avoidance by increasing vigilance or by reducing exposure. Under an increased predation risk, foraging birds may decrease the chance of being killed by a predator by enhancing scanning rates, moving more often from perch to perch, or selecting more sheltered feeding positions (Suhonen 1993, Mozetich and Carrascal 1995 and references therein). Given that the chance of an individual flocking bird being preyed upon depends on flock size and composition, we studied how the hypothesised changes in flock structure in fragments affect anti-predator responses of birds. In particular, we investigated whether scanning and hopping rates increase in fragments, and whether this response is

related to the reduction in flock size or to the loss of species that could be especially able to detect predators and advertise their presence to flock mates (Barnard and Thompson 1985, Cimprich and Grubb 1994, Dolby and Grubb 1998). We also studied whether birds complement these behaviours with the use of more protective feeding substrata (Caraco et al. 1980a, Ekman 1986, Lima and Dill 1990, Suhonen 1993). We selected the blue tit, *Parus caeruleus* (L.), as a model species to test these predictions because it occupies in winter the whole range of fragment sizes in our study area (Tellería and Santos 1995, 1997).

3) *Body condition*. We finally investigated whether fragmented forests are a conflicting scenario for blue tits to cope with the trade-off between predation and starvation (Lima 1986, McNamara and Houston 1990). At mid to high latitudes, birds need to accumulate a moderate to extensive amount of body reserves to secure self-maintenance during winter nights and unpredictable food-shortages (Blem 1990). Environmental instability is important in determining how much reserves are enough; the more unpredictable the environment, the larger the energy stores necessary for the birds to assure survival. However, energy storage has important costs related to flight performance. When putting on fat, a bird increases its body mass at the expense of reducing both the speed and the angle of ascent in take-off according to simple physical laws (Pennycuik 1989). In turn, this impairs the ability of fat individuals to escape predators (Metcalf and Ure 1995, Kullberg et al. 1996, Lind et al. 1999). The theory predicts that birds will manage body reserves in a different manner depending on food predictability and predation risk (McNamara and Houston 1990, Witter and Cuthill 1993). The reduction of suitable habitat in fragmented forests or the potentially reduced possibility to join flocks may decrease either the availability or the predictability of food resources, forcing birds to increase body reserves. This can be affected, however, by two additional factors related to the effects of fragmentation that predict opposite patterns: 1) If birds actually perceive an increased risk of predation in fragments because of being forced to assemble in smaller flocks (see above), they could accumulate less fat in fragments than in forests to improve predator avoidance (Rogers 1987, Witter and Cuthill 1993, Gosler et al. 1995, Adriaensen et al. 1998). 2) Field observations and experiments have shown that interspecific competition restricts the access to food by subordinates, which usually respond by acquiring extra body reserves (Krams 1998a). If forest fragmentation is related to the exclusion of some dominant species from flocks, subordinate species could decrease their body reserves to improve predator avoidance.

## Methods

### Study area

#### *Floristic and physiognomic features*

The study was conducted during the winters of 1994–1995 and 1995–1996 in the vicinity of Lerma (Central Spain 42°5'N, 3°45'W). This area is located at 800 m a.s.l. in the western slopes of the Sistema Ibérico, a mountain range subjected to frequent frosts and snowfalls during winter. We selected for the study a forest archipelago with 18 fragments (ranging from 0.1 to 3 ha and together making up an extension of 12.2 ha; hereafter fragments) located to the north from Santa Cecilia village, and two large contiguous forests (Quintanilla, 280 ha, and Torduelas, 150 ha; hereafter forests). Both fragments and forests show a similar shrubby appearance with trees averaging 5 m in height. The holm oak, *Quercus ilex* L., is the dominant tree species in the area (reaching 30% cover), followed by the Spanish juniper (*Juniperus thurifera* L., 4%) and the Lusitanian oak (*Quercus faginea* Lam., 1.4%). The shrub layer, dominated by the rockrose, *Cistus laurifolius* L., covers around 26% of the forest ground (see Tellería and Santos 1995 for further details).

#### *Two different situations of predator abundance*

As a part of our routine fieldwork in this area, we recorded the number of raptors observed in fragments and forests every work session. Interestingly, our study coincided with a noticeable increase in raptor abundance from the first to the second winter (Fig. 1). This circumstance, probably related to the hard and persistent cold wave which lashed north-western Europe during the 1995–1996 winter, allowed us to evaluate the role of changing predation risk in determining behavioural responses of tits to forest fragmentation. Because we could have recorded the same individual raptor more than once in a single day, we measured raptor abundance as the percentage of study days in which each raptor species was detected in fragments or forests (Fig. 1). So, here we consider that the likelihood of contacting a raptor during our fieldwork was a good indicator of the risk of predation that birds were facing in each year. As we were mainly concerned with bird-eating predators, we discarded records of buzzards, *Buteo buteo* L. (a mice and vole predator), red kites, *Milvus milvus* L., and griffon vultures, *Gyps fulvus* Hablizl (two scavengers). Raptor species considered were specialised in hunting birds inside forests or in clearings in the wood (sparrowhawk, *Accipiter nisus* L., and goshawk, *A. gentilis* L.), or in the open landscape with which the forest archipelago is interspersed (hen harrier, *Circus cyaneus* L., kestrel, *Falco tinnunculus* L., and peregrine falcon, *F. peregrinus* Tunstall).

### Bird sampling methods

#### *Flock structure*

Because flock structure may change in relation to time of day and weather conditions (Matthysen 1990), we sampled flocks throughout the day, calling the fieldwork off in snowy or windy days. When a flock was detected, we recorded its species composition, the number of individuals of each species, and the behaviour of one individual blue tit in the flock. The behaviour of solitary blue tits was also recorded. In some cases we could not record the flock size because it was impossible to individually identify all birds in the flock.

#### *Blue tit behaviour*

We studied scanning and hopping rates as two measures of anti-predator behaviour of blue tits. We considered that birds were scanning when they stopped food searching and moved their head in a vigilance attitude while standing on a perch. We decided that one scanning event had finished when the bird resumed its normal feeding behaviour. Hops consisted of cavorts and short flights between feeding positions. We did not record pecking rates (a measure of feeding activity) because blue tits persistently poked about in bark, lichens and other secretive substrata, which made it

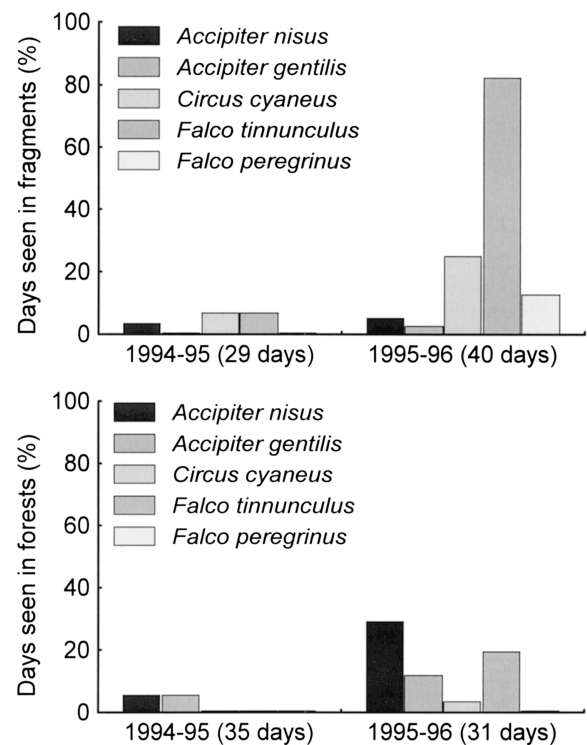


Fig. 1. Occurrence of bird-eating raptors in the area of Lerma during both study winters. The percentage of fieldwork sessions in which each raptor species was seen in fragments or forests is shown.

impossible to know whether the bird was just searching for food or pecking on some meal. As soon as one foraging blue tit came in sight we started its focal tracking, which lasted as long as possible but never less than 10 s. During the time keeping, we noted the number of scannings and hops done by the focal bird. When the bird moved out of sight, we stopped time-tracking until the bird was relocated, unless we were not sure it was the same individual. From these data, we computed scanning and hopping rates as number of events per unit time (10 s).

Together with changing scanning or hopping rates, the selection of more sheltered feeding substrata could be also involved in the anti-predator response of tits, as moving into secretive sites would reduce exposure to predators (Suhonen 1993). Thus, we studied whether blue tits preferred to forage on more sheltered positions in fragments than in forests. Tits are more visible when moving on exposed branches, and so focal individuals (which obviously were always at sight) did not make up a random sample for this analysis. Because of this, we conducted a complementary sampling aimed to gather data on the use of foraging substrata. When a blue tit other than the focal individual came in sight, we noted where it was foraging by classifying feeding substrata as inner (if the bird was on branches well inside the canopy) or outer (on leaves and twigs at the canopy surface). As in the case of focal observations, we recorded data on feeding substrata of one single individual per flock. Nevertheless, we also recorded these data for the focal tits in order to control for possible changes in scanning or hopping behaviour in relation to the use of sheltered or bare sites.

We conducted a log-linear analysis to study the changes between years in the use of more or less protective foraging sites in forests and fragments. This method manages multi-factor cross-tabulations (in our case a three-way contingency table combining degree of fragmentation, year and substrate type) by partitioning the variation in frequency data into the different factors, allowing one to test for interactions among them in a way similar to analysis of variance. The log-linear model is defined by the minimum number of interactions necessary to account for the distribution of observed frequencies. To obtain this model, we utilised a method that first proceeds in a backwards way by fitting all  $n$ -factor interactions (from  $n = 3$  to  $n = 1$  in our case) to the correspondent null hypothesis that all of them are simultaneously zero. As soon as the reduction in the order of interactions causes a lack of fit to the correspondent null hypothesis, the analysis selects (this time by means of a forward procedure) those terms that significantly contribute to explain the distribution of frequencies, thus generating the final log-linear model that best fits the data (Sokal and Rohlf 1995).

#### *Body condition of blue tits*

During January and February of 1996, we mist-netted blue tits in forests and fragments. We captured 34 individuals, 17 in fragments and 17 in forests. By using the birds whose age or sex could be accurately determined (according to Svensson 1992), we found that age-ratios (9 adults and 8 juveniles in forests, 8 and 8 in fragments) and sex-ratios (7 males and 7 females in forests, 7 and 8 in fragments) were not biased in relation to fragmentation. Hence, in order to keep a sample size large enough, we did not consider sex or age in our analyses. We weighed tits with a Pesola spring balance (0.5-g precision), and measured the wing maximum chord, the length of the straightened tail (both with a ruler to the nearest half mm) and the tarsus length (to the last scale before the toes, with a 0.05-mm precision calliper, see Svensson 1992 for details about measurements). We evaluated the amount of subcutaneous fat stored by tits according to a five-score scale, ranging from 0 (no visible fat) to 4 (interfurcular cavity bulging with fat; Jordano 1989), although we assigned half-score values to individuals whose fat deposits were intermediate in size between two values in the scale. It is known that body mass and the amount of fat accumulated by birds show different patterns of daily variation, which are largely dependent on environmental predictability (Blem 1990). Therefore, we captured birds all around the day to study possible differences in fattening patterns between fragments and forests.

We used the residuals of body mass on body size as a measure of body condition (Brown 1996). To derive a suitable index of body size, we performed a PCA with all body dimensions but body mass (Rising and Somers 1989, Freeman and Jackson 1990). The first component extracted by this PCA can be used as an index of structural size, which is independent of the nutritional condition of individuals (Piersma and Davidson 1991). Birds carrying much body reserves (i.e. with a large residual mass) will have less problems for self-maintenance under changing environmental conditions (Blem 1990), but also have an increased wing load and hence will be more vulnerable against the attacks of predators (Metcalf and Ure 1995, Bednekoff 1996).

#### **Some statistical considerations**

Our observations were done on unmarked individuals, which therefore were not individually recognisable. Although we captured some birds, we decided not to mark them with colour-rings because of two reasons. First, we were interested in studying the effects of different landscape configurations (fragments or forests) on tit behaviour, for which we needed to survey flocks over a too large area without using feeders or any other means that would allow multiple records of

Table 1. Changes between forests and fragments in the mean number of individuals and the percentage of occurrence of each species in flocks during each study year. Also shown are the mean flock size and the number of species per flock in each landscape type and year (means  $\pm$  se).

	Forests		Fragments	
	1994–1995	1995–1996	1994–1995	1995–1996
Blue tit, <i>Parus caeruleus</i>	3.4 (76%)	2.8 (65%)	1.3 (64%)	1.7 (67%)
Great tit, <i>P. major</i>	2.4 (74%)	1.7 (71%)	0.3 (20%)	0.3 (17%)
Crested tit, <i>P. cristatus</i>	1.1 (42%)	1.6 (40%)	–	–
Coal tit, <i>P. ater</i>	–	0.4 (17%)	–	–
Long-tailed tit, <i>Aegithalos caudatus</i>	3.1 (34%)	2.2 (20%)	0.02 (5%)	0.8 (7%)
Firecrest, <i>Regulus ignicapillus</i>	4.8 (90%)	4.1 (85%)	1.0 (55%)	1.5 (61%)
Goldcrest, <i>R. regulus</i>	0.2 (4%)	0.2 (9%)	–	–
Chiffchaff, <i>Phylloscopus collybita</i>	0.1 (4%)	0.2 (9%)	0.02 (7%)	0.6 (25%)
Short-toed treecreeper, <i>Certhia brachydactyla</i>	0.5 (38%)	0.6 (43%)	–	0.01 (1%)
Nuthatch, <i>Sitta europaea</i>	0.1 (4%)	0.02 (2%)	–	–
Flock size	15.5 $\pm$ 2.6	15.8 $\pm$ 2.5	2.7 $\pm$ 3.0	5.7 $\pm$ 2.5
Number of species	3.7 $\pm$ 0.4	3.5 $\pm$ 0.4	1.4 $\pm$ 0.5	1.9 $\pm$ 0.4

individual birds. Therefore, we should have conducted a massive ringing effort for gathering a sample of marked birds large enough to conduct individual-based studies. Second, no intensive survey program was to be conducted in our study area that could benefit from that marking, which hence would have been an unworthy nuisance for the birds. Notwithstanding this, the probability of having repeated observations of the same birds was actually low. Supporting this we did not recapture any of the birds ringed during our study of body condition, nor did we see any of them during observations of tit behaviour.

We could not be so safe, however, that we did not observe the same flocks more than once, since the dynamic structure of flocks complicated their individual identification between work sessions. This problem is more important because our analyses of tit behaviour needed to control for flock characteristics (size or species composition). Even though all individual tits considered in our study were different, sharing flocks would have led to pseudoreplication. As well, observations made in the same site would be less independent because of the effect of particular site characteristics (e.g. fragment size and structure) on tit behaviour. To avoid these flaws, we used the sites where we observed foraging tits as the appropriate sampling units for comparing between years or degrees of fragmentation. Although we acknowledge there is a chance that some flock moved among different sites used in the study (note however that the area includes many other neighbouring woodlots), we considered that repeating exactly the same flocks at different sites was unlikely. Hence, using sites (16 fragments and two forests) as sampling units would have buffered the possible inflation of power in our analyses due to the use of non-independent observations. To avoid losing information contained in the original data, we first estimated the between-sites effect nested within landscape types (fragments or forests), which allowed us to compute ade-

quate error terms and degrees of freedom for estimating the other effects in our analyses.

## Results

### Flock structure

In total, we found ten species joining flocks considering both study years (Table 1). We found a reduction from forests to fragments both in the number of individuals and the frequency of occurrence of each species in flocks, with the most abundant and frequent species in forest flocks being also the best represented in fragment flocks (Spearman's rank correlations; mean number of individuals in flocks: 1994–1995  $r_s = 0.73$ ,  $n = 9$  species,  $P = 0.026$ ; 1995–1996  $r_s = 0.78$ ,  $n = 10$ ,  $P = 0.008$ ; frequency of occurrence in flocks: 1994–1995  $r_s = 0.66$ ,  $P = 0.051$ ; 1995–1996  $r_s = 0.62$ ,  $P = 0.057$ ). Blue tits and firecrests were abundant and widely distributed species in both forests and fragments. However, other species which were also abundant in forest flocks (such as long-tailed tits, *Aegithalos caudatus* L. or great tits, *Parus major* L.) dropped to low abundances under fragmented conditions. Finally, some species had a very low abundance in fragments or, in the extreme case, were only found in forests (Table 1). As a consequence of these species-specific distribution patterns, flocks were composed of less species in fragments than in forests during both study winters, and flock size also decreased in fragments compared to forests (Tables 1, 2).

### Anti-predator behaviour of blue tits

#### Selection of feeding substrata

The log-linear analysis conducted to study changes in substrate use in relation to year and degree of fragmen-

Table 2. Results of ANOVAs analysing the components of flock structure in relation to year and landscape structure. Study sites where observations of flocks were done (16 fragments and two forests) are the levels of the "site" factor, which has been nested within landscape types (forests or fragments). The sum of squares and degrees of freedom of the "site" effect make up the error term for the other effects in the analysis, which have thus been computed with sites as sampling units.

	d.f.	Species per flock			Individuals per flock		
		SS	F	P	SS	F	P
Fragmentation	1	12.573	83.69	<0.0001	2.320	62.27	<0.0001
Year	1	0.163	1.08	0.314	0.016	0.43	0.521
Fragmentation × year	1	0.377	2.51	0.133	0.104	2.79	0.114
Site (nested)	16	2.404	1.50	0.103	0.596	1.27	0.219
Residual for site	197	19.731			5.779		

tation was unable to discard the highest-order interaction between fragmentation, year and substrate type (chi-square of goodness of fit to the absence of the three-way interaction:  $\chi^2 = 3.88$ , d.f. = 1,  $P < 0.05$ ). This means that the consideration of all three factors together was necessary for suitably explaining the distribution of observed frequencies. Overall, fragmentation was associated with a more frequent use of sheltered sites, as shown by the significant association between landscape configuration and substrate type ( $\chi^2 = 13.2$ , d.f. = 1,  $P < 0.001$ ). However, the partial association between year and substrate type, which accounts for overall changes in tit behaviour in relation to year, was not significant ( $\chi^2 = 0.06$ , d.f. = 1,  $P = 0.80$ ). This was nevertheless consistent with the strong difference in the shape of this effect between landscape types, evidenced by the significant three-way association. Indeed, blue tits foraged more frequently on sheltered sites during the second study year, when predators were more abundant in our study area, although such an effect took place in fragments but not in forests (Fig. 2). Thus, the overall model showed that whether or not year was important in determining changes in the selection of feeding substrata depended on the degree of fragmentation.

#### Scanning and hopping rates

Controlling for year effects in an ANCOVA with year as factor and flock size and number of species as covariates, scanning rates were found to be negatively correlated to flock size ( $\beta = -0.49$ ,  $F_{1,89} = 7.57$ ,  $P = 0.0072$ ) but were not significantly affected by the number of species in the flock ( $\beta = -0.14$ ,  $F_{1,89} = 0.62$ ,  $P = 0.43$ ). Hopping rates did not depend, however, on any of these aspects of flock structure (flock size,  $\beta = 0.15$ ,  $F_{1,86} = 0.39$ ,  $P = 0.53$ ; number of species  $\beta = -0.05$ ,  $F_{1,86} = 0.04$ ,  $P = 0.85$ ). According to these preliminary results we controlled for flock size in the analysis of scanning rates, but not when analysing hopping behaviour.

We designed a general linear model to analyse the variation in scanning rates in relation to landscape type, year, feeding substrata (factors) and flock size (covariate). We first tested for interactions between

each factor and the covariate. Non-significant interactions between year and flock size ( $F_{1,14} = 0.79$ ,  $P = 0.61$ ) and between feeding substrata and flock size ( $F_{1,14} = 0.72$ ,  $P = 0.59$ ) were excluded from the final model. The results of this analysis (Table 3), first showed that flock size strongly affected scanning rates in fragments, but lost importance in large forests (Fig. 3). Thus, controlling for year effects flock size explained 33% of variance of scanning rates in fragments ( $F_{1,52} = 27.95$ ,  $P < 0.0001$ ), but only 4% in forests ( $F_{1,35} = 1.52$ ,  $P = 0.22$ ). Controlling for this changing effect of flock size, scanning rates were higher in fragments than in

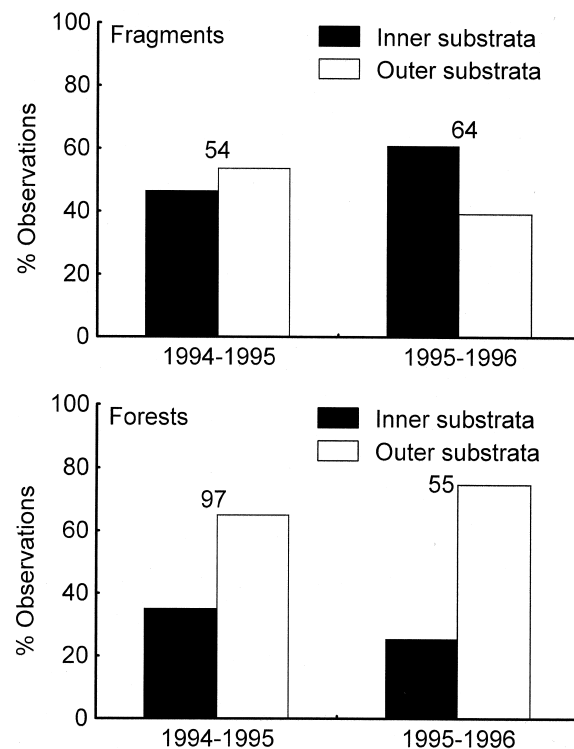


Fig. 2. Changes between years in the use of inner or outer feeding substrata by blue tits in fragments and forests. Numbers on the top of bars are sample sizes.

Table 3. Results of the general linear models analysing scanning and hopping rates of blue tits in relation to fragmentation, year and feeding substrata. Scanning rates have been analysed controlling for flock size. The effects have been estimated as described in Table 2 with sites where focal observations of blue tits were done (14 fragments and two forests).

	Scanning rates				Hopping rates			
	d.f.	SS	F	P	d.f.	SS	F	P
Fragmentation	1	0.345	13.01	0.0029	1	0.054	1.46	0.247
Year	1	0.286	10.79	0.0054	1	0.415	11.22	0.0048
Feeding substrate	1	0.008	0.29	0.596	1	0.002	0.05	0.818
Fragmentation × year	1	0.233	8.79	0.0102	1	0.010	0.27	0.609
Year × substrate	1	0.001	0.03	0.859	1	0.056	1.51	0.239
Fragmentation × substrate	1	0.004	0.14	0.712	1	0.127	3.43	0.085
Three-way interaction	1	0.030	1.12	0.307	1	0.013	0.35	0.566
Flock size	1	0.481	18.13	0.0008	–	–	–	–
Fragmentation × flock size	1	0.263	9.93	0.0071	–	–	–	–
Site (nested)	14	0.371	0.81	0.659	14	0.518	0.69	0.774
Residual for site	66	2.169			80	4.268		

forests, and even more so in the year with larger abundance of predators (Fig. 4).

We conducted a similar analysis to study hopping rates, although because this behaviour did not depend on flock characteristics we did not include any covariate in the model. Hopping rates were similar between landscape types and feeding substrata, the year effect being the only significant term in the model (Table 3). During the second year, when predators were more abundant in the area, foraging blue tits changed more frequently between feeding positions by hopping (Fig. 4).

Once we had demonstrated the role of flock size, year and fragmentation in determining the anti-predator behaviour of blue tits, we explored to what extent the specific composition of flocks could have influenced such a behaviour. To do so, we designed a model with the terms that had been significant in the former analysis (shown in Table 3), but also including the number of individuals of each species recorded in flocks as covariates. Overall, the relevant trends depicted by the model without species effects remained in this new model although, as it would have been expected, to consider the abundance of each species changed the effect of flock size and its interaction with fragmentation (Table 4). Thus, this new analysis was consistent with the former in showing different scanning rates between years in fragments but not in forests (the landscape type × year interaction, as shown in Fig. 4), and an effect of flock size on scanning rates in fragments but not in forests (the landscape type × flock size interaction as shown in Fig. 3, although this time the pattern was not significant). Among the species occurring in flocks, the great tit, *Parus major*, was the only one whose abundance significantly influenced scanning rates of blue tits (Table 4). This effect did not change in relation to fragmentation (landscape type × great tit abundance interaction:  $F_{1,14} = 0.33$ ,  $P = 0.57$ ) nor between years (year × great tit abundance interaction:  $F_{1,14} = 0.03$ ,  $P = 0.86$ ). Thus, whether in forests or in

fragments and in both study years, blue tits mitigated their anti-predator behaviour when great tits were more abundant as flock mates (Fig. 3).

### Body condition of blue tits

The PCA with body measurements extracted a PC1 accounting for 53.2% of variance (factor loadings:

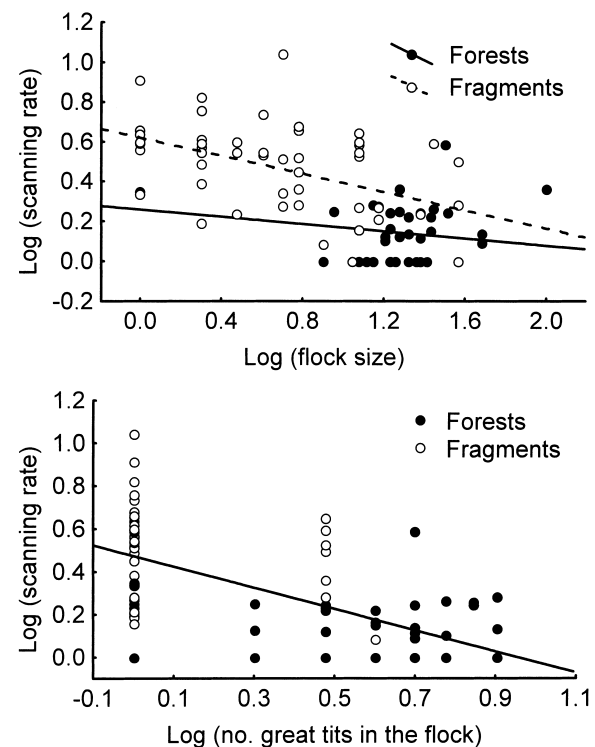


Fig. 3. Above, changes in the relationship between flock size and blue tit scanning rates in relation to fragmentation. Below, the effect of the number of great tits in the flock on the scanning rate of blue tits. This effect did not significantly change in relation to fragmentation.

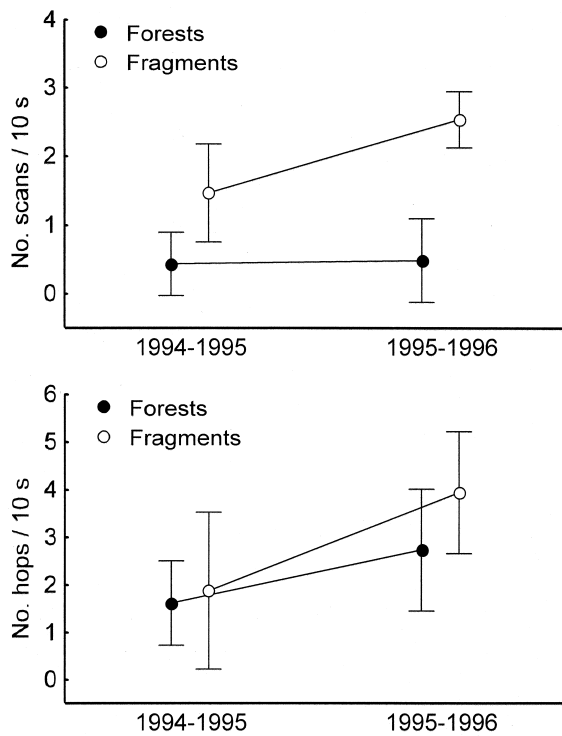


Fig. 4. Changes between years in the scanning and hopping rates of blue tits observed in forests and fragments. Shown are means and standard errors.

tail = 0.521, tarsus = 0.727, wing = 0.892; eigenvalue = 1.60), which we considered to be appropriate for measuring structural size of blue tits. We derived measures of size-corrected body mass (hereafter body condition) by computing the residuals of the regression of body mass of blue tits on PC1 scores ( $r = 0.42$ ,  $F_{1,32} = 6.74$ ,

Table 4. Results of the general linear model analysing scanning rates of blue tits in relation to fragmentation, year, flock size and number of individuals of each species in flocks. The effects have been estimated as described in Table 2 with sites where focal observations of blue tits were done (14 fragments and two forests). The scientific names of species are given in Table 1.

	SS	d.f.	F	P
Fragmentation	0.128	1	5.25	0.038
Year	0.018	1	0.73	0.406
Fragmentation × year	0.132	1	5.44	0.035
Flock size	0.105	1	4.32	0.056
Fragmentation × flock size	0.027	1	1.10	0.313
Blue tits (other than focal)	0.001	1	0.05	0.832
Great tits	0.162	1	6.66	0.022
Coal tits	0.005	1	0.22	0.644
Crested tits	0.028	1	1.13	0.305
Long-tailed tits	0.001	1	0.03	0.860
Short-toed treecreepers	0.010	1	0.41	0.532
Firecrests	0.004	1	0.16	0.698
Chiffchaffs	0.053	1	2.18	0.162
Site (nested)	0.341	14	0.82	0.645
Residual for site	1.900	64		

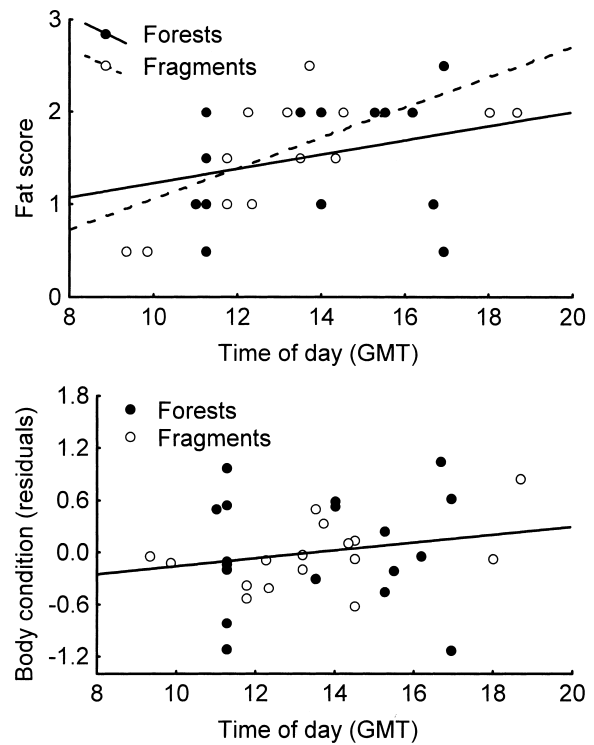


Fig. 5. Above, changes in the daily patterns of fat accumulation of blue tits in relation to fragmentation. Below, daily patterns of weight increase (once corrected for body size), which did not change between forests and fragments. Note that the dispersion of residual body mass values was lower in fragments compared to forests.

$P < 0.05$ ). Body condition did not significantly depend on fat scores (linear regression with the logarithm of the squared fat scores to meet linearity and normality:  $r = 0.13$ ,  $F_{1,32} = 0.59$ ,  $P = 0.45$ ). One-way ANCOVA analyses with fragmentation (forests vs fragments) as the factor and time of capture as a covariate failed to detect any significant effect of fragmentation on body condition ( $F_{1,31} = 0.12$ ,  $P = 0.73$ ) or fat scores ( $F_{1,31} = 0.63$ ,  $P = 0.43$ ). Although the body condition of birds did not significantly change throughout the day in fragments nor in forests (time of capture  $F_{1,31} = 1.28$ ,  $P = 0.27$ , interaction fragmentation × covariate time of day  $F_{1,30} = 0.34$ ,  $P = 0.57$ , Fig. 5), blue tits did put on fat from morning to dusk, leading to a significant effect of time of day on fat scores ( $F_{1,31} = 11.2$ ,  $P = 0.002$ ). Despite that no significant interaction could be detected between the effects of fragmentation and time of capture on fat scores ( $F_{1,30} = 1.93$ ,  $P = 0.18$ ), a closer insight into the relationship within each landscape type evidenced that blue tits actually put on fat throughout the day in fragments, but did not accumulate fat significantly in forests (Fig. 5). Thus, time of capture explained 56% of variance of fat scores in fragments ( $r = 0.75$ ,  $F_{1,14} = 18.1$ ,  $P = 0.0008$ ) but less than 9% in



forests ( $r = 0.29$ ,  $F_{1,16} = 1.56$ ,  $P = 0.23$ ). Parallel to this pattern of daily fat storage in fragments, blue tits showed less variation in body condition in fragments compared to forests, as shown by an ANOVA on the absolute deviations of residual body mass values from their mean in each landscape type (that is, a Levene's test of homogeneity of variances between forests and fragments:  $F_{1,32} = 6.28$ ,  $P = 0.017$ , Fig. 5).

## Discussion

### Flock size and composition

The loss of species in fragments described in this paper was similar to that recorded in a study on the distribution of this guild in a set of 31 woodlots of different size in the same area (Tellería and Santos 1995). In both cases, the most specialist species occurred in forests but were the first to disappear from fragments. These species are thought to experience an increasing difficulty to meet their particular habitat requirements in fragments below a critical size (Tellería and Santos 1995, 1997). In this study, specialist species are those that prefer to forage on rare tree species (for instance the coal tit and the crested tit which chiefly rely on Spanish junipers, *Juniperus thurifera*, in the area), or on other scarce substrata like trunks and large branches (for example the nuthatch and the short-toed treecreeper). Contrasting with these specialists, the species that forage on holm oak foliage (the most abundant substrate in both forests and fragments), like blue tits or firecrests, were able to occupy a broad range of fragment sizes. The marked decline of great tit abundance in fragments, a species that usually feeds on the forest ground in this area (Tellería and Santos 1995), could be related to the rapid depletion of food resources important for this species. Wood mice, *Apodemus sylvaticus* L., from the surrounding fields overcrowd during winter the small fragments, depleting the oak acorns and fruits on which great tits rely (Tellería et al. 1991, Santos and Tellería 1994, 1997). Thus, the species composition of flocks in fragments seemed to be determined by environmental restrictions related to the particular habitat requirements of each species (Tellería and Santos 1995, 1997). This depletion of resources with decreasing fragment size may also explain the decrease in the number of individuals per flock of the species that did occur in fragments. The lack of differences in flock structure between years (coinciding with a noticeable change in the abundance of bird-eating raptors in the area) suggests that birds did not overcome the increased predation risk by gathering in larger flocks, contrasting with that found in other studies (Morse 1977, Caraco et al. 1980b). Our results suggest that, because the small size of fragments prevents the assemblage of large flocks, birds adjusted individual behaviour to face different situations of predation risk, as shown in blue tits.

### Blue tit anti-predator behaviour

Flock structure affected anti-predator behaviour of blue tits. Birds increased scanning rates when sharing flocks with fewer individuals, as shown in other studies of tit behaviour (Matthysen 1990). Surprisingly, however, the abundance of great tits as flock mates arose as an important predictor of the scanning rates of blue tits, both in fragments and forests and independently of flock size. Dominant species like great tits – the largest European tit species – frequently exclude subordinates from the preferred sites (for example good feeding patches), so that these heterospecific associations can only be sustained if subordinates obtain counterbalancing benefits (Cimprich and Grubb 1994, Dolby and Grubb 1998). It has been suggested that one such pay-off accrued to subordinates could be gaining in foraging time by taking advantage of the efficient anti-predator vigilance of dominants. Although some studies of single-species flocks have given some support to this idea (Hegner 1985, Hogstad 1986, Krams 1998b, Lahti 1998), there is little evidence that such a mechanism could work also at the interspecific level. Cimprich and Grubb (1994) failed to detect increased scanning rates in subordinate Carolina chickadees, *Parus carolinensis*, when dominant tufted titmice, *Parus bicolor*, were experimentally excluded from wintering flocks. However, the lack of both species significantly increased the vigilance of *Picoides pubescens* and *Sitta carolinensis* (Dolby and Grubb 1998). Our study suggests that interspecific relationships among European tits are similar to those described for tufted titmice and Carolina chickadees, since great tits are dominant over blue tits and other pariforms (Morse 1978, Dhondt and Eyckerman 1980). The observed decrease in the vigilance of blue tits when sharing flocks with many great tits could well compensate the costs of interspecific interactions.

According to these results, the inadequacy of fragments to support large flocks and the inability of great tits to colonise fragments could be two major determinants of the increased anti-predator behaviour of blue tits in small woodlots. However, after controlling for changes in flock structure, scanning rates remained significantly affected by the degree of fragmentation, with an increased vigilance in fragments. This suggests that blue tits perceived a higher predation risk in fragmented landscapes regardless of flock size or composition. In fact, birds foraging in fragments are more exposed to predators while gleaning at the borders of woodlots, and also face an additional risk of being preyed upon by open-land raptors when moving among forest patches. The changes between years in the components of anti-predator behaviour studied support that both the realised and the perceived risk of predation actually increased in the second year, when we saw more raptors in the area. Thus, blue tits foraged in more sheltered positions during the second winter, and

also increased scanning and hopping rates that year. The lack of association between the use of more or less exposed feeding positions and the changes in scanning or hopping rates suggests that birds reinforced anti-predator behaviour by combining the selection of protected sites with an increase of vigilance. However, this apparently higher predator pressure in the second year had a different effect on anti-predator behaviour of blue tits depending on the degree of fragmentation. The trend towards selecting more protective feeding patches the second year only emerged in fragments, and scanning rates increased during the second winter in fragments but not in forests. As well, the degree of forest fragmentation differentially affected the relationship between anti-predator behaviour of blue tits and flock size, as this effect took place only in small woodlots. In short, fragmentation played an important role in shaping the effect of changing predation risk on the behavioural responses of blue tits.

Hopping was the component of anti-predator behaviour that showed less clear changes in relation to fragmentation or flock structure. Thus, hopping rates were larger in the second year in both landscape types and did not depend on flock size. Although hopping has been thought to reduce exposure, some tree-gleaning passerines increase vigilance without changing the time spent on a given patch when feeding under the risk of predation (Mozetich and Carrascal 1995). In our study, the increase in hopping rates when predator abundance was higher agrees with the idea that movement contributes to defence. However, the lack of differences in relation to fragmentation or feeding substrata reflects that blue tits do not use this strategy to adjust anti-predator behaviour at local or microdistribution scales.

### **Blue tit body condition**

Predation pressure and energy stress are likely to be the main causes of winter mortality in insectivorous forest passerines (Lima 1986, Rogers 1987, McNamara and Houston 1990). Blue tits do not hoard food, so they have to negotiate body reserves according to environmental conditions to manage with habitat unpredictability. This reinforces the value of body mass and fat stores as indicators of the way blue tits cope with changing environmental restrictions. Blue tits showed a similar body mass in fragments and forests, and did not differ in the amount of fat stored in each landscape type. Given that observations of behaviour indicated that predation risk was higher in fragments, these results contrast with theoretical views that postulate a decrease in body mass under the risk of predation. However, fragmentation not only increases the risk of predation, but also reduces the predictability of resources. Because of the lower availability of resources

in fragments, birds face the uncertainty of finding a suitable food supply when moving between fragments. Moreover, the limitation of flock size would further accentuate the problems of acquiring enough food in fragmented forests. As a consequence, fragmentation may alter the relative importance of predation and starvation risk as determinants of fat accumulation. In our study area, blue tits increased fat scores along the day in fragments but not in forests. This contrasts with that expected from the enhanced anti-predator behaviour observed in fragments, as putting on fat may increase the vulnerability of blue tits against the attacks of predators (Metcalf and Ure 1995; see however Kullberg 1998). Supporting that predation risk involved mass-dependent costs of fat storage in small woodlots, blue tits showed a closer adjustment of body mass to body size in fragments than in forests, as shown by differences in relation to fragmentation in absolute residual mass values. These results suggest that the combination of an increased unpredictability of resources and a higher risk of predation in fragments could press blue tits to manage body reserves in a restrictive manner, with selection acting against both too thin and too heavy individuals and hence leading to the observed stabilization of body mass relative to body size. In fledgling blue tits, which benefit from being heavier (i.e. in good condition) as well as individuals wintering in unpredictable habitats, stabilizing selection on body mass under the risk of predation has been demonstrated by comparing the shape of the relationship between fledgling mass and survival among years with or without sparrowhawks (Adriaensen et al. 1998). Therefore, our results suggest that small woodlots are unpredictable habitats where fat accumulation is necessary to avoid starvation, but also dangerous sites where overweight may put birds under the risk of being killed.

### **Conclusions**

This paper presents an example of the insights that behavioural ecology can bring to the study of the consequences of habitat fragmentation. Fragmentation affects the structure of mixed-species flocks of forest passerines, and anti-predator behaviour and energy management strategies of blue tits in particular, suggesting that fragments are relatively unpredictable and risky habitats compared to unfragmented forests. The lack of social facilitation related to flock reduction has been proposed to reduce survival of flocking birds (Allee effects; Reed 1999), which is consistent not only with the hypothesised role of flocking on tit biology (Matthysen 1990), but also with the reduced body condition and increased winter mortality of birds found by experimentally reducing mixed-species flocks (Dolby and Grubb 1998). Hence, because the effects of forest

fragmentation on the behaviour of flocking passerines are likely to appear in other taxa and habitat types, it seems promising to consider individual behaviour as an additional response variable in fragmentation studies.

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