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NUTHATCHES *SITTA EUROPAEA* DO NOT DELAY POSTFLEDGING DISPERSAL IN ISOLATED FOREST FRAGMENTS

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Abstract. We followed the fate of colour-ringed Nuthatch *Sitta europaea* fledglings in six territories within a large forest and eight territories within small (<15 ha) forest fragments. Almost half of the young birds had disappeared by day 8 after fledging, before any dispersal was expected to have occurred. This high level of mortality was probably mainly due to predation. After day 15 the rate of disappearance increased markedly due to dispersal, and all young had left the study areas by day 28. The pattern of disappearance was highly similar in both study areas, suggesting that dispersal was not delayed in forest fragments, nor was the pattern of early fledgling mortality different from a large forest.

Key words: habitat fragmentation, dispersal, juvenile mortality, Nuthatch.

INTRODUCTION

Natal dispersal of birds and other animals is commonly defined as the movement between the place of birth and the site of first reproduction (GREENWOOD, 1980). Dispersal involves a behavioural sequence of acts or decisions, most of which are still poorly understood. For instance, it is possible to distinguish between a «leaving», a «transfer» and a «settling» phase (cf. SMALL *et al.*, 1993; IMS & YOCOZ, 1997). Although an increasing number of studies have attempted to follow the entire dispersal sequence by radiotracking (see BELTHOFF & RITCHISON, 1989; GONZALEZ *et al.*, 1989; SMALL *et al.*, 1993 for avian examples), information on dispersal patterns remains largely based on separate observations per phase.

Recently the study of dispersal has acquired additional relevance in the context of habitat fragmentation. Conservation biologists want to know, for instance, to what extent dispersal flows are channeled or arrested by landscape elements (MADER, 1984; Saunders & HOBBS; 1991, ROSENBERG *et al.*, 1997), or how isolation of habitat patches affects gene flow, immi/emigration balance and recolonization probability (WAUTERS *et al.*, 1994; HANSKI & GILPIN, 1997). The magnitude of these landscape effects probably depends on

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the nature of the costs and benefits of dispersal, which vary across species (JOHNSON & GAINES, 1990; MATTHYSEN, 1994). In addition there may be differential effects in each phase.

Nuthatches (*Sitta europaea*: Aves) have repeatedly been shown to be less abundant in more isolated forest fragments, suggesting that dispersal is insufficient to overcome isolation (OPDAM & SCHOTMAN, 1987; VERBOOM *et al.*, 1991). In previous papers we have presented information on the «transfer» and «settling» phases in a highly fragmented habitat (MATTHYSEN *et al.*, 1995; MATTHYSEN & CURRIE, 1996). These studies showed that almost all Nuthatches leave the natal patch to settle elsewhere, but also suggested a high cost related to dispersal. Here we present more detailed observations on the «leaving» phase. In particular, we test the prediction that if there is a barrier effect associated with isolation of forest fragments (STAMPS *et al.*, 1987), Nuthatch fledglings should disperse later in fragments compared to a large forest.

METHODS

In the summer of 1994 we monitored the rate of disappearance of colour-ringed juveniles from their natal territories in 14 broods. Six territories were chosen within a 30 ha study plot in a forest of more than 200 ha (Peerdsbos). The eight remaining territories were located in six different forest fragments within a 4x4 km area in a highly fragmented landscape, described in more detail elsewhere (MATTHYSEN *et al.*, 1995; MATTHYSEN & CURRIE, 1996). Five fragments were small (2 to 12 ha) forest stands dominated by mature Common Oak *Quercus robur* with some Beech *Fagus sylvatica*, each containing one or two breeding pairs, and separated from one another by at least 500 m of agricultural land. The sixth fragment was a narrow belt of ornamental trees (mainly Beech) in a small town, almost 2 km in length and 10 ha in size. Here two territories out of the four present were chosen for observation.

All nestlings were individually colour-ringed, weighed and sexed when 10 to 15 days old (MATTHYSEN *et al.*, 1995). Brood sizes varied from six to eight except for one fragment brood with two nestlings only. Nestlings fledged when they were approximately 22 days old. It is assumed that all ringed nestlings survived to fledging; nestling loss at this stage is unusual in Nuthatches (MATTHYSEN, 1998). All territories were checked at least once during the first week (day 2-8) after fledging, and subsequently all were checked about twice a week and the number of fledglings recorded, and, if possible, their identity. Parent-offspring interactions were also noted. Fledglings were initially located by their conspicuous calls but as they became more mobile, playback was used to locate adults as fledglings associated with their parents in relatively cohesive family groups until they disappeared. Fledglings never responded to the playback. Territories were monitored until all the fledglings were found to be absent on several successive visits.

We characterized between-brood variation in dispersal by maximum dispersal date per brood, which is the day the last fledgling was seen on territory (range: 10 to 27 days after fledging). We also computed a median date of disappearance of the fledglings still alive on day 8, assuming that no dispersal occurred before this age (see further). Since this parameter was closely correlated with maximum dispersal date ($r=0.82$, $n=14$) but probably

more subjected to observational errors since it is based on counts rather than presence/absence, we only present data on maximum dispersal date. Since we predicted that dispersal would, if anything, be delayed in fragments, one-sided tests were used to compare timing in the two study areas.

RESULTS

All fledglings disappeared from their natal territories within 28 days after fledging. During observations for another purpose in neighbouring fragments (MATTHYSEN & CURRIE, 1996), two fledglings were resighted on days 14 and 17 at distances of 1.7 and 2.8 km, in both cases with at least one sibling still on the natal territory. Parents were no longer observed to feed fledglings after day 11 although begging continued to day 18. In this period we frequently saw fledglings chase their parents and beg intensely for food, which in two cases elicited aggressive responses from adults (on days 17 and 18).

Maximum dispersal dates were very similar in the large forest (mean \pm S.D.: 21.0 ± 5.9 days, $N=8$) and in the forest fragments (20.3 ± 4.5 days, $N=6$; $U=22$, one-sided $P>0.5$). The difference in median date was even opposed to the one-sided prediction (means: 19.8 and 20.3 days, respectively). With the two study areas pooled, there was no correlation between maximum dispersal time and brood size (Spearman rank correlation, $n=14$, $R_s=0.34$), fledging date ($R_s=-0.16$, $n=14$) or mean chick weight ($R_s=0.28$, $n=13$) (all $P>0.1$). Using the pooled standard error of the two samples we calculated a one-sided confidence interval for the difference in maximum dispersal time between group means. The interval allows us to conclude with 95% confidence that fragment broods dispersed not more than 3.8 days later than broods from the large forest.

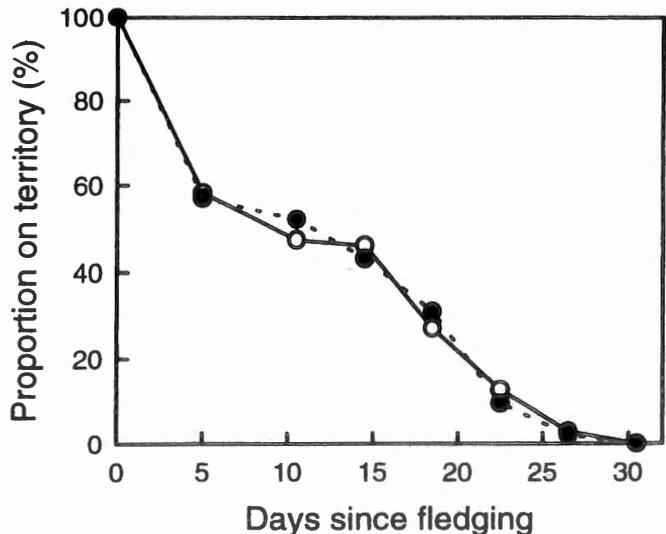


Fig. 1. — Mean proportion of fledglings per brood remaining on territory in a large forest (filled circles, $n=6$ families) and forest fragments (open circles, $n=8$ families). Data points are means for four-day periods, except for the first point giving a mean for day 2 to 8 (mean observation date in this interval = day 5.3 in both areas).

In both study areas, fledglings disappeared from the territory at a very similar rate which appeared to increase after day 15 (Fig. 1). This is illustrated by mean loss rates per 8-day period: 42% disappeared between days 0 and 8, 33% from day 8 to 16, 70% from day 16 to 24 and 100% from day 24 to 32 (only taking into account broods counted on or near days 8, 16 and 24). The difference between the first three periods is nearly significant (Kruskal-Wallis analysis of variance, $H=5.3$, $P=0.07$, total $n=21$ territory/period combinations).

DISCUSSION

In this study, Nuthatches born in isolated forest fragments disappeared from their natal territories at a similar rate as those born in a larger forest. We estimate that the true difference did not exceed a 3.8-day delay in fragments. This is much smaller than the natural variation within years and areas which easily covers two to three weeks (MATTHYSEN, 1989). A potential critique is that we sampled broods in a single large forest only. An obvious reason is the scarcity of large forests in our landscape and the practicalities of working in distant study areas at the same time (cf. LENS & DHONDT, 1994). We believe that our results are still of general significance because (i) the large forest and fragments differed little except in the variable of interest, *i.e.* the spatial isolation of territories; they were geographically close (<20 km), very similar in habitat and also in reproductive parameters of the Nuthatch population (MATTHYSEN & ADRIAENSEN, in press); and (ii) the single large forest appeared sufficiently representative of the «unfragmented» condition, since it differed little in population density and reproductive parameters from oak stands within two more distant large forests (MATTHYSEN & ADRIAENSEN, in press; MATTHYSEN, unpubl.).

The earliest known age for Nuthatch dispersal is 8 days after fledging for a bird settling close to the natal territory (MATTHYSEN, 1998) and 10 days for longer dispersal (STECHOW, 1937). This coincides with a phase of restlessness observed in captive young from around day 14 (LÖHRL, 1958). Therefore losses before day 10 are best regarded as early mortality. The extended length of stay of at least some young, up to two weeks after cessation of feeding, suggests a limited role for parental aggression to force juveniles to disperse (HOLLEBACK, 1974; DAVIES, 1978). The proportion of Nuthatches that disappeared by day 8 (nearly 50%) is much higher than reported on Marsh Tits *Parus palustris* where only 4% disappeared in the first 11 days (SMITH, 1967), and Black-capped Chickadees *Parus atricapillus* where 12% disappeared in the three to four weeks preceding family break-up (NILSSON & SMITH, 1985). Predation is probably a major cause of disappearance, as we witnessed attacks by both Jay *Garrulus glandarius* and Sparrowhawk *Accipiter nisus* (on days 2 and 20, respectively) as well as several chases by Jays. Jays and other corvids were very common in all study areas. However, contrary to many studies on nest predation, we found no suggestion for a higher predation rate in fragments (*e.g.* ANDRÉN & ANGELSTAM, 1988; NOUR *et al.*, 1993).

Variation between broods in maximum dispersal time could not be explained by fledging date, brood size or mean nestling weight condition. A comparable study on Crested Tits *Parus cristatus* found a seven-day delay in pine forest fragments of 10-50 ha compared to a large forest (LENS & DHONDT, 1994). When comparing their original data

(L. LENS, *in litt.*) with our results, we found a significant species \times area interaction (ANOVA, $F_{1,20}=8.3$, $P<0.01$) suggesting that the different results are not due to lack of statistical power in our own analysis. Lens & Dhondt (1994) suggested that Crested Tits dispersed later in fragments because of their lower body mass at fledging. In our case mean nestling body mass did not differ between fragments ($24.3\pm 0.8\text{g}$) and large forests ($22.6\pm 0.7\text{g}$; Mann-Whitney U-test, $U=12$, $P>0.1$), and an even smaller difference was found in a more extensive comparison over several years (MATTHYSEN & ADRIAENSEN, *in press*). Thus, the most parsimonious explanation for the difference between the two studies is that there is no barrier effect delaying dispersal from fragments, and that the delay in Crested Tits is caused by a lower fledgling weight. The conclusion that there is no barrier effect, is consistent with the long dispersal distances travelled by at least some Nuthatches and the low rate of local recruitment in both studies (LENS & DHONDT, 1994; MATTHYSEN *et al.*, 1995). However, the absence of a barrier effect does not preclude that disperser success is affected by habitat fragmentation (see MATTHYSEN & CURRIE, 1996).

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