

S10-4 Consequences of habitat fragmentation for birds: comparison between Europe and North America

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Abstract Much semi-natural habitat in Europe and North America now exists as small patches in landscapes dominated by agriculture, industry or urban sprawl. European landscapes, such as in eastern England, have existed in this state for a much longer period of time (> 1 000 yrs) than landscapes in the central United States (< 200 years). We compare the population and community responses of birds in small woodland patches in agricultural landscapes in eastern England and central US (Ohio), focusing on the family Paridae. In both England and the US, decreased reproductive success in small woods was observed, but differing causal mechanisms may be involved. Decreased food supply and increased foraging costs due to greater travel distances between patches may result in chick loss, reduced fledging weights and, therefore, reduced recruitment in England. The main cause of low reproductive success in our study in the US, however, was interspecific nest-site competition in relation to wood patch structure. Parental time and energy budgets may also be adversely affected by increased exposure to poor weather conditions in small woods. Birds in small English woods bred later than pairs in large woods, possibly due to microclimatic effects on vegetation development and invertebrate availability. Molting and breeding are both energetically costly and are usually separated in time; therefore, late breeding is followed by late molting. Late molting is associated with lower overwinter survival and subsequent breeding success, which may result from poorer plumage quality in late-molting birds. In the US, lower survival rates were also detected in small woods, especially those without supplemental food. These locations also contained birds with narrower feather growth bars, indicating lower nutritional condition. Habitat fragmentation may therefore reduce habitat quality due to changes in bird community structure, a lack of resources and increased exposure to stressful conditions, resulting in reduced breeding success, increased costs of rearing young, late molting and reduced survival. Our results suggest that there are generalities to be drawn in landscapes where habitat patches are small, despite differences in time since fragmentation.

Key words Feather quality, Habitat fragmentation, Reproductive success, Survival, Woodland birds

1 Introduction

The consequences of habitat fragmentation for the persistence of native species (e.g., Fahrig, 2002) and for current worldwide declines in biodiversity (Heywood, 1995) are the focus of much current concern. A neglected aspect of this phenomenon is the extent to which organisms may have adapted evolutionarily to habitat fragmentation. Due to such adaptation, one might expect that negative effects associated with fragmentation should decrease with time since fragmentation. Accordingly, we compare responses to forest fragmentation by one group of woodland birds, family Paridae, in midwestern USA (Ohio) and eastern England (Cambridgeshire). Today landscapes in these regions resemble one another with their islands of woodlands in a matrix of row-crop agricultural land, yet those in Europe have been fragmented for over 1 000 years longer (Rackham, 1986). The comparative studies herein were conducted without recourse to common methodology, so close comparisons of the same variables measured in the same way are not possible. Instead, we probe more diffusely for findings

that might suggest increased adaptation to fragmentation, as evidenced by greater reproductive success and survival among the parids of England than in Ohio. Both sites are the scenes of continuing long-term demographic studies of parids and other species, from 1990 in Cambridgeshire and from 1995 in Ohio.

2 Methods

In Cambridgeshire, reproductive success in great (*Parus major*) and blue (*P. caeruleus*) tits has been studied since 1993 using nest boxes (total *c* 170) located in up to 45 woods of different sizes (0.1–157 ha). Boxes are checked at approximately weekly intervals; the components of breeding success recorded are given in Table 1. Relationships between these variables and woodland area were investigated using mixed linear models incorporating both fixed and random effects. Only data from first broods and first breeding attempts were used. Full details are given in Hinsley et al. (1999).

To measure survival, turnover of individual breeding

Table 1 Breeding performance of great and blue tits in a 1-ha woodland compared to that in a 150-ha woodland

Variable	Great tit	Blue tit
Timing of laying (1st egg date)	7 days later	8 days later
Clutch size	same	same
Number of young at 11 days	-1.2	-1.8
Mean mass of young, g	-1.4	same
Total mass of young, g	-30.0	-22.5
Number fledged	-1.4	-2.4

The difference due to woodland area was estimated from linear mixed models based on tit performance in 5 breeding seasons (1993 to 1997) in Cambridgeshire, England. Mass of nestlings was measured at day 11 post-hatching (Hinsley et al., 1999).

birds in a maximum of 16 small woods (0.51 ± 0.27 ha) was estimated for several species from color-banding (Table 2). All adult breeders of the target species were color-banded each year and their presence/absence noted in subsequent years. Full details are given in Hinsley et al. (1994).

To compare the timing of molt in large and small woods, post-nuptial primary molt scores of great and blue tits were recorded as a matter of routine during various aspects of the long-term study. Molt scores were recorded by the standard procedure of the British Trust for Ornithology (Ginn and Melville, 1983). Full details are given in Hinsley et al. (2003).

To assess feather quality, the effects of molt rate were investigated by increasing its speed in an experimental group of European starlings (*Sturnus vulgaris*) in comparison with a control group which molted more slowly. Rate of molt is increased by shortening photoperiods, and thus different rates were achieved by exposing the groups to either long (slow molt) or shortening (fast molt) days. The characteristics of resulting primary feathers are shown in Table 3. Full details are given in Dawson et al. (2000). Details of the study area can be found in Hinsley et al. (1995).

3 Results

3.1 Reproductive success

Between 1993 and 2002, great and blue tits in England bred earlier and fledged more young in large (27–157 ha) than in small (0.1–1.1 ha) woodland patches. Furthermore, great tits in small woods reared lighter young. These differ-

ences are highlighted in a comparison between production in 1 ha and 150 ha woodlots that was based on the models of trends in components of breeding success/woodland area for the years 1993 to 1997 (Hinsley et al., 1999; Table 1).

In Carolina chickadees (*Poecile carolinensis*) in Ohio, the probability of a nest fledging successfully was a positive logistic function of woodlot size, with an inflection point at 6.8 ha. In woodlots of < 6.8 ha and > 6.8 ha, respectively, 30% and 72% of nests fledged successfully. A manipulative experiment demonstrated that chickadee reproductive success was lower near a woodland edge and, furthermore, that chickadees preferred to nest in woodlot interiors when given a choice (Doherty and Grubb, 2002a). As the edge-to-interior ratio is greater in small than in large woodlots, the increased nest failure near edges could have accounted for the difference in nest success in small and large woodlots. The cause of chickadee nest failure came predominantly from nest site competition with house wrens (*Troglodytes aedon*), a well-known forest-edge species.

3.2 Survival

In England, individuals of several songbird species disappeared from small (0.51 ± 0.27 ha) woodlands at a rate considerably higher than mortality rates reported in the literature (Hinsley et al., 1994; Table 2). While the divergence from published rates was not extreme in the two species of tits, winter wrens (*Troglodytes troglodytes*), European robins (*Erithacus rubecula*), and chaffinches (*Fringilla coelebs*) underwent almost complete annual turnover in the study plots, a far higher rate than previously reported. Turnover rates in color-marked

Table 2 Percentage loss of banded birds between 1990 and 1991 from small woodlots in Cambridgeshire, England, compared to published mortality estimates (Hinsley et al., 1994)

Species (<i>n</i> = number of woodlots)	% loss in small woodlots	Published annual mortality estimates
great tit (<i>n</i> = 16)	67	50 ¹
blue tit (<i>n</i> = 14)	58	70 ¹
winter wren (<i>n</i> = 16)	96	63 ²
European robin (<i>n</i> = 15)	95	62 ³
chaffinch (<i>n</i> = 13)	85	33 ⁴

¹ Perrins (1979); ² Hawthorn and Mead (1975); ³ Lack (1965); ⁴ Newton (1972).

Table 3 Quality of primary feathers of European starlings in relation to rate of molt measured experimentally in Cambridgeshire, England

Parameter	Fast molt	Slow molt
Duration of molt (days)	73	103
7th primary, fresh mass (mg)	51.7	55.6
9th primary, mass after 9 months' wear (mg)	57.2	71.1
Rachis keratin hardness (kg/mm ²)	10.0	12.3
Deflection under standard load (mm)	16.7	13.2
8th primary, Young's modulus (Gpa)	2.6	2.3

Rate of molt was manipulated by exposing birds to different photoperiods (constant long days = slow molt; shortening days = fast molt, from Dawson et al., 2000).

birds were up to 167% greater than estimates of species presence/absence based on an annual census of breeding birds. In other words, although all species were present in the second year, nearly all the individuals were new birds.

In Ohio, annual survival of adult chickadees across a sample of 47 woodlots varied from about 40% in very small woodlots with no supplemental food to about 65% in large woodlots that contained supplemental food in the form of permanent bird feeders (Fig. 1). Similar trends were recorded in the tufted titmouse (*Baeolophus bicolor*), white-breasted nuthatch (*Sitta carolinensis*) and downy woodpecker (*Picoides pubescens*) (Doherty and Grubb, 2002b). The importance of adequate winter nutrition and shelter was further emphasized by the finding that rate of energy expenditure in free-ranging chickadees was greater in winter than during breeding (Doherty et al., 2001).

3.3 Timing of molt and feather quality

Analysis of molt scores from great and blue tits showed that, on average, molt was delayed by about 8 days in small woods compared to large woods (Hinsley et al., 2003). This matched differences found in timing of breeding



Fig. 1 The calculated relationship between woodlot size and annual survivorship of adult Carolina chickadees in an agriculture landscape in Ohio, USA

The upper and lower curves, respectively, indicate survival in woodlots with and without supplemental food in the form of winter-long bird feeders (Doherty and Grubb, 2002b).

(Table 1). Although we have no information about the effects of timing of molt on tit feather quality, later-molting starlings showed a reduction in quality as a result of molting faster. Faster-grown primary feathers had less mass, were composed of softer keratin, were more prone to wear and were more flexible (Dawson et al., 2000, Table 3). However, Young's modulus, which depends on the structure of feather keratin (Bonser and Purslow, 1995), did not vary with rate of molt, suggesting that the measured differences were due simply to a shortage of keratin in the faster-grown feathers.

4 Discussion

In both Cambridgeshire, England and in Ohio, reduced reproductive success was found in small woodlots. Possible causes include diminished food supply, increased foraging costs, especially if birds incur increased travel costs from foraging in more than one woodlot (Hinsley, 2000), and, in Ohio, interspecific nest-site competition. Nest-site competition was not a significant factor in England, but nest losses due to predation were more common in larger woodlots. This was probably because predators such as the grey squirrel (*Sciurus carolinensis*), which is also affected by fragmentation (e.g., Fitzgibbon, 1993), were less common in small woodlots and/or because nestboxes were too few to create an active search response. Thus, nest failure in relation to woodlot size is more complex than the often assumed scenario of greater losses in smaller patches due primarily to predation (also Friesen et al., 1999; Huhta et al., 1998).

In both England and Ohio, low survival (indexed by lower persistence) was recorded in small woodlots. One possible cause may be the increased exposure to cold and windy winter weather in smaller woodlots, and hence increased energy expenditure (Doherty et al., 2001). Birds in small English woods bred and molted later than those in large woodlots. Molting later after the summer solstice exposes birds to shorter days and hence they molt faster (Morton and Morton, 1990). As demonstrated for starlings, faster molting can reduce feather quality (Dawson et al., 2000). Although we did not investigate the thermoregula-

tory ability of European starlings in relation to rate of molt, work by Nilsson and Svensson (1996) showed that late breeding (and hence presumably, late molting) blue tits had higher thermoregulatory costs in winter than earlier breeders, and suffered higher overwinter mortality.

In Ohio, birds in small woodlots without supplemental food had the lowest survival rates. In winter, this same category of birds also grew induced feathers with the narrowest growth bars, indicating poor nutritional condition (Grubb, 1995). Such reduced nutritional condition may have resulted from food shortage coupled with high winter metabolic rates. Hence slow feather growth-rates in small woodlots may result from nutritional/energetic constraints.

In conclusion, our data from the two continents indicate that, despite differences in time since fragmentation, there are some generalities to be drawn in landscapes where habitat patches are small. We found no evidence for adaptation to fragmentation, judged by the recorded declines in breeding success with woodlot size in both studies. Survival in Ohio chickadees was influenced by supplemental food in relation to woodlot size, and it is likely that such an effect also operates in England. Up to 75% of householders there provide some food for birds in their gardens, and blue and great tits are recorded at nearly 100% of feeders monitored by the BTO Garden Bird Feeding Survey (Glue, 2002). Causes for the deleterious effects of fragmentation may differ in detail, but in general, lack of resources (especially food) and exposure to inclement weather are basic elements. We anticipate tightening future comparisons by coordinating our methodologies.

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