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Local settlement in woodland birds in fragmented habitat: effects of natal territory location and timing of fledging

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Abstract

Factors such as early fledging and natal territory location have been shown to influence dispersal and settlement success of woodland birds. Early fledging allows for earlier dispersal, increasing the chances of an individual locating good quality habitat. However, for birds in fragmented woodland, the advantages of early dispersal may be modified by natal territory location in relation to the availability of suitable habitat in the surrounding landscape. Connecting habitat corridors may promote dispersal, and connectivity in landscapes is usually considered as positive, but this may not always be the case. In landscapes where habitat is highly fragmented, corridors may promote departure, but leave dispersers with little chance of success.

An individual-based Spatially Explicit Population Model was used to investigate the effects of timing of fledging, natal territory location and proximity to potential dispersal corridors on local settlement rates. Modelling was based on both hypothetical and real woodlands and used marsh tit as an example woodland bird. For each modelled scenario, the number of young that settled was recorded for each territory, the overall results being expressed as the mean percentage settlement rate per territory.

Territory location and edge effects were both found to influence dispersal and settlement rate. Fledging early clearly demonstrated a general advantage for local settlement success. However, territory location, in relation to the likelihood of dispersing out of the wood was found to interact with fledging order. Fledglings from internal territories had an advantage over those from edge territories and local settlement rate could be reduced by a location favourable to emigration. In general, the effect of exits was to reduce the settlement rate of early fledging young while that of later young tended to increase. In highly fragmented woodland, fledging late from a well-connected edge territory would appear to be the worst case scenario.

Keywords

Fledging order, juvenile dispersal, marsh tit, PatchMapper, SEPM

1. Introduction

Post-fledging survival and recruitment in birds usually decline with time through the breeding season (e.g. Morton 1992, Verboven and Visser 1998, Verhulst and Nilsson 2008). Detrimental effects of timing may also affect fitness of fledglings in later life (Haywood and Perrins 1992, Visser and Verboven 1999). Thus, in general, early fledging should be associated with greater lifetime reproductive success (Nilsson 1989a, Visser and Verboven 1999). Early young can make the transition to independence while food is still abundant and, by virtue of greater experience, may have a competitive advantage over later fledging conspecifics (Kluijver 1951, Nilsson and Smith 1985). Early fledging also correlates with earlier onset of post-juvenile moult (Bojarinova et al. 1999) which should ensure adequate nutrition and optimum daylength for the production of good quality plumage (Dawson et al. 2000).

Fledging early also allows for earlier dispersal and for potentially longer dispersal distances which may in turn increase the ability of an individual to locate good quality habitat (Nilsson 1989a, Matthysen et al. 1995). Timing of dispersal and establishment in winter flocks has frequently been shown to influence social dominance, survival and later reproductive success (e.g. Hogstad 1987, Nilsson and Smith 1988), with earlier birds having the advantage. While the timing of dispersal in nuthatches *Sitta europaea* in small forest patches was not affected by isolation (Matthysen and Currie 1996), that of crested tits *Lophophanes cristatus* was delayed (Lens and Dhondt 1994). Thus in more sedentary species and those reluctant to cross open spaces (Russell 2001, Bélisle and Desrochers 2002, Desrochers and Bélisle 2007), connecting habitat corridors may promote dispersal. Connectivity in landscapes is usually considered to be positive, (Taylor et al. 1993, With et al. 1997, Bailey 2007, but also see Simberloff et al. 1992, Willson et al. 2001), but where habitat is highly fragmented and most patches are small and scattered, corridors may promote departure, but then leave dispersers with long search times and relatively little chance of success.

In this paper, we investigate the influences of natal territory location, relative to the locations of potential dispersal corridors, and timing of fledging on post-fledging settlement within a focal woodland. We use an individual-based Spatially Explicit Population Model (SEPM) (Alderman et al. 2005, Alderman and Hinsley 2007) and use the marsh tit *Poecile palustris* as an example to show that the potential for successful establishment after initial natal dispersal may be affected by natal territory location within a woodland patch and that this influence may be positive or negative depending on the availability of surrounding woodland. The marsh tit is largely confined to mature deciduous woodland, seldom breeds in habitat patches of less than 4-5 ha and is relatively sedentary (Cramp and Perrins 1993, Broughton et al. 2006, Hinsley et al. 2007). Natal dispersal is poorly understood in this species, with one Swedish study finding typical movements of 0.8 – 1.0 km (Nilsson 1989a). In Britain, natal and breeding dispersal is considered to be similarly short, with 85% of 108 ringing recoveries being less than 5 km from the place of ringing, and only 1% greater than 20 km (Sellers 1984). In contrast, in British blue tits *Cyanistes caeruleus* and great tits *Parus major*, 95% of observations of dispersal distances in the first three months after fledging were up to 8 – 11 km (Wernham et al. 2002).

Although many factors may influence dispersal and settlement success, in the lifetime reproductive success of the marsh tit, timing of fledging is vital; initial post-fledging settlement success, dominance in winter flocks and subsequent breeding success are all linked with early fledging and early dispersal (Nilsson and Smith 1985, Nilsson and Smith 1988, Nilsson 1989a and b). In continuous woodland, or well-wooded landscapes, early dispersers have the advantage. However, for birds in highly fragmented woodland, the advantages of early dispersal may be modified by natal territory location. An individual from a territory in close proximity to a connecting hedgerow, or other potential habitat corridor, may leave its natal wood, but have little chance of finding other suitable habitat. Thus territory location within the interior of a wood, reducing the initial likelihood of encountering a habitat corridor, may confer an advantage in landscapes where most habitat is in small and scattered patches.

2. Methods

2.1. Study Area

The study area was based on Monks Wood National Nature Reserve, which is located in Cambridgeshire, eastern England ($52^{\circ}24'N$, $0^{\circ}14'W$) (Fig. 1). Monks Wood is a 157 ha deciduous woodland, dominated by mature Common Ash *Fraxinus excelsior*, Pedunculate Oak *Quercus robur* and Field Maple *Acer campestre* with scattered areas of Silver Birch *Betula pendula* and European Aspen *Populus tremula* and some areas of elm *Ulmus* spp. (Broughton et al. 2006). The understorey is dominated by Common Hazel *Corylus avellana*, hawthorn *Crataegus* spp. and Blackthorn *Prunus spinosa*, with scattered Honeysuckle *Lonicera periclymenum*, Dogwood *Cornis sanguinea* and Wild Privet *Ligustrum vulgare* (Broughton et al. 2006). The wood is criss-crossed by wide and narrow rides and is interspersed with glades, patches of scrub and young trees and areas of rough grassland. It also includes 9.4 ha of open fields and is adjoined along part of its southern boundary by a 37 ha, largely conifer, plantation (Bevill's Wood).

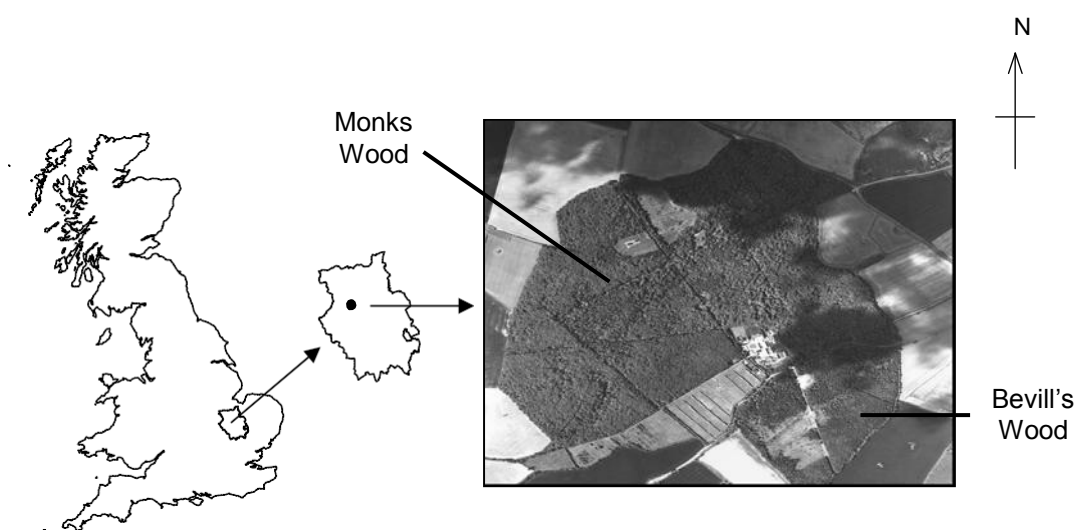


Figure 1: The location of Monks Wood and its position within the county of Cambridgeshire in eastern England, UK.

2.2. Model Description

2.2.1. Introduction

This study uses PatchMapper, an individual-based SEPM, which combines an individual-based population simulator with a grid-based representation of the landscape. Coded in Java, for portability, a set of interactive screens control the simulation and enable user-selection of life history, dispersal and territorial parameters. Different habitat configurations and landscape management scenarios can be evaluated with a choice of landscapes, either input from a GIS or user generated. During a simulation run, the locations of individuals are superimposed on the landscape, presenting a real-time visual output to the user. PatchMapper is further described in Alderman et al. (2005), with typical applications given in Alderman et al. (2005) and Alderman and Hinsley (2007). The description of the model configuration used for the investigations detailed in this paper which follows is based on the Overview, Design concepts and Details (ODD) protocol as proposed by Grimm et al. (2006), for describing individual based models.

2.2.2. Purpose

The model was configured to use the marsh tit as an example woodland bird, with both hypothetical and real woodlands used as model landscapes. The objective was not to model marsh tit dispersal per se, but rather to investigate how location of the natal territory, influencing the probability of dispersal out of the natal wood, and the relative timing of dispersal affected the success of the rapid initial settlement phase (see below). The modelling therefore concentrated on the basic strategy of locating and occupying territory vacancies, with the possible outcomes being successful initial settlement, dispersal out of the wood or mortality.

2.2.3. State variables and scales

The model comprises two connected levels: individuals and landscapes. Individuals are described using the state variables age, gender, identification of the territory which the individual occupies and identification of the wood in which the territory is located.

Landscapes were digitised onto 600 x 600 square celled lattices, with a resolution of 3 m per cell length. In the model, landscapes are described using state variables identifying each cell as habitat (wood) or non-habitat (matrix) and whether a habitat cell is also a territory cell. Territories have three possible states: unoccupied, occupied by a single bird of either gender or occupied by a pair.

Individuals move across the landscape using a vector-based correlated random walk. The walk characteristics are based on the state variables identifying the main dispersal direction, the turn angle either side of the main dispersal direction and the number of steps between turns. When reaching the edge of a wood a state variable allows or denies exit. During dispersal, reference is made to the grid-based landscape to determine behaviour appropriate to the wood extent and territory location and number.

2.2.4. Process overview and scheduling

The model proceeds in yearly cycles. Each cycle starts with winter mortality. Surviving single birds then disperse, with the aim of forming a breeding pair. Breeding then takes place. Surviving fledglings then disperse throughout the wood and either settle in a territory, leave the landscape or suffer dispersal mortality. The final stage of the year is to record the number of young fledging from each territory and those that successfully settle. The model cycle is given in figure 2.

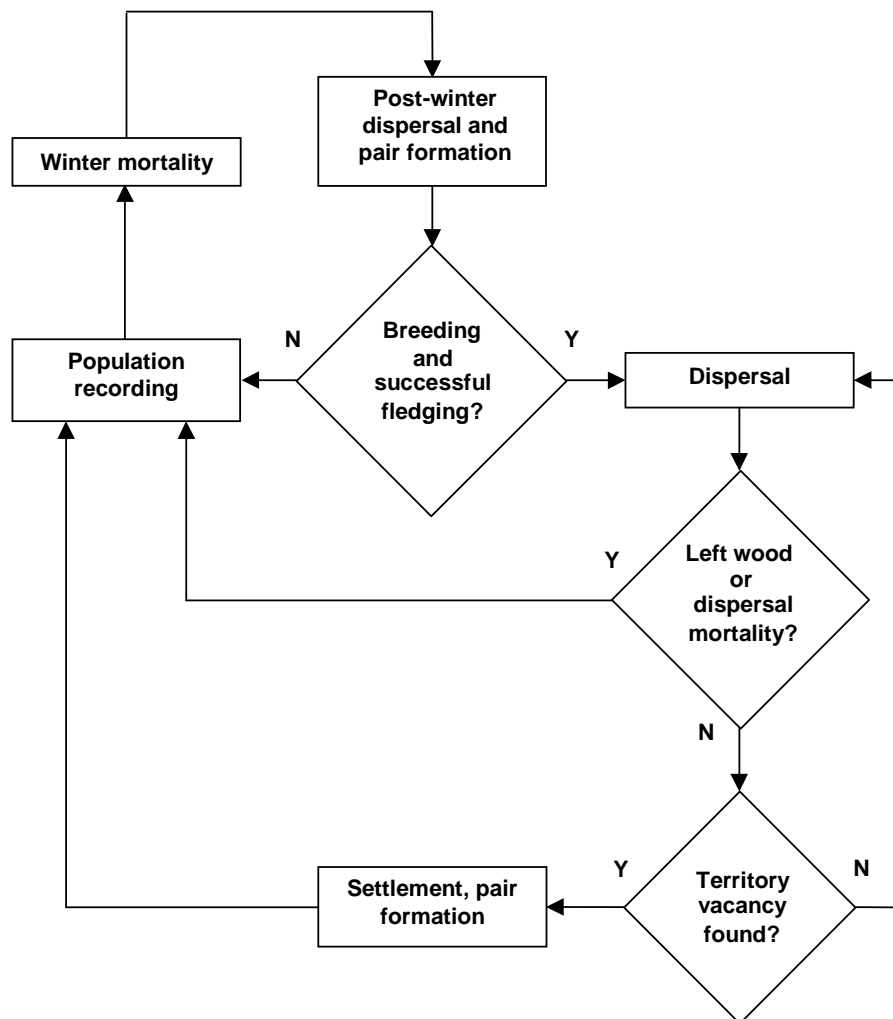


Figure 2: The model cycle, showing the stages executed during each 'year'. The simulation starts by seeding each territory with a breeding pair, whereupon the user-selected number of annual cycles are executed, starting with the winter mortality phase.

2.2.5. Design concepts

Species Modelling

The British marsh tit is a small (c. 10 g), hole-nesting bird, largely confined to mature deciduous woodland (Cramp and Perrins 1993, Broughton et al. 2006, Hinsley et al. 2007). The species is sedentary, with pairs maintaining mutually exclusive territories between February and June (Broughton et al. 2006). Breeding takes place in the spring and the species is single brooded (Cramp and Perrins 1993). After fledging, the young disperse from the natal territory and attempt a rapid initial settlement in a territorial vacancy or in a subdominant position within territory/homorange occupied by adults (Nilsson and Smith 1988, Nilsson 1989a). Dispersal of all young in a fledged brood was assumed to occur on the same day, as recorded by Morley (1953), although there is evidence that this is not always the case (Nilsson and Smith 1985). Marsh tit juvenile dispersal was modelled by applying behavioural rules based on these life-cycle characteristics with reference to the structure of the wood, including territory shape and location, an approach in which both habitat structure and species' characteristics govern population sizes and distribution (Alderman et al. 2005).

Including sub-dominant settlement (based on an assumption of, for example, two such vacancies permitted per territory) would not have changed the relative effects of natal territory location or timing. The following values were used to model the success of juvenile dispersal, i) fledging success (of hatched young): 80-90%; ii) number of fledged young: 7-9; iii) gender ratio of young: 50:50; iv) adult winter mortality: 45-55%; v) juvenile winter mortality: 64%; vi) dispersal mortality: 0.01 % per 3 m step; (parameters estimated from Broughton and Carpenter unpubl. data).

Landscape Modelling

Two sets of landscapes, one hypothetical and one real, were employed. To illustrate the general effects of territory location and timing of fledging on juvenile post-fledging settlement rate, a hypothetical square woodland map, with fixed territory sizes and exit points, was used (Fig. 3). To investigate these effects on actual settlement rate, a map of Monks Wood, including the number, location and spatial extent of the actual marsh tit territories recorded in 2007, was used (Fig. 4).

The hypothetical landscape

The hypothetical map comprised 25 territories, and to avoid any scale effects, used a modelled territory size of 4 ha corresponding to the mean marsh tit territory size (4.1 ha) previously recorded for Monks Wood (Broughton et al. 2006). To model emigration from the natal wood via connecting habitat corridors, any birds which reached the corner areas, marked by the black lines in figure 3, left the landscape. The exit areas extended 20 pixels either side of the corners themselves, giving a scale exit area of 120 m at each corner. Any birds reaching all other edges reflected back into the wood at a randomly chosen angle within ± 80 degrees of the reciprocal of mean dispersal direction.

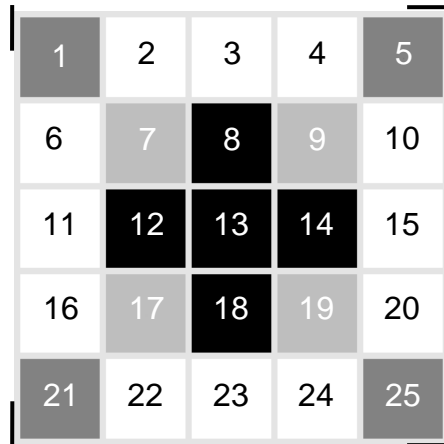


Figure 3: The modelled hypothetical landscape, showing the numbered territories. Birds were allowed to leave from the corners of the map if they reached an edge adjacent to the black lines, as detailed in the text. For clarification and reference in the text, the squares have been shaded to denote ‘central’ (black), ‘internal’ (light grey), ‘edge’ (white) and ‘corner’ (dark grey) territories. The territory numbers were used for the modelling and for reference in the text.

The real landscape

The modelled real landscape was based on the areal extent of Monks Wood and included the 22 marsh tit breeding territories as mapped in 2007 (Broughton, unpubl. data). Territory size was a little larger than that recorded for 2004 (Broughton et al. 2006), ranging from 3.6 ha to 9.6 ha, with a mean of 5.7 ha. Points at the wood edge adjoined by hedgerows or additional woodland likely to act as exit points for emigration were also identified, labelled A-H in figure 4a. These ‘exit points’ are discussed further in the section covering species modelling.

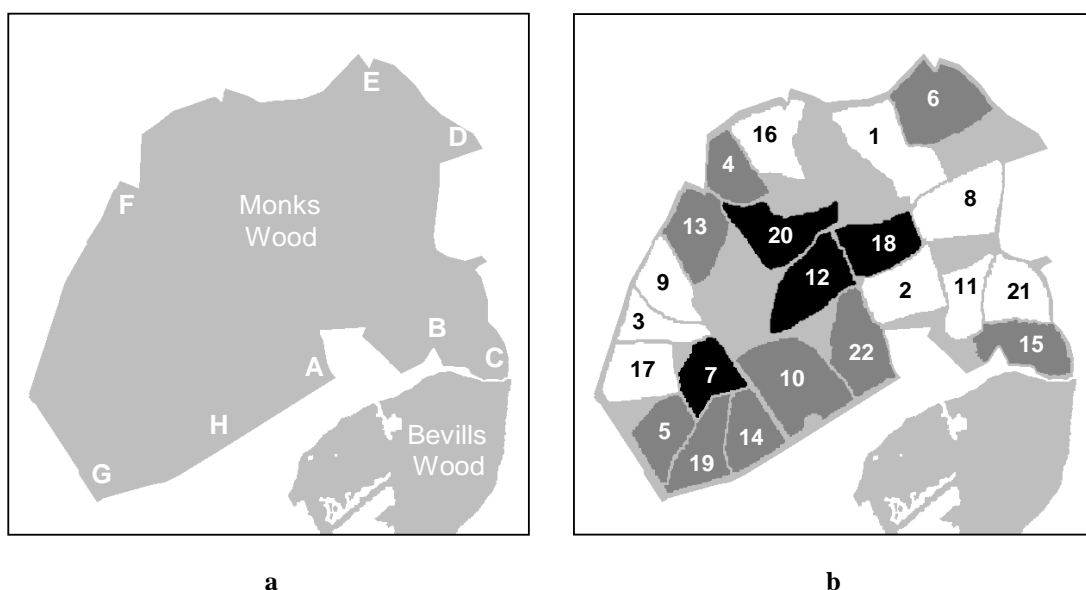


Figure 4: The modelled real landscape. Fig. 4a shows the modelled wooded area. Possible exit points, where hedgerows join the wood are marked A-H. Exit points B and C mark the gap between Monks and Bevill's Woods, formed by a minor road which the birds cross readily. Fig. 4b shows the location and extent of the 22 modelled marsh tit territories as mapped during the 2007 breeding season. For clarification and reference in the text, the squares have been shaded to denote 'internal' (black), 'edge-near-exit' (dark grey) and 'edge' (white) territories. The territory numbers were used for the modelling and for reference in the text. The un-numbered light grey areas were unoccupied by breeding marsh tits in 2007 (most of the unoccupied internal area is unsuitable or low quality habitat).

Dispersal modelling

In the model, dispersing marsh tits search for a territory by traversing the wood with a correlated random walk. Individuals moved a $\pm 0 - 35$ degree zig-zag course, centred about a main dispersal direction, with a modelled 3 m - 45 m movement before each change of direction. The number of steps between directional changes and the directional changes themselves were determined at random from a uniform distribution. The result was a nearly straight dispersal path; such paths are thought to maximise the chance of habitat detection over a perfectly straight one (Zollner and Lima 1999). To model the possibility of mortality during dispersal, a per-step dispersal mortality probability of 0.01 % per 3 m step was applied.

Whenever a territory was encountered it was checked for a vacancy. Depending on its occupancy status and the gender of the dispersing bird, the territory was either occupied as a lone bird or a pair formed. If no suitable vacancy existed, the disperser was forced to search for further suitable vacant territories within the wood. In these cases, the correlated random walk was interrupted and the bird followed the edge of the territory until a non-territory cell in the dispersal direction was encountered, when the correlated random walk was resumed (Fig 5a).

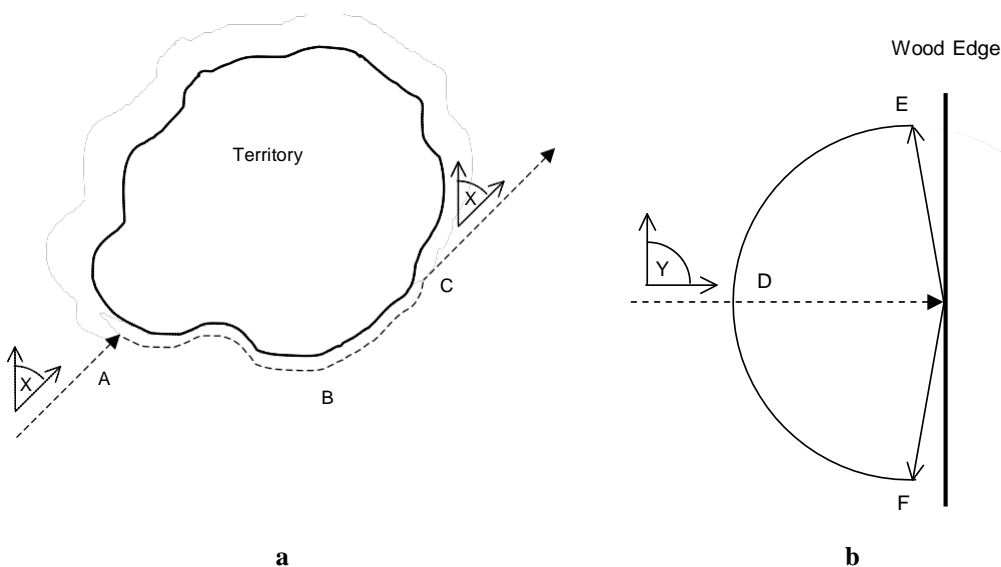


Figure 5: The principles behind modelling encounters with (a) territory edge and (b) wood edge. When an occupied territory edge is encountered (Fig. 5a, track A), the territory edge is followed (track B)

until a non-territory cell in the encountering dispersal direction (X) is detected. When this occurs, the territory edge is left (track C). Tracks A and C lie in the same dispersal direction (X). When a wood edge is encountered (Fig. 5b, track D at bearing Y), a reflecting angle ± 80 degrees of the reciprocal of track D is calculated and used as the mean dispersal angle (bearings E-F).

The unoccupied areas of the wood shown in figure 4b usually coincided with the presence of open fields and areas of scrub and young trees which constitute zero or poor quality habitat (Broughton et al. 2006, Hinsley et al. 2007). Observations of marsh tits leaving Monks Wood showed that birds avoided crossing significant expanses of open ground but instead used habitat corridors such as connecting hedgerows and the cover offered by the proximity of Bevill's Wood (Fig. 4a) (Broughton and Bellamy, pers obs). Therefore, to model these observations, any birds that reached the wood edge at an exit area (Fig. 4a) dispersed out of the wood into the landscape via the habitat corridor. Any birds reaching parts of the woodland edge which were not exit areas reflected back into the wood at a randomly chosen angle within ± 80 degrees of the reciprocal of mean dispersal direction (Fig. 5b). The exit areas varied in length, as set out in table 1. The exit areas themselves were points at which connecting hedgerows met Monks Wood. The length of each exit area was chosen to reflect the portion of wood edge from which the connecting hedgerows were thought to be visible by a marsh tit. One exception to this is exit area B, which borders a minor road between Monks and Bevill's Woods. Birds leaving from all exits points, other than point B, were not disallowed from returning but in practice very few did and too few to affect the results. To avoid biasing the results, any bird reaching edge B moved into Bevill's Wood, but was not allowed to return. Marsh tits are generally considered to be poor dispersers and unlikely to cross open spaces, thus this scenario of restricting emigration to habitat corridors would also apply to other species reluctant to leave cover.

Exit Area	Pixel Edges	Scale Edge Length, m
A	26	78
B	195	585
C	17	51
D	27	81
E	87	87
F	21	63
G	26	78
H	26	78

Table 1: The number of pixel edges and their equivalent scale length for the modelled wood exit areas, based on the location of real habitat corridors..

To ensure that only local settlement was modelled, immigration into the landscape was not allowed. Birds reaching the landscape edge, after leaving Monks Wood, were absorbed (i.e. they were removed from the model), which is a more realistic approach

than modelling with reflective or wrapped boundaries (e.g. Pulliam et al. 1992, Tischendorf and Fahrig 2000).

3. Tests

In order to determine the effects of territory location and fledging order, i.e. relative timing of fledging between territories, on settlement rate, three sets of tests were conducted. The first test set used the hypothetical square landscape, with the remaining two sets using the Monks Wood study area itself. All test sets were run for 50,000 yearly cycles. After each cycle, the number of young dispersing and the number of young that settled were recorded for each territory and the overall results were expressed as the mean % settlement rate. The test sets were as follows:

Test Set 1: Effects of territory location and fledging order in a hypothetical square woodland

The null hypothesis is that natal territory location and fledging order have no effect on local settlement rate. To investigate any general effects of the interaction of territory location and fledging order on settlement rate, the three scenarios detailed in table 2a were run using the square landscape (Fig. 3). The order of the randomly fledging territories was randomised for each yearly cycle. To avoid bias, for the groups of territories fledging first, an individual bird fledged from each territory in the group in turn, until all had left, with the order being randomised for each yearly cycle (Fig. 2). Dispersing birds were allowed to leave the landscapes if they reached the exit corner cells (Fig. 3).

Landscape/Location	Fledging Order
a) Square Woodland	<p>All territories in random order</p> <p>Centre territories (8, 12, 13, 14, and 18) first, the remainder in random order</p> <p>Edge territories (2, 3, 4, 6, 10, 11, 15, 16, 20, 22, 23 and 24) first, the remainder in random order</p>
b) Monks Wood	<p>All territories in random order, without exit from wood</p> <p>All territories in random order, exit from wood allowed</p> <p>Edge territory not adjacent to an exit point (3) first, the remainder in random order</p> <p>Edge territory adjacent to an exit point (6) first, the remainder in random order</p> <p>Internal territory (12) first, the remainder in random order</p>

Isolated edge territory adjacent to an exit point (15) first, the remainder in random order

Table 2: Details of the three scenarios (a) testing the effects of territory location and timing of fledging using the hypothetical square wood (test set 1) and the six scenarios (b) used to test the effects of territory location, early fledging and exit points using the real Monks Wood landscape (test set 2).

Test Set 2: Effects of territory location and fledging order in the real Monks Wood landscape

Young dispersing from territories located near exit points may be more likely to leave the wood. Young from such territories may therefore have a lower initial local settlement rate than those from other territories. To test this hypothesis separately from any effects of fledging order, two tests (table 2b) were run in which all territories fledged in random order for each yearly cycle, but with the first test restricting the birds to Monks Wood (i.e. no exit points) and the second one allowing the birds to leave at the exit points (Fig. 4).

Fledging order should influence local settlement rates for individual territories. Those that fledge first should be more successful, but it is likely that location will also influence the results. Interior territories are surrounded by other territories, with no immediate access to exit points. Therefore, local settlement rate may increase with increasing distance from the wood edge. To test this hypothesis, one territory of each of three types of territories with increasing distance from exit points (table 2b) was allowed to fledge first. The order of the randomly fledging territories was randomised for each yearly cycle, with dispersing birds being allowed to leave the wood if they reached the exit points (Fig. 4a).

Test Set 3: Comparison of modelled and observed local settlement rates in the real Monks Wood landscape

The local settlement rate for individual territories is likely to depend on both location and timing of fledging. As a comparison with the scenarios used in test sets 1 and 2, the model was run using the observed timing of breeding and territory locations recorded for Monks Wood marsh tits in 2007. During the 2007 breeding season, all territories (Fig. 4) and nest sites in the wood were located (see Broughton et al. 2006 for methods). Of the 22 territories, 21 contained nests which progressed as far as hatching young and thus the relative order of fledging across territories was estimated from the hatch dates. Nestlings were individually colour-ringed before fledging in 15 nests. Of the other six nests, two were inaccessible for ringing (territories 5 and 15) and four failed to produce young due to predation or flooding (territories 13, 18, 21 and 22). A pair was present on territory 19, but the female arrived relatively late in the season and no evidence of a nest was found. In July/August 2007, following post-fledging dispersal, the wood was searched for colour-marked birds and the numbers of juveniles from each territory that had achieved initial settlement were recorded. The numbers which subsequently bred in the wood in 2008 were also determined. The observed initial settlement rate, and eventual establishment to breed, was compared with the predictions of the model of mean settlement rate in relation to fledging order

and territory location. Breeding in marsh tits tends to be highly synchronous (as might be expected given the importance of timing) (Wesolowski 1998) and thus broods from different territories could fledge on the same day. This was observed to occur within Monks Wood and the identified groups of territories and their estimated order of fledging are given in table 3. Within each group of territories, an individual bird dispersed from each territory in the group in turn, until all had left, with the order being randomised for each yearly cycle. The test was run allowing birds to exit from the wood, as described above, and also without allowing exit.

Group	Territories Fledging
1 st	6,12,17,20
2 nd	3
3 rd	8,13
4 th	1,2,10,18
5 th	7,9
6 th	16
7 th	4,5,14
8 th	15,21
9 th	11,22

Table 3: The groups of territories in their estimated fledging order, as described in the text.

3. Results

Test Set 1: Hypothetical square woodland

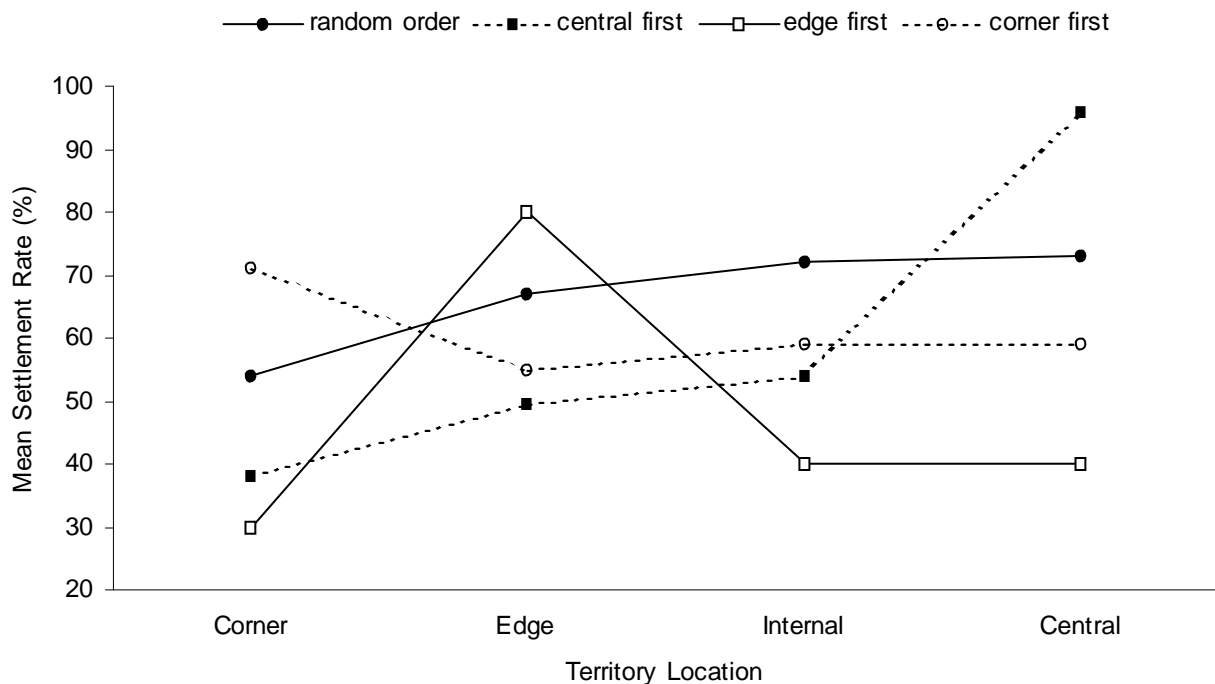


Figure 6: Settlement rate in relation to territory location and fledging order in a hypothetical square woodland. Territories are grouped according to location, namely corner (n = 4), edge (n = 12), internal (n = 4) and central (n = 5), as shown in Fig. 3. Points indicate the mean settlement rates for the groups when, i) fledging occurs in random order (solid circles, solid line), ii) central territories fledge first (solid squares, dotted line), iii) edge territories fledge first (open squares, solid line) and iv) corner territories fledge (open circles, dotted line). For clarity, points within each of scenarios i) to iv) are joined by lines. Note: \pm SE ranges are not shown, as they are too small to be visible beyond symbols.

When fledging in random order, settlement success increased with distance from an exit point due to the greater chance of encountering a territory vacancy before reaching an exit point (Fig. 6). Hence the lowest chance of success was predicted for the territories (1, 5, 21 and 25) in the corners adjacent to the exit points. The advantage of a central territory location (8, 12, 13, 14 and 18) was further enhanced by fledging early, and consequently also reduced the success of the remaining territories compared to random order. Fledging early from an edge territory again conferred an advantage and reduced the success of the other territories. This scenario also demonstrated an effect of competitor abundance; with nearly half the territories (2, 3, 4, 6, 10, 11, 15, 16, 20, 22, 23, 24) fledging early, the chance of success of young from the later territories was much reduced, even for the central territories. Fledging early from a corner territory again increased settlement rate, but less so than for edge, and especially, central territories because of the proximity to the exit points and increased chance of emigration out of the wood.

Test Set 2: Real Monks Wood Landscape
Fledging in random order with and without exits

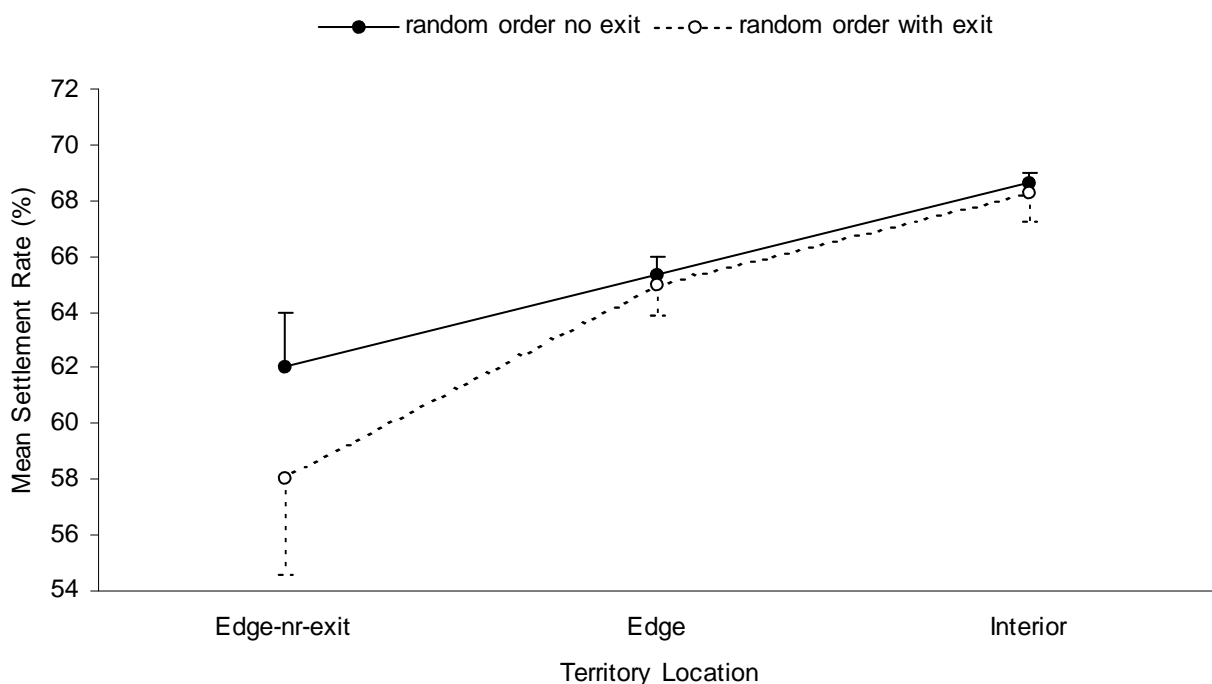


Figure 7: Settlement rate in relation to territory location and fledging order in Monks Wood. Territories are grouped according to location, namely edge-near-exit (n = 9), edge (n = 9) and internal (n = 4), as shown in Fig. 4. Points indicate the mean (+ or - SE) settlement rates for the groups when, i) fledging occurs in random order and birds are not allowed to exit the wood (solid circles, solid line, + SE) and ii) fledging occurs in random order and birds can leave from exit points (open circles, dotted line, - SE). For clarity, points within each scenario are joined by lines.

When fledging in random order without allowing exit from the wood, the overall pattern was similar to that found for the square landscape. Young from the most central (internal) territories (7, 12, 18 and 20, Fig 4) had the greatest settlement rates compared to those on the edges (Fig. 7). Even without allowing birds to leave the wood, settlement rates tended to be lowest for edge territories located near exits. This was probably an isolation effect which reduced the birds' chances of encountering territory vacancies (see below, Interaction of fledging order and location). Adding the possibility of leaving the wood at an exit point made surprisingly little difference except for the edge-near-exit territories. This was probably due to the more complex shape of the real wood and the variation in size and shape of the real territories compared to the square landscape. This is considered further in the discussion.

Interaction of fledging order and location

For edge-near-exit territory 6, edge territory 3 and interior territory 12 fledging first increased settlement rate substantially. For territory 6, settlement rate when fledging first was 83% compared with 55% in random order (mean \pm SE for edge-near-exit territories in random order = $58 \pm 3.4\%$), for territory 3, 95% compared with 69% (mean for edge territories, random order = $65 \pm 1.3\%$), and for territory 12, 96% compared with 72% (mean for interior territories, random order = $69 \pm 1.2\%$). However, for edge-near-exit territory 15, in its isolated position in the corner of the wood and adjacent to the large exit point into Bevill's Wood (table 1), there was little advantage, settlement rate when fledging first was 40% compared with 34% in random order and was less than the mean of $58 \pm 3.4\%$ for edge-near-exit territories fledging in random order. Overall, there appeared to be little difference in the advantage of fledging first from edge or interior territories, but the overall success of fledging first from edge-near-exit territories was less than for both these other locations, and especially so when connectivity, and hence the likelihood of emigration, was large.

Test Set 3. The real Monks Wood landscape

Observed and modelled fledging order and initial settlement

Fledging order, both as modelled and as estimated from the field data, had a large influence on settlement success (Fig. 8). Three of the four territories which fledged first contributed the six individuals which remained to breed in the wood in the following year. Location also appeared to have an effect. The percentage of edge-near-exit territories from which at least one juvenile was observed to have settled in late summer was 38%, compared to 75% and 67% of interior and edge territories respectively (excluding territory 19). When running the test without allowing the birds to exit from the wood, settlement rate increased for some territories and decreased for

others; the overall pattern of the difference when exit was allowed was that settlement decreased a little for the earliest broods, but tended to increase for the later ones (Fig. 9). The largest discrepancy in this general pattern was due to Territory 15, the most isolated territory with the greatest opportunity for exit (Fig. 4).

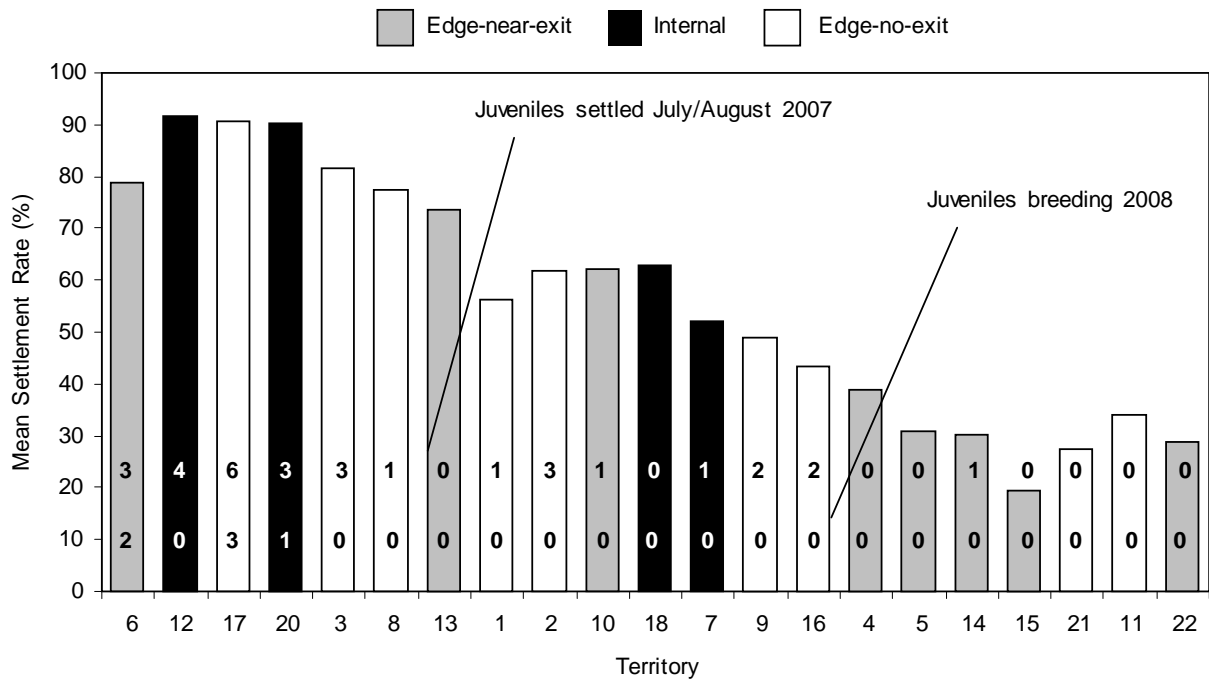


Figure 8: Modelled and observed settlement rate in Monks Wood in relation to territory location and fledging order. The bars show the results of the model run using the real landscape with the territories identified in 2007. Territories are arranged in estimated order of fledging for 2007, starting with the earliest on the left. The two rows of numbers at the bottom of the bars show the actual recorded number of juveniles from each territory settled in July/August 2007 (upper row) and the number of them observed to go on to breed in 2008 (lower row). Territory 19 is omitted, as nesting did not occur during 2007.

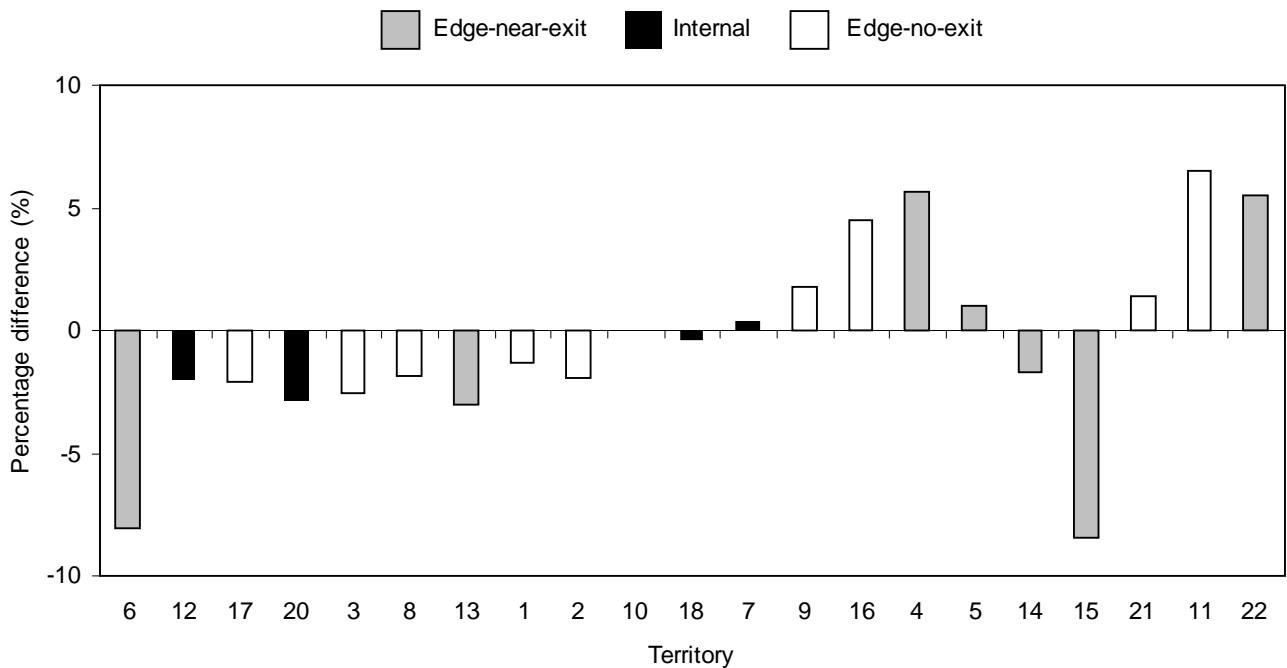


Figure 9: The percentage difference (calculated as success with exit minus success without exit) between settlement rate for birds fledging from territories within Monks Wood modelled with and without exits. The model was run with the territories identified in 2007 fledging in the order in which they were estimated to do so in 2007.

Discussion

In sedentary woodland species such as marsh tit and nuthatch, the importance of early fledging and rapid territory establishment by juveniles appears to drive several aspects of the species ecology (Wesołowski 1998). Breeding starts relatively early in the season, late replacement/second broods are rare and there is evidence of reduced clutch size and incubation times in later breeders (Nilsson and Smith 1985 and 1988b, Matthysen 1998, Wesołowski 2000). For birds breeding in large tracts of continuous woodland, fledging early should confer a competitive advantage in acquiring vacant territories, prospective mates and dominance in winter flocks (Nilsson 1989a, Nilsson and Smith 1988). In more fragmented woodland, natal territory location may become more important if location affects access to territory-based resources. The results of this study for both the hypothetical landscape and for Monks Wood clearly showed the general advantage of early fledging. Fledglings from internal territories had an advantage, even when fledging occurred in random order (Figs. 6, 7), because they were more likely to encounter more territories, with an associated chance of establishment, before dying or reaching an exit point and leaving the wood. However, depending on the degree of competition for resources within a bird's natal wood, there might be an advantage in fledging near to connecting habitat. Fledglings from territories near potential exit points would have more chance to exploit opportunities in surrounding woodland, but such opportunity would depend on the quality of other woods (Boudjemadi et al. 1999) as well as connectivity (Brooker and Brooker 2002). In sparsely wooded landscapes dominated by small patch sizes, dispersal from a rare large wood could have little chance of success and hence fledging from a well connected edge territory could be doubly unfavourable (Figs. 7, Test Set 2), i.e. slower access to potential internal territories and a greater chance of leaving the wood.

In Monks Wood, the effect of territory location with respect to the presence of exit points appeared to be relatively small compared to the effects of fledging order on settlement success (Figs. 7, 8 and 9). However, due to the shape (approximately oval) and relatively small size of the wood, the distinction between internal and edge territories was small. In a larger wood with more interior, the distinction between internal and edge territories would be greater, as illustrated by the hypothetical landscape (Fig. 6). In addition, the exits from Monks Wood are fairly evenly spaced (Fig. 4) again reducing contrast in relation to location. However, Territory 15, the most isolated and well connected edge territory did indicate how local settlement success could be reduced by a location favourable to emigration (Figs. 8 and 9, Test Set 2). These results for Monks Wood do illustrate an additional peril of woodland fragmentation for specialist woodland species. Monks Wood is the largest deciduous wood in Cambridgeshire and yet has little 'internal' habitat; only four of the 22 marsh tit territories are internal and even then they are only one territory away from the edge (Fig. 4). Thus even patches considered to be relatively large have a high proportion of

edge; smaller woods are essentially all edge which, coupled with competition for habitat space, will tend to promote emigration of young into a potentially hostile landscape. We are currently exploring effects of wood size, quality and density in the landscape on settlement rates in conjunction with emigration, timing and territory location.

When modelling success in relation to the estimated fledging order in Monks Wood in 2007, the advantage of early fledging was again clear; initial settlement success in late summer and breeding establishment in 2008 were both associated with early fledging (Fig. 8). However, territory location, in relation to the likelihood of dispersing out of the wood, interacted with fledging order. In general, the effect of exits was to reduce the settlement success of early fledging young while that of later young tended to increase (Fig. 9), i.e. dispersal out of the wood by early young decreased the competition faced by later young. In a well-wooded landscape, such an advantage for later young could be cancelled out by the arrival of early fledging immigrants, but not if surrounding woodlands were sparse, scattered and small. In highly fragmented woodland, fledging late from a well connected edge territory would appear to be the worst case scenario, as indicated by the results for Territory 15 (Test Set 2).

Timing of fledging within any given breeding season depends on both territory and parental quality (Svensson and Nilsson 1995, Verhulst et al. 1995). It has also been noted that the tendency for certain territories to be early can persist for considerably longer than the life-times of particular territory owners (Wilkin et al. 2007). However, studies detailing the joint effects of natal territory location and timing of fledging within contiguous woodland appear to be lacking. In a study of dispersal by great tits and blue tits in fragmented woodland, Matthysen (2002) investigated if the location of the nest site, and in particular its proximity to the woodland edge, influenced the tendency of fledglings to leave the patch and the direction of emigration (determined by the location of the first breeding attempt). He concluded that the tendency to disperse was independent of proximity to the edge and that the decision to emigrate was largely independent of intra-patch movements and edge effects. However, great tits and blue tits are less sedentary than marsh tits, disperse greater distances over a longer time period (Dhondt 1979, Greenwood et al. 1979), and do not show the immediate territory seeking/establishment behaviour typical of newly independent juvenile marsh tits. Thus movements by great tit and blue fledglings within their natal woods could well be disconnected from the tendency to disperse. Matthysen (2002) did find that great tits tended to disperse in a direction consistent with that of the edge nearest to their natal site. He suggested that this might arise from pre-dispersal exploratory movements beyond the natal patch borders and might even occur in the company of parents during extensive post-fledging movements. Blue tits did not show this effect and no directional dispersal was detected in a different study (Sharp et al. 2008) of long-tailed tits. Marsh tit family parties can move more widely than the 4-5 ha of the breeding territory, but will remain in its general vicinity (due to the adults' attachment to their territory) and will not leave the wood (Nilsson and Smith 1985). The fledglings also disperse within 15 days and thus there is no extensive post-fledging movement of young prior to independence. Therefore, although our conclusion that territory location and edge effects can influence dispersal and settlement rate in marsh tits differs from that of Matthysen (2002) for great and blue tits, this may simply reflect genuine ecological differences between the species.

Landscape modification by human activity tends to reduce semi-natural habitat to small, scattered patches (Sala et al. 2000, Hinsley et al. 2009). Pressures on land use produce a fine-grained landscape within which large tracts of particular habitat types are usually rare. For habitat specialists confined to such larger patches, territory quality may be influenced by location within the patch. Fledging success may be influenced by the shape and connectivity of the patch and a territory's location within the patch. When the surrounding landscape contains little alternative habitat, such effects may reduce patch quality more than expected from area alone and may contribute to threshold effects in population collapse (e.g. Jansson and Angelstam 1999, Radford et al. 2005).

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