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Patterns of nest placement in a population of Marsh Tits *Poecile palustris*.

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Abstract

There is a limited understanding of the factors influencing nest placement among territorial birds, including the roles played by habitat, conspecific attraction and female experience of a previous nesting location. We used seven years of Marsh Tit (*Poecile palustris*) nest site and territory data, and high-resolution vegetation models derived from remote sensing, to investigate spatial patterns of nest placement with regard to previous female experience and age, conspecific attraction, and habitat in a woodland environment. We found no evidence for an effect of conspecific attraction or previous nest location on nest placement within the territory. However, first-year (FY) females placed nests in a random spatial pattern within their territories, and after first-year (AFY) females predominantly placed nests within the central parts of their territories, away from conspecifics.

Nest sites were located in areas of comparatively taller overstorey and less understorey than other parts of the territory, although absolute differences were not substantial. Both female age groups nested in areas of the territory where the overstorey contained relatively more Common Ash (*Fraxinus excelsior*) than elsewhere. A concentration of this tree species within the core areas of the territories of AFY females may have explained the tendency for that age group to place nests preferentially in those areas. There was no concentration of Common Ash within the territory cores of FY females, which may have explained the random placement of nests within their territories.

Keywords: Lidar, Marsh Tit, Nest placement, Remote sensing.

Introduction

The factors affecting nest site selection are a recurrent theme in ornithological research. For territorial species, studies of nest placement have reported an influence of habitat (Atiénzar et al 2009), topography (Bayard and Elphick 2010), previous experience (Muller et al. 1997) and the spatial arrangement of conspecifics (e.g. Ramsay et al. 1999; Melles et al. 2009). Among the *Poecile* genus of cavity-nesting tits and chickadees of the Holarctic, the results have been conflicting. While some studies have found a positive association between nest location and habitat, such as tree canopy volume (Smith 1976) or the density of large trees (Sedgwick and Knopf 1990), Ramsay et al. (1999) were unable to support the hypothesis that habitat is a major factor in nest site selection. There is also little evidence of an effect of female experience on nest placement. Mennill et al. (2004) concluded that Black-capped Chickadees (*P. atricapillus*) selected nest sites based on conspecific attraction, with females that were paired to low-ranking males placing their nests close to the territories of high-ranking neighbouring males. This behaviour did not facilitate extra-pair copulations, however, and the advantage was unclear. The Marsh Tit (*P. palustris*), a 10-12 g sedentary woodland species, adopts a similar breeding strategy to the Black-capped Chickadee, whereby pairs occupy exclusive spring territories and nest sites are selected by the female (Morley 1953; Broughton et al. 2006), but there is no information for the Marsh Tit on the factors governing nest placement within the territory.

The understanding of the influence of vegetation structure and composition on patterns of bird distribution is being advanced by the increasing use of remote sensing methods (Bradbury et al. 2005; Gottschalk et al. 2005). For woodland birds in particular, lidar (light detection and ranging) technology can describe the three-dimensional habitat structure at a

high spatial resolution and at a landscape-scale (Broughton et al. 2006; Martinuzzi et al. 2009; Goetz et al. 2010), while optical imagery can provide information on the vegetation species composition (Goetz et al. 2010; Hill et al. 2010). The combination of habitat datasets derived from remote sensing and bird distribution data derived from field surveys can permit powerful analyses of bird-habitat interactions (Fuller et al. 2005; Goetz et al. 2010).

We aimed to investigate the influence of habitat, female experience of previous nest locations, and conspecific attraction on Marsh Tit nest placement, using seven years of territory, occupancy and nest site data. The application of comprehensive, high-resolution models of canopy and understorey vegetation, derived from airborne remote sensing, enabled detailed spatial analysis of nest sites, territory configurations, habitat structure and vegetation composition.

Methods

Territory and nest data

The study was conducted in 153 ha of woodland in the Monks Wood National Nature Reserve in Cambridgeshire, UK (52° 24'N, 0° 14'W; hereafter 'Monks Wood'), and six neighbouring patches of woodland that lie within 4 km to the east of that site (hereafter the 'Eastern Woods'), four of which are 4-7 ha in size and the other two 27 ha and 70 ha. Monks Wood is a lowland, semi-natural ancient woodland, dominated by Common Ash (*Fraxinus excelsior*), English Oak (*Quercus robur*) and Field Maple (*Acer campestre*) in the tree canopy, with small amounts of Silver Birch (*Betula pendula*), European Aspen (*Populus tremula*) and elm (*Ulmus* spp.). The understorey layer is dominated by hawthorn (*Crataegus*

spp.), Blackthorn (*Prunus spinosa*) and Common Hazel (*Corylus avellana*) (Broughton et al. 2006). Monks Wood was clear-felled around 1918 and has regenerated naturally since that time, with 90% of the wood being unmanaged. The Eastern Woods are predominantly mature, unmanaged woodland with an overstorey dominated by Common Ash and English Oak, with some elm and Field Maple, and an understorey of Common Hazel, Blackthorn and hawthorn.

Almost the entire population of Marsh Tits in Monks Wood were individually marked with colour-rings between 2003 and 2010. Birds were sexed and aged as first-years (FY) or older (after first-years: AFY) according to Broughton et al. (2008). Six female spring immigrants that could not be aged before the post-breeding moult were assumed to be FY, because this age group formed 92% of the female immigrants of known age (Broughton et al. 2010). Each spring, the boundaries of all 21-23 Marsh Tit territories in the wood were delineated and digitised in a Geographical Information System (GIS), based on observations of territorial behavior between February and May (Broughton et al. 2006, 2010). A total of 117 nest locations (112 in natural cavities, five in nest-boxes) were identified in Monks Wood during intensive surveying of each territory in April and May of 2004-2010. Nest locations were digitised using coordinates from a hand-held GPS receiver (*Garmin eTrex H* model), with further correction based on reference to features in digital habitat models (see below), giving an estimated accuracy of 3-12 m. Only nests from a pair's initial breeding attempt each year were included in analyses, as second attempts may be constrained by the availability of time (Wesołowski 2000).

The Eastern Woods were used to test the wider applicability of nest-habitat interactions observed in Monks Wood (see below), and were each surveyed 4-8 times during April-May

in 2008 or 2010 in order to determine the approximate territory positions of their un-ringed Marsh Tit populations, using territory-mapping techniques that included the use of playback of recorded calls (Bibby et al. 2000). The boundaries of 15 territories were estimated and digitised, and were termed 'approximate territories' to acknowledge the lower precision than that achieved for the digitised Monks Wood territories. The locations of nests within these territories were digitised as per Monks Wood.

Nest placement in relation to patterns of social hierarchy among males was assessed in Monks Wood using male age as a proxy for dominance, as age-related prior residency correlates strongly with social status in the *Poecile* genus (Nilsson and Smith 1988; Koivula et al. 1993; Schubert et al. 2007). For each nest, the age disparity between the resident male and the male in the nearest territory to the nest was calculated. A positive value indicated that the neighbouring male was older than (and socially dominant to) the resident male, and a negative value indicated that the neighbouring male was younger than (and sub-dominant to) the resident. Values of zero indicated males of the same age where dominance could not be inferred, and were excluded from analyses. To investigate whether females were placing nests closer to the borders than to the centres of their territories, we defined the territory core as the area containing all points that were closer to the geographical centre (centroid) than to the territory border. The remainder of the territory was defined as the margin, containing the area that was closer to the border than to the centroid. If females were placing nests with regard to the social hierarchy of neighbouring males, we predicted a greater proportion of nest placement within the territory margins than by random chance, and these locations would be associated with a positive age disparity between the nearest neighbouring male to the nest and the resident male.

In order to test for an effect of previous female experience of nest locations on placement of nests in Monks Wood, we measured the distance between nests of the same female in subsequent years, where the territory centroid fell within the previous year's territory and where the previous year's nest was successful. This distance was then compared with that between the nests of new FY females nesting within an area for the first time, where the new territory centroid fell within the previous territory, and the successful nest of the previous female in the preceding year.

Habitat models of woodland canopy overstorey and understorey structure

Digital habitat models of Monks Wood and the Eastern Woods were used to investigate the role of habitat selection in relation to nest placement within the territory. For each territory and approximate territory, 25 m buffers were defined around nest sites to encompass the mean maximum distance used by foraging adults when provisioning nests at Monks Wood (Carpenter 2008), and were then used to compare habitat within the remainder of the territory. To assess woodland structure, a 0.5 m resolution raster canopy-height model (CHM) of the woods was generated during leaf-on conditions from airborne lidar data acquired in June 2005 (Hill and Broughton 2009). Lidar is an active remote-sensing technique whereby a short pulse of near-infrared light is fired at the ground by an aircraft-mounted laser scanner. The timing and intensity of the reflected return signals from the surfaces below are then used to calculate a ranging measurement (Lefsky et al. 2002), with the first-return signal measuring the range to the first object encountered (e.g. a tree top) and the last-return signal measuring the range to the last object encountered at or above the ground at the same location (e.g. sub-canopy shrubs or the ground). The CHM of the woods thus described the structure of the woodland canopy surface, containing height information

for the tallest vegetation structure present in each 0.5 m grid cell using the first-return data (Hill and Broughton 2009). Based on field observations (Hill et al. 2010), height values of > 8 m were considered to represent the overstorey layer of mature tree crowns, and were extracted to create a separate overstorey height model. This model was used to determine mean values of overstorey height for the nest buffers and the corresponding remaining parts of the territories, and for the territory cores and margins. The results from the comprehensive multiple-year territory data at Monks Woods were assessed for wider applicability using the smaller single-year dataset from the Eastern Woods.

The CHM height values of 1-8 m corresponded to the understorey vegetation (Hill and Broughton 2009). The CHM from first-return data during leaf-on conditions contained only limited information on the understorey layer, as much of it was hidden beneath the overstorey in the airborne lidar data. Therefore, a leaf-off CHM (from April 2003) was also acquired using last-return data in order to derive additional information on the understorey coverage that was exposed beneath the dormant overstorey (Hill and Broughton 2009). Height values in the range 1-8 m in either the leaf-on or leaf-off CHMs were extracted as the total understorey data. The mean height and spatial coverage of this understorey vegetation was generated for each nest buffer and corresponding territory, and each territory core and margin. As with the overstorey, the Eastern Woods were used to assess the wider applicability of the results derived from Monks Wood.

Overstorey tree species composition model

A 1 m resolution raster map of the six tree species comprising the Monks Wood overstorey was produced from a supervised classification of time-series Airborne Thematic Mapper

(ATM) data acquired in 2003. The distribution of overstorey in this map was determined using a corresponding 1 m resolution lidar-derived CHM acquired in June 2000 (Hill and Thomson 2005), applying a vegetation height threshold of > 8 m, as above. Each 1 m grid cell, where the canopy was 8 m or taller, was thus assigned to a tree species, and the remaining grid cells (below 8 m in height) were assigned to an unclassified category. The resulting canopy tree species model had a surveyed overall accuracy of 88% (Hill et al. 2010), and was used to compare the proportions of tree species within the overstorey of each nest buffer and corresponding territory, and the territory cores and margins.

Statistical analysis

Mean overstorey height, understorey height and understorey coverage were treated as paired data for nest buffers and their corresponding territories, and for territory cores and their corresponding margins. We applied angular transformation to proportional data, and non-parametric tests were employed where normalisation of data could not be achieved by transformation. All tests were two-tailed. To investigate patterns of nest placement, we carried out randomization tests by generating single random points within each territory over 999 iterations, determining the frequency with which points fell within the territory cores. The position of the observed frequency of nests within cores on the frequency distribution was used to calculate statistical significance. Nest placement within the territory was compared between FY and AFY females, and examined for age groups combined.

To test whether the proportion of tree species in the overstorey differed between the nest buffers and territories, the proportional values required transformation to address the problem of non-independence, i.e. the mutually-exclusive relationship between each tree species in a

limited area whereby an increase in the proportion of one species must be at the expense of one or more others. We therefore divided each proportion value by that of the unclassified vegetation category in the same defined area, and took the natural logarithm of each ratio to leave the transformed values unbounded. Using these transformed values as the response variable, we performed a three-way ANOVA with nest identity, spatial category (nest buffer or territory remainder) and tree species as factors, predicting a significant interaction of spatial category and tree species if Marsh Tits were selecting for particular tree species around nest sites.

Results

Nest placement within the territory

Of the 117 nests located in Monks Wood, 95 nest cavities were unique, and no birds were observed that were unable to acquire a nest cavity. This indicated that nest sites were not limiting for Marsh Tits in Monks Wood, as the proportion of unique nest sites exceeded that recorded for this species in the primeval conditions of Białowieża forest, Poland, where holes are super-abundant (Wesołowski 2006). Monks Wood territory sizes ranged from 1.45-14.12 ha (mean = 5.55, SD = 2.03, $n = 153$) and, for those territories used in nest placement analyses, geometry determined that the area of the territory core was substantially smaller than that of the territory margin (cores: mean = 1.42 ha, SD = 0.48; margins: mean = 4.09 ha, SD = 1.42; $n = 117$). For Monks Wood nests, all AFY females had nested in the area as first-years, and 42.4% of birds in the AFY age category nested in more than one year. Breeding attempts by the same female in different years were treated as independent, however, as all territory boundaries, 81.2 % of nest sites and the arrangement of neighbours between and

within years were unique. In addition, we found no evidence of an effect of previous female site-selection in nest placement, as AFY females did not place nests closer to successful sites in the previous year ($n = 45$), when compared to naïve FY females nesting in the same area for the first time ($n = 26$) (Mann-Whitney U -test: $U = 1058.0$, $P = 0.15$). For all females combined, nests were located in the territory core more frequently than random points (Table 1). This was also true of AFY females when the age groups were considered separately, but there was no statistical difference between the distribution of the nests of FY females among the territory cores and margins when compared to that of the random points (Table 1).

The median age of males paired to FY females was 1 year old (range = 5 years), this being significantly younger than the 3 years of age (range = 7 years) of males paired to AFY females (Mann-Whitney U -test: $U = 2666.0$, $P < 0.01$). For females of all ages, there was no relationship between the nests placed in the territory core or margin and the age disparity (younger or older) between the resident male and the nearest neighbouring male to the nest ($\chi^2 = 0.18$, $DF = 1$, $P = 0.67$). This was also true when considering FY females in isolation (Fisher's Exact Test, $P = 0.46$), despite their greater tendency to locate their nests within the territory margin (Table 1). Furthermore, for FY females, nest placement within the margin was not associated with the age of their breeding partner ($\chi^2 = 0.15$, $DF = 1$, $P < 0.68$). These results indicated that the age difference between neighbouring males and the resident males was no greater for nests placed within the territory margins compared to those placed within the territory cores, and that the pattern of nest location of females paired to young males did not differ from that of females paired to older males.

Habitat in the nest buffers compared with the territories

For females of all ages in Monks Wood, overstorey height in the nest buffers was significantly taller than that of the corresponding territories (Table 2), but only by 3.8%. For all females in the Eastern Woods, mean overstorey height within the nest buffers was 6.8% taller than in the remainder of the approximate territories, and this result approached statistical significance (Table 2). This pattern was also observed when considering female age-groups separately in Monks Wood (Table 2), and there was no difference in the overstorey heights of nest buffers between FY and AFY females (two-sample *t*-test: $t = 0.40$, $P = 0.69$).

As shown in Table 3, Silver Birch, European Aspen and elm accounted for a negligible proportion of the overstorey in the Monks Wood nest buffers and territories, and these species were excluded from further analyses. For the remaining tree species (English Oak, Common Ash and Field Maple), a three-way ANOVA using transformed proportions (see statistical analyses) found a significant effect for nest identity ($F_{116,580} = 1.96$, $P < 0.01$) and tree species ($F_{2,580} = 64.94$, $P < 0.01$), with a significant interaction of tree species and spatial category (nest buffer or territory remainder) ($F_{2,580} = 7.23$, $P < 0.01$) indicating an inconsistent difference in the proportions of tree species between the nest buffers and territories. Of these tree species, the absolute proportion of only the tallest, Common Ash, was substantially greater in the nest buffers than in the territories (Wilcoxon Signed Rank *W*-test: $W = 5423.0$, $P < 0.01$; Table 3), although there was no difference between FY and AFY females in the proportions of this species in the nest buffers (two-sample *t*-test: $t = 0.93$, $P = 0.36$).

For all females combined, understorey height in the nest buffers was significantly less than in the corresponding territories in Monks Wood and the Eastern Woods, and this effect persisted

when female age groups were considered separately (Table 2). Understorey height was greater in the nest buffers of FY than AFY females (Mann-Whitney U -test: $U = 3840.0$, $P < 0.02$), though only by 6.8%, although values for the remainder of the territories indicated that understorey was comparatively taller across the entire territory of FY females. The proportion of understorey coverage was significantly lower in the nest buffers than the remainder of the territories for all females in Monks Wood and the Eastern Woods, and for the FY and AFY female age groups in Monks Wood. There was no difference in understorey coverage between the nest buffers of FY and AFY females (two-sample t -test: $t = 0.62$, $P = 0.54$).

Habitat in the territory cores and territory margins

Although AFY females appeared to nest disproportionately within the territory cores, compared to FY females, the original analyses of social and habitat factors did not account for this difference. We therefore performed additional analyses on habitat within the territory cores and margins, and related these to the results from the nest buffers, in an attempt to detect habitat differences between the territories of FY and AFY females to explain the difference in the patterns of nest placement. As both age groups had shown an apparent selection for greater overstorey height and proportion of Common Ash, and less understorey, in the nest buffers, we limited analyses to these variables.

For all females, overstorey height was slightly greater in the territory cores of Monks Wood and the Eastern Woods compared with the territory margins, as was the proportion of Common Ash in Monks Wood, while understorey height and understorey coverage were both greater in the margins than the cores (although the difference in height in the eastern Woods was not significant, Table 4). There was no difference between FY and AFY females in

overstorey height in the territory cores, understorey height, or the proportion of understorey coverage in Monks Wood (Table 5). There was, however, a significant difference in the proportion of Common Ash within the territory cores, with that of AFY females being 17.8% greater than that of FY females (Table 5). The proportion of Common Ash within the territory cores of FY females was similar to that in the margins (core mean (SD) = 0.45 (0.21), margin mean (SD) = 0.43 (0.17); paired *t*-test on angular-transformed data: $t = 1.23$, $P = 0.22$), while for AFY females the proportion in the cores was significantly greater than in the margins (core mean (SD) = 0.53 (0.20), margin mean (SD) = 0.50 (0.16); paired *t*-test on angular-transformed data: $t = 2.38$, $P = 0.02$), indicating a concentration of Common Ash within the territory cores of AFY females that was not apparent in the territories of FY females.

Discussion

Although Marsh Tits are secondary cavity-nesters, and thus reliant on pre-existing tree holes, the very low rate of cavity re-use indicated that nest sites were abundant throughout Monks Wood. On this basis, we excluded the possibility that female choice of nest placement was significantly constrained by nest site availability. We nevertheless found no evidence that the pattern of nest placement by female Marsh Tits was influenced by conspecific attraction. Indeed, placement by FY females was essentially random within the territory, while AFY females appeared to site their nests preferentially within the territory core, away from conspecifics. This conflicted with the detailed work by Mennill et al. (2004), which found that females of the closely-related Black-capped Chickadee placed their nests close to their territory border. They suggested that this may have been due to conspecific attraction, although geometry determines that the part of a convex polygonal territory which is closer to

the boundary is always much larger in area than that which is closer to the centre. Thus nests have a higher probability of being located nearer the territory boundary by chance and not necessarily selection. By dividing each territory into a core and margin and using random points to derive expected patterns of nest placement, we were able to circumvent this issue. However, this discrepancy does not explain the finding of Mennill et al. (2004) that nests of females with low-ranking partners were close to neighbouring high-ranking males, a result that we could not replicate using age as a proxy for male rank in the Marsh Tit. This may be because age was an insufficient surrogate for social rank in our analyses, or that Marsh Tits differ from Black-capped Chickadees in this aspect of their social behaviour.

There were differences in habitat structure between the nest buffers and the remainder of the territories, although a statistically significant difference in mean overstorey height in Monks Wood amounted to just 3.8%. This result nevertheless supports the finding that Marsh Tit occupation was associated with taller canopy height at this site (Broughton et al. 2006), and the trend was also replicated in the smaller dataset for the Eastern Woods. The overstorey of territory cores was significantly taller than that of the margins, although there was no difference in the height of nest-buffers between female age groups. Understorey height and coverage were significantly lower in the nest buffers of Monks Wood and the Eastern Woods, compared to the remainder of the territories, and the same trend was found in territory cores when compared to the margins. The absolute differences between the habitat variables were not large, but indicated that the breeding territories were centred on areas of relatively taller trees and with a relatively lower density of understorey shrubs, compared to the territory margins. This pattern was also observed at a more localised scale around nest sites, with nest buffers having a taller overstorey and less understorey than the rest of the territory.

These results contrast with those of Hinsley et al. (2007) and Carpenter et al. (2010), who concluded that Marsh Tit occupation and abundance at the scale of whole territories was positively associated with the density and coverage of understorey. The failure to detect this trend around nest sites in this study may suggest that selection for understorey might not be directly related to nesting behaviour and, in particular, nest site selection. It is possible that greater visibility around nest sites confers some advantage in relation to predator detection and avoidance. The differences in canopy and understorey structure between territory cores/nest buffers and margins/reminders of territories (Tables 2 and 4) might have been generated at least in part by edge effects. In the relatively small Eastern Woods, territories inevitably included woodland edges characterised by taller, denser shrubs and shorter trees. In Monks Wood, some territories lacked external woodland edges, but internal edges along large rides and glades could have contributed to the same effect.

Carpenter (2008) found that Common Ash was the tree species most frequently used for foraging in Monks Wood, when provisioning young, and we detected a significantly higher proportion of this species in the overstorey of the nest buffers compared to the rest of the territories. As Common Ash was the tallest common tree species, however, it was initially unclear whether selection of nest buffer characteristics by Marsh Tits was operating on the basis of tree species or vegetation height. Common Ash was also more common in the overstorey of the territory cores compared to the margins, however, but not for FY females. Aside from a discrepancy in understorey height, this difference in Common Ash between the two groups of females was the only age-related inconsistency among the habitat results. Both female age groups showed an apparent selection for Common Ash in the nest buffers, indicating that all females sought out areas rich in this species for nest placement, in accordance with Carpenter's (2008) observation that Common Ash was preferred for

foraging. Only the territory cores of AFY females contained a concentration of Common Ash, however, suggesting that older females occupied territories centred on breeding habitat of a higher quality than FY females. This may, therefore, explain why AFY females nested disproportionately within the territory cores, as their territories contained a relative abundance of Common Ash in these areas. The FY females, meanwhile, nested in areas that were locally rich in Common Ash yet spaced more randomly within their territories, due to there being no concentration of this species within the territory cores of this age group. As AFY females tended to be paired to older and, presumably, higher-ranking males than the breeding partners of FY females, it is likely that these experienced and dominant birds were better able to assess and acquire high-quality habitat resources than the younger, sub-dominant birds.

Why Common Ash should be selected over other tree species as foraging habitat is unclear. We have no information on food availability on the various tree species within the study site, and Carpenter's (2008) finding that Common Ash was preferred while foraging may have merely reflected its abundance around nest sites. Alternatively, Carpenter's (2008) suggestion that Marsh Tits may have been competitively excluded from preferred foraging areas by other tit species may offer another explanation. Marsh Tits may not select for Common Ash *per se*, but, rather, be avoiding competition with more dominant species in areas rich in, for example, English Oak, which offers high quality habitat for Great Tits (Wilkin et al. 2009).

We conclude, therefore, that Marsh Tit nest-placement ultimately appeared to be based on habitat variables at our study site, with birds locating nests in areas where the overstorey was rich in Common Ash. Selection for this tree species may have been responsible for the second main observation, of nests being placed among relatively tall trees within the territory, as

Common Ash was the tallest common species within our study site. There was also an apparent preference for nesting areas that had relatively less understorey than other areas of the territory. Our use of age as a proxy for male social rank detected no effect of conspecific attraction, and we also discounted female experience as an explanatory factor in the spatial pattern of nest placement.

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Tables

Table 1. Observed nest placement by Marsh Tits within the territory cores (areas closer to the territory centroid than to the boundary) compared to results of a randomization test using 999 iterations to generate a random point within each territory. FY = first-year females, AFY = after first-year females.

	Observed number of nests in territory core (%)	Median (range) of random points in territory cores	<i>P</i>
All females (<i>n</i> = 117)	44 (37.61)	29 (27)	< 0.01
FY females (<i>n</i> = 58)	14 (24.56)	14 (20)	0.13
AFY females (<i>n</i> = 59)	30 (50.85)	15 (24)	< 0.01

Table 2. Mean habitat variables in the nest buffer and remainder of the territory for each breeding territory in Monks Wood (MW, $n = 117$) and the Eastern Woods (EW, $n = 15$) for all females. Comparisons performed using paired t -tests and Wilcoxon Signed Rank W -tests, with angular transformation being applied to proportion data before testing. FY = first-year females, AFY = after first-year females.

	Nest buffers	Territories	Test statistic	P
Overstorey mean height (m)				
MW: all females	15.99 (2.14)	15.38 (1.33)	$t = 3.99$	< 0.01
MW: FY females	16.07 (1.94)	15.32 (1.25)	$t = 3.24$	< 0.01
MW: AFY females	15.91 (2.33)	14.44 (1.41)	$t = 2.36$	0.02
EW: all females	17.92 (3.24)	16.70 (3.02)	$t = 2.07$	0.06
Understorey mean height (m)				
MW: all females (median (range))	2.87 (4.48)	3.28 (1.75)	$W = 855.00$	< 0.01
MW: FY females (median (range))	2.97 (2.13)	3.34 (1.69)	$W = 149.00$	< 0.01
MW: AFY (median (range))	2.78 (4.40)	3.26 (1.67)	$W = 305.00$	< 0.01
EW: all females (mean (SD))	3.05 (0.38)	3.44 (0.43)	$t = 3.17$	< 0.01
Understorey mean coverage (proportion)				
MW: all females	0.39 (0.09)	0.43 (0.06)	$t = 4.83$	< 0.01
MW: FY females	0.40 (0.09)	0.44 (0.05)	$t = 3.59$	< 0.01
MW: AFY females	0.39 (0.09)	0.42 (0.06)	$t = 3.22$	< 0.01
EW: all females	0.44 (0.11)	0.50 (0.10)	$t = 2.36$	0.03

Table 3. Mean proportional composition of overstorey tree species in 25 m radius nest buffers ($n = 117$), the corresponding remainder of the Marsh Tit territories, and the whole of Monks Wood (MW). Mean heights (and SD) of each tree species in the overstorey of the whole of Monks Wood are also given, derived from height values of the 1 m grid cells assigned to each species.

	Mean (SD) proportion in nest buffers	Mean (SD) proportion in territories	Proportion of MW	Mean (SD) height in MW (m)
Common Ash	0.54 (0.22)	0.45 (0.16)	0.48	16.22 (3.05)
European Aspen	0.05 (0.08)	0.05 (0.04)	0.06	14.17 (3.11)
Silver Birch	0.01 (0.01)	0.02 (0.02)	0.02	12.15 (2.54)
Elm	< 0.01 (0.01)	< 0.01 (0.01)	0.01	17.50 (3.98)
Field Maple	0.15 (0.12)	0.12 (0.07)	0.12	15.93 (3.30)
English Oak	0.11 (0.12)	0.15 (0.08)	0.18	14.88 (2.87)
Unclassified vegetation	0.13 (0.15)	0.20 (0.10)	0.15	11.95 (2.52)

Table 4. Habitat variables in the territory cores and margins for each breeding territory in Monks Wood (MW, $n = 117$) and the Eastern Woods (EW, $n = 15$) for all females. Paired t -tests were used for parametric data, and Wilcoxon Signed Rank W -tests for non-parametric data. Angular transformations were applied to proportion data before testing.

	Territory cores	Territory margins	Test statistic	P
MW overstorey mean height (m) (mean (SD))	15.85 (1.80)	15.24 (1.27)	$t = 5.71$	< 0.01
EW overstorey mean height (m) (mean (SD))	17.53 (3.24)	16.42 (3.00)	$t = 2.95$	0.01
MW understorey mean height (m) (median (range))	3.00 (2.68)	3.34 (1.88)	$W = 922.00$	< 0.01
EW understorey mean height (m) (median (range))	3.27 (1.22)	3.35 (1.39)	$W = 31.00$	0.11
MW proportion coverage of understorey (mean (SD))	0.42 (0.06)	0.45 (0.06)	$t = 5.64$	< 0.01
EW proportion coverage of understorey (mean (SD))	0.46 (0.09)	0.51 (0.10)	$t = 2.61$	0.02
Proportion of Common Ash in MW	0.49 (0.21)	0.45 (0.17)	$t = 2.51$	0.01

Table 5. Comparison of habitat variables in the territory cores of first-year (FY) and after first-year (AFY) females in Monks Wood. Two-sample *t*-tests were used for parametric data and Mann-Whitney *U*-tests for non-parametric data, with angular transformations being applied to proportion data before testing.

	FY females (<i>n</i> = 58)	AFY females (<i>n</i> = 59)	Test statistic	<i>P</i>
Overstorey mean height (m) (mean (SD))	15.85 (1.66)	15.84 (1.94)	<i>t</i> = 0.02	0.99
Understorey mean height (m) (median (range))	2.98 (1.97)	3.07 (2.60)	<i>U</i> = 3494.00	0.70
Proportion coverage of understorey (mean (SD))	0.42 (0.06)	0.42 (0.07)	<i>t</i> = 0.10	0.92
Proportion of Common Ash (mean (SD))	0.45 (0.21)	0.53 (0.20)	<i>t</i> = 2.03	0.045