

Marsh Tit *Poecile palustris* territories in a British broad-leaved wood

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We used individual colour-marking and territory mapping to quantify the spatial extent of 32 Marsh Tit *Poecile palustris* territories in Monks Wood, eastern England, during spring of the years 2002–04. A mean territory size of 4.1 ha was identified. All 2004 spring territories were located, allowing a breeding density of 14 pairs/km² to be calculated. Availability of airborne digital remote sensing (LiDAR) data for Monks Wood allowed the characterization of the canopy structure in territories and non-breeding areas using a three-dimensional canopy-height model. The difference between the mean canopy height of the 2004 territories and that of the unoccupied area of the study site in the same year was 1.8 m, or 14%. Sampling the unoccupied area, with hypothetical 'pseudo-territories', showed a statistically significant difference of 1.6 m (13%) between the mean canopy heights of the 'taller' 2004 territories and the unoccupied pseudo-territories. A comparison by field survey of tree and shrub species composition between the 2004 territories and pseudo-territories found no difference in species richness or the mean density of shrubs or mature trees (> 30 cm diameter at breast height, dbh). The mean density of medium-sized (5–30 cm dbh) and small (< 5 cm dbh) trees was, respectively, 1.9 and 3.9 times greater in the pseudo-territories, values that were statistically significant. Overall, Marsh Tits in Monks Wood appeared to require mature trees with a shrub layer beneath the top canopy, but avoided areas with large numbers of young and immature trees.

The Marsh Tit *Poecile palustris* is a small (body mass c. 10 g), hole-nesting bird, largely confined to mature deciduous woodland. Unlike many other tits in Britain, the species seldom breeds in secondary habitats such as hedgerows. Pairs maintain relatively large, year-round territories in which they hoard food (Cramp & Perrins 1993). The species has undergone a significant decline in Britain since the 1960s and has been added to the Red List of *Birds of Conservation Concern* (Gregory *et al.* 2002, Perrins 2003). Reasons for this decline are unclear, but may include increased woodland fragmentation and isolation, changes in woodland management and structure, and changes in predator pressure and/or competition (Fuller *et al.* 2005). Although the Marsh Tit is relatively well-studied among the less-abundant species of European tits (Cramp & Perrins 1993), most recent work has focused on the nominate race, *P. p. palustris*, in Scandinavia and Poland (Nilsson & Smith 1985, 1988, Nilsson 1989,

Wesolowski 1996, 1998, Haftorn 1997). The only detailed studies of the social and territorial behaviour of the race occupying England, Wales and western France, *P. p. dresseri*, date from the middle of the last century (Southern & Morley 1950, Hinde 1952, Morley 1953), before the population decline.

The highly sedentary nature of the Marsh Tit is well known (Perrins 1979, Sellers 2002), and the investment that birds make in territory defence appears to be significant (Southern & Morley 1950, Haftorn 1997). There has, however, been little detailed attention paid to the woodland structure or vegetation composition of Marsh Tit territories in England or elsewhere (Cramp & Perrins 1993). Territories may be delimited by observation of colour-ringed individuals (Bibby *et al.* 2000) or, for some species, by radiotelemetry (e.g. Hodder *et al.* 1998). Although ground surveys can provide useful information on detailed habitat composition and structure in more open environments (Tye 1992, van den Berg *et al.* 2001, Gołowski & Dombrowski 2002), the three-dimensional complexity of woodland

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habitats, and the relatively large size of Marsh Tit territories, make it particularly difficult to quantify these characteristics comprehensively using field-based methods. The airborne remote sensing technique of LiDAR (light detection and ranging) provides the capability of collecting such data at both a high spatial resolution and at the scale of whole woods (Lefsky *et al.* 2002, Hill *et al.* 2003).

This paper describes the use of individual colour-marking and territory mapping over three years to identify areas of woodland exclusively defended as breeding territories by Marsh Tits. The spatial characteristics of the territories are described, and the identification of all territories in one breeding season enabled the determination of breeding density for that year. Airborne remotely sensed LiDAR data were used to compare the structural characteristics of territories with those of areas of woodland not occupied by Marsh Tits, and with overall woodland structure. In addition, vegetation surveys throughout the woodland enabled a comparative investigation of woody species composition between territories and non-breeding areas.

METHODS

The study site was the 157-ha Monks Wood National Nature Reserve (NNR) in Cambridgeshire, eastern England (52°24'N, 0°14'W) (Steele & Welch 1973, Gardener & Sparks 2005). Monks Wood NNR is a lowland (6–46 m above Ordnance Survey Datum), semi-natural 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. The understorey is dominated by Common Hazel *Corylus avellana*, hawthorn *Crataegus* spp. and Blackthorn *Prunus spinosa*, with scattered Honeysuckle *Lonicera periclymenum*, Dogwood *Cornus sanguinea* and Wild Privet *Ligustrum vulgare*. 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. Overall, the structure and species composition are very heterogeneous. The 9.4 ha of open fields within the study area (Fig. 1) were excluded from any calculations.

Marsh Tits have been recorded in Monks Wood since at least 1926 (Steele & Welch 1973). Numbers have possibly increased in recent years as the regenerating wood has matured following widespread felling in the first half of the 20th century (Hinsley *et al.* 2005).

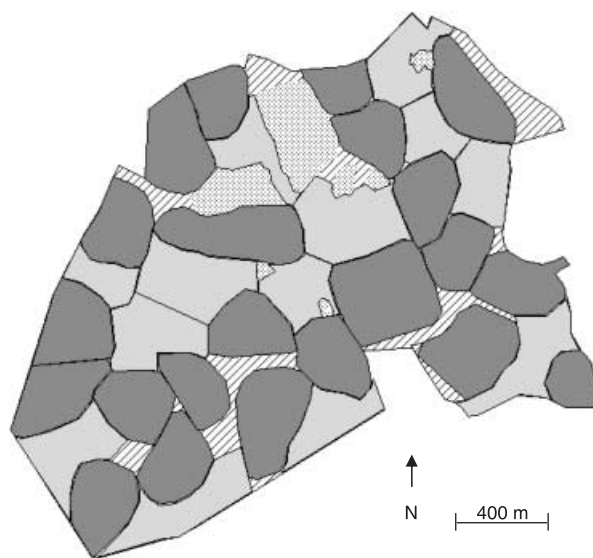


Figure 1. Location of 2004 territories (dark grey) and pseudo-territories (light grey) in Monks Wood. Stippled areas are open fields, hatched areas are unsampled woodland.

Marsh Tits have been trapped and colour-ringed at Monks Wood since 1998, although efforts were made between 2002 and 2004 to colour-ring as many territorial birds as possible. Birds were caught using a portable drop-door trap baited with sunflower seeds. In addition to a uniquely numbered aluminium ring (British Trust for Ornithology) on one leg, birds were fitted with individually identifiable combinations of two colour rings on the other leg. They were then weighed, the wing measured, and they were aged and sexed (Svensson 1992, King & Muddeman 1995) before release at the point of capture.

Searches for marked birds were conducted during the main territorial and breeding period (February to June) from 2002 to 2004. Each bird or pair was searched for every 1–5 days in the general area of their territory, and followed for 2–4 h. Initial locations of marked birds and all subsequent movements were recorded on 1 : 10 000-scale maps in the field, with notes made on behaviour. Particular attention was paid to the location of territorial behaviour, such as boundary disputes and singing. The registration data from the field maps were stored in a database that was loose-coupled to ArcView Geographical Information System (GIS) (version 3.2). Accuracy of the mapped and digitized locations was estimated to be within 30 m.

Visual registrations of colour-marked birds tend to be unsuitable for objective methods of territory or home-range estimation, owing to the inherent bias

imposed by the difficulties of observing birds in dense vegetation, poor light or bad weather. Such objective methods rely on systematic and unbiased registrations collected via remote methods, such as telemetry. These methods, e.g. kernel estimation, and also minimum convex polygons, exclude or limit consideration of behavioural observations and physical features in the environment (such as field boundaries or other barriers) that aid significantly in the interpretation of registrations. Standard territory mapping techniques (Bibby *et al.* 2000) were therefore applied to the registrations in the database to estimate the extent of approximately half of all defended spring territories in 2003 ($n = 9$) and all spring territories in 2004 ($n = 22$), and also one from 2002. Territories were considered to be those areas occupied exclusively by pairs between February and June, or those occupied by unpaired or widowed birds if they were defended throughout the spring period. Territory borders were identified and digitized through areas of regular confrontation between neighbouring birds, with these often being along linear features such as the rides and paths which formed many territory boundaries. Where birds met no opposition at the edge of their territory, perhaps due to the territory adjoining open fields or unused woodland, the boundary was delineated subjectively using the registrations of visual records of the areas used exclusively by a bird or pair (cf. Bibby *et al.* 2000). All 2004 territories contained a breeding pair, and territories occupied by the same birds, with similar boundaries, in successive years were included only once in the analyses.

A digital canopy height model (DCHM) of Monks Wood was derived from airborne laser scanning data acquired for the wood in June 2000. Airborne laser scanning is an active remote-sensing technique working on the principle of LiDAR (Lefsky *et al.* 2002, Bradbury *et al.* 2005). As the aircraft flies over the target area, a short pulse of near-infrared light is fired at the ground by the laser scanner and the timing and intensity of the reflected return signal from the surface is used to calculate a ranging measurement. For Monks Wood, one elevation measurement was recorded approximately every 5 m² on the ground. These point-sample data contain information on the elevation of both the ground surface and features on the ground such as buildings, trees and bushes. By interpolating the point data into raster grids with a 1-m² pixel size, extracting those pixels that represent the ground surface and interpolating elevation across the data gaps under surface features, a digital terrain model (DTM) describing the land surface can be created. A DCHM

describing the top surface of the vegetation canopy can then be calculated by subtracting the DTM values from the elevation of pixels identified as vegetation. The DTM had a root mean square error of ± 0.51 m, whilst canopy height was underestimated in the DCHM by an average of 1.02 m for shrubs and 2.12 m for trees (Gaveau & Hill 2003). The DCHM was therefore calibrated using a linear relationship between height and height underestimation (Patenaude *et al.* 2004). Full details of LiDAR data acquisition and processing are given in Hill *et al.* (2002) and Hill and Thomson (2005). The Marsh Tit territories were digitized within the GIS and used as templates to select and 'cookie-cut' the corresponding sections of the Monks Wood DCHM. The spatial extent and canopy height parameters for each territory were then derived from the matching section of the DCHM using ArcView and ArcInfo (version 8) GISs. The percentage of canopy falling within specified height classes for each territory was also determined by calculating the frequency of pixel height values falling within those ranges.

Previous work in Monks Wood (Hinsley *et al.* 2002) has shown that canopy height, measured using LiDAR, was closely related to field-based estimates of tree canopy vegetation density in 25-m-radius sample plots (canopy vegetation density = $-0.826 + 2.54 \log_{10}$ canopy height, $r^2 = 0.86$, $P < 0.001$, $n = 36$). Areas of mature trees should have a taller canopy than young trees and therefore canopy height can act as a surrogate for maturity/density of the tree canopy. Marsh Tits are considered to prefer mature deciduous woodland (Cramp & Perrins 1993), and, in order to test this, the height characteristics of the Monks Wood Marsh Tit territories were compared with those of the wood as a whole. The 2004 territories were then compared with those areas of the wood not occupied by Marsh Tits in that year, as follows. Within the GIS, 13 'pseudo-territories' were located in the unoccupied fraction of the wood by manually digitizing areas that approximated the size and shape of the existing territories (Fig. 1). The DCHM was not visible during pseudo-territory digitization and selection so as to avoid any bias with regard to physical features. The canopy height parameters of the pseudo-territories were then derived by cookie-cutting the DCHM and extracting the values using the GIS, as was done for the real territories. The mean canopy height of each pseudo-territory was compared with those of the 2004 territories in a randomization test (Manly 1991), using 5000 simulations. This routine tested the statistical significance

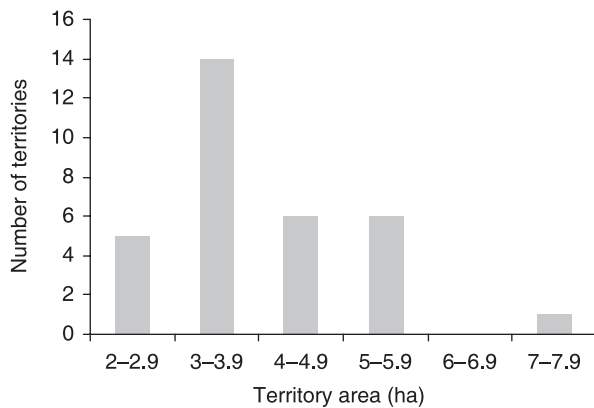


Figure 2. Frequency of occupied territory areas 2002–04 ($n = 32$).

of any differences in mean canopy height between the 2004 territories and the pseudo-territory samples of the unoccupied area. Marsh Tit territories, which are occupied all year round, frequently remain constant from one year to the next with little shift in boundary (Southern & Morley 1950, Haftorn 1997), suggesting that data for 2004 would be sufficiently representative of other years.

The LiDAR-derived DCHM supplied data only for the top tree canopy and thus information concerning the shrub layer beneath the trees was lacking. Marsh Tits frequently forage in the shrub layer (Perrins 1979) and therefore shrub species richness, and shrub and tree density, were assessed by field survey within each of the 2004 territories and pseudo-territories. A transect 100 m long and 10 m wide was aligned randomly through the central point (located using the GIS and estimated on the ground) of each territory and pseudo-territory. The number of individuals of each tree or shrub species located within each transect was then recorded, with trees also being classified by size according to the main stem diameter at breast height (dbh) (small ≤ 5 cm, medium = 5–30 cm,

large ≥ 30 cm). The results were compared in randomization tests (Manly 1991), using 5000 simulations. Species excluded from species density calculations, owing to their rarity and low frequency in the transects, were Dog Rose *Rosa canina*, Wild Service Tree *Sorbus torminalis*, willow *Salix* spp. and Crab Apple *Malus sylvestris*. Tree and shrub species richness between the territories and pseudo-territories was also compared using the randomization test, including all species recorded.

RESULTS

The areas of all spring territories (2002–04) ranged from 2.1 ha to 7.3 ha, with a mean \pm sd of 4.1 ± 1.2 ha ($n = 32$). Despite the apparently large range of territory size values, there was a clear bias towards territories with an area of between 3 and 3.9 ha, with this size classification accounting for 44% of the total number (Fig. 2). Most territories (81%) were within a limited range of between 3 and 6 ha, with just one territory (3%) above this range and five (16%) below.

The range in territory areas in 2004 alone was identical to that for the whole 2002–04 data set and the mean \pm sd was very similar at 4.0 ± 1.2 ha ($n = 22$). The 2004 territories occupied 59% of the wood (Fig. 1), at an overall density of one breeding pair per 6.9 ha of wooded ground (or 14 pairs/km²). The pseudo-territories, derived from the 41% of the wood that was not occupied by Marsh Tits in 2004, ranged in size from 2.9 ha to 6.0 ha with a mean \pm sd of 3.9 ± 1.2 ha ($n = 13$).

The mean canopy height of the 2002–04 territories was 0.4 m (3%) higher than that of the wood as a whole (Table 1). The mean canopy height of the 2004 territories alone was slightly higher again, being 0.8 m (6%) greater than that for the overall wood. The difference was greater still when the mean canopy height of the 2004 territories was compared with the mean value for the total area not occupied by Marsh Tits

Table 1. Mean canopy height values for the territories, unoccupied areas and the whole wood. The pseudo-territories were representative samples of the 2004 unoccupied area.

	Minimum mean canopy height (m)	Maximum mean canopy height (m)	Mean (m)	sd	<i>n</i>
2002–04 territories	8.1	15.1	12.2	1.7	32
2004 territories	9.8	15.1	12.6	1.7	22
2004 unoccupied area	–	–	10.8	–	1
Pseudo-territories	7.8	14.4	11.0	2.3	13
Whole wood	–	–	11.8	–	1

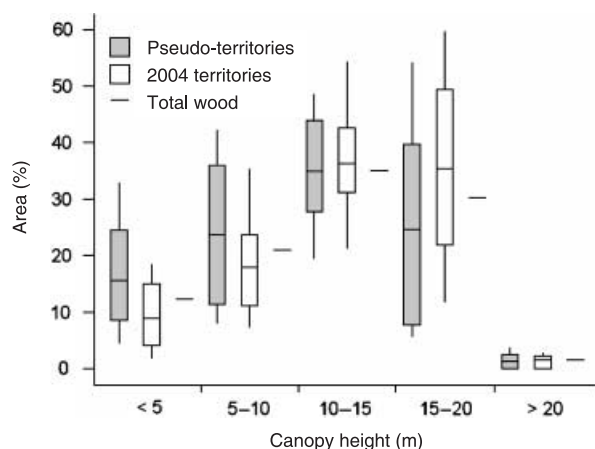


Figure 3. Mean area proportions in categories of canopy height for the unoccupied pseudo-territories ($n = 13$), the occupied 2004 territories ($n = 22$) and the whole wood. The data show the interquartile range (box), mean (bar) and data extent (whiskers) for the percentage of area in each height band.

Table 2. Species richness (mean \pm sd) of shrubs, trees and all woody species in the 2004 territories ($n = 22$) and pseudo-territories ($n = 13$).

	Territories	Pseudo-territories	<i>t</i>	<i>P</i>
Tree species	3.9 \pm 0.9	3.7 \pm 0.8	0.78	1.00
Shrub species	5.5 \pm 1.3	5.5 \pm 1.3	0.08	1.00
Shrub + Tree species	9.5 \pm 1.9	9.2 \pm 1.8	0.42	1.00

in that year, the former being 1.8 m (14%) taller. The difference in mean height between the 2004 territories and the pseudo-territory samples of the unoccupied area was similar at 1.6 m (13%). The randomization test showed that this 1.6-m difference between the mean canopy height of the 2004 territories and the pseudo-territories was statistically significant ($P = 0.02$). No relationship was found between territory size and mean canopy height.

Within the 2004 unoccupied pseudo-territories, a greater proportion of the area was in the combined two lower height classes, below 10 m, when compared with the actual 2004 territories (pseudo-territories = 39%, 2004 territories = 27%, t -statistic = 1.99, $df = 33$, one-sided $P = 0.02$, Fig. 3). The 2004 territories had a greater proportion of their area in the 15–20 m height class (pseudo-territories = 25%, 2004 territories = 35%, t -statistic = 1.98, $df = 33$, one-sided $P = 0.02$). There was no significant difference between 2004 territories and pseudo-territories in the proportion of the area in the 10–15 m height class (t -statistic = 0.46, $df = 33$,

one-sided $P = 0.31$), and there was little habitat in the wood as a whole that was taller than 20 m (Fig. 3).

There was no difference in the species richness of trees or shrubs between the 2004 territories and the pseudo-territories, expressed as the mean number of tree and shrub species in each (Table 2). Similarly, there were no statistically significant differences in the mean densities of any species of tree (classified by size) or shrub between the territories and pseudo-territories in which they occurred (Table 3). There were also no statistically significant differences in the mean density of any tree species when all size classes were combined, either across all territories and pseudo-territories or only in those in which they occurred (results not shown due to lack of significant differences). When tree species were grouped by size, there was no difference in the mean density of large trees (> 30 cm dbh) between territories and pseudo-territories (Table 3). However, the mean density of medium-sized trees (5–30 cm dbh) was almost twice as high in the pseudo-territories, and the difference was significant (two-sided $P = 0.03$). The mean density of saplings and small trees (< 5 cm dbh), where present, was almost four times higher in the pseudo-territories than in the territories, which was also significant ($P = 0.049$, Table 3).

DISCUSSION

The mean size and size range of the spring territories from throughout the study period were similar to previously reported figures for English Marsh Tits. Southern and Morley (1950) reported breeding territories (March–August) of 2.3–4.6 ha in a mature oak wood, while Hinde (1952) identified three territories of between 1.5 and 2.2 ha in mixed woodland. A study of the nominate race in Germany (Ludescher 1973) found mean territory sizes of 5.8 ha, but this included ranges outside of the breeding season. Observation in Monks Wood suggested that home ranges outside of the breeding season, which are not exclusively defended, are larger than the mean of 4.1 ha recorded here for spring territories (our pers. obs.). Although insufficient data are currently available to delimit home ranges, it was nevertheless apparent that the spring territories contained the core year-round activity for established birds. These territories are much larger than those generally reported for Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major* (Cramp & Perrins 1993), which occurred in the same habitat, and this may be influenced by the Marsh Tit's year-round occupation of territories and food-storing behaviour: availability of sufficient resources

Table 3. Mean density and sd (per 0.1-ha transect) of trees by species and size class (large (l) ≥ 30 cm dbh, medium (m) = 5–30 cm dbh, small (s) ≤ 5 cm dbh), and of shrub species, in the 2004 territory (total $n = 22$) and pseudo-territory (total $n = 13$) transects in which they occurred. dbh = diameter (of main stem) at breast height.

Species	Territories	sd	<i>n</i>	Pseudo-territories	sd	<i>n</i>	<i>t</i>	<i>P</i>
TREES								
Ash (l)	4.5	3.8	18	5.1	4.2	11	0.38	1.00
Ash (m)	16.6	14.4	22	27.2	33.2	13	1.09	0.25
Ash (s)	16.9	20.7	16	32.2	28.4	8	1.36	0.15
Oak (l)	3.9	3.9	17	2.5	1.2	10	1.35	0.33
Oak (m)	3.5	5.0	11	3.5	2.6	4	0.02	1.00
Oak (s)	1.3	0.6	3	2.0	1.4	2	0.63	1.00
Maple (l)	2.8	2.0	12	2.2	1.6	5	0.67	1.00
Maple (m)	7.3	3.4	21	7.4	5.9	11	0.03	1.00
Maple (s)	2.3	1.9	6	1.5	1.0	4	0.92	1.00
Birch (l)	1.3	0.6	3	0	–	0	–	–
Birch (m)	1.2	0.4	10	15.2	20.8	4	1.35	0.13
Birch (s)	1.0	0.0	2	71.5	99.7	2	1.00	1.00
Elm (l)	0	–	0	17.0	0.0	1	–	–
Elm (m)	0	–	0	40.3	65.6	3	–	–
Elm (s)	2.0	1.7	3	65.7	90.4	3	1.22	0.10
Aspen (l)	2.0	0.0	1	1.0	0.0	1	–	–
Aspen (m)	3.2	2.6	5	11.0	12.4	5	1.37	0.37
Aspen (s)	5.5	6.4	3	32.0	10.5	3	3.50	0.22
All trees (l)	8.5	6.6	22	7.9	6.2	13	0.26	1.00
All trees (m)	26.6	14.7	22	52.8	46.2	13	1.98	0.032
All trees (s)	16.2	19.5	19	64.0	92.9	11	1.69	0.049
SHRUBS								
Hawthorn	27.9	19.0	22	25.8	16.3	13	0.35	1.00
Hazel	10.0	7.7	19	9.6	6.3	9	0.14	1.00
Blackthorn	23.6	32.1	16	16.3	24.4	7	0.60	1.00
Dogwood	10.5	12.3	13	14.2	25.7	9	0.40	1.00
Honeysuckle	9.9	10.5	13	12.8	16.6	9	0.46	1.00
Privet	9.4	13.24	12	4.2	4.5	8	1.25	0.37
Bramble	3.1	2.6	9	2.5	1.7	4	0.50	1.00
All shrubs	72.2	34.0	22	63.2	25.0	13	0.89	0.42
All trees and shrubs	121.3	36.4	22	178.1	121.3	13	1.64	0.056

during the winter may require defence of those resources throughout the year. There is evidence that the larger territories belong to older, higher-ranking males that annex neighbouring areas of territory when they become vacant (Southern & Morley 1950, Broughton 2006). Such annexations may provide more resources for breeding or winter survival, access to more females for extra-pair copulations (Broughton 2006), or perhaps serve to isolate the paired female from seeking or receiving the attentions of neighbouring males for the same reason. Such extra-pair mating is relatively common in the related Black-capped Chickadee *Poecile atricapillus* (Mennill *et al.* 2004), where females most frequently engaged in extra-pair copulations with high-ranking males, who

in turn had significantly larger territories than lower-ranking males. Such activity resulted in 33% of nests containing extra-pair offspring.

The breeding density of Marsh Tits in Monks Wood, established for 2004 at 14 pairs/km² (and again in 2005, our pers. obs.), was low in comparison with the 22–28 pairs/km² found elsewhere in England (Bagley Wood, Oxfordshire) by Southern and Morley (1950). Glue (1973), however, found just 2.3 pairs/km² in another English location (New Forest, Hampshire). The lack of widespread figures and previous data for Monks Wood makes it impossible to put these values into context with regard to the decline in the British population of Marsh Tits since the 1960s; factors such as habitat differences may also be involved. The

density estimate for the semi-natural ancient woodland of Monks Wood is similar to that for deciduous habitats reported for *P. p. palustris* in eastern European primeval forest (Tomiałojć *et al.* 1984), where the breeding densities of many forest species are relatively low (Fuller 1995, Tomiałojć & Wesolowski 2004). Other breeding density estimates for the nominate race in Europe are more similar to those of Southern and Morley (1950) (Cramp & Perrins 1993), indicating that the density for Monks Wood may indeed be relatively low. The percentage of wooded ground occupied in Monks Wood, however, is similar to that reported for Bagley Wood (Oxfordshire) by Southern and Morley (1950), the values being 59% and 50–75%, respectively.

Tree and shrub species composition seemed to be relatively unimportant to territorial Marsh Tits in Monks Wood, as the richness of tree and shrub species was similar in both the territories and the pseudo-territories. This may, however, have been a consequence of the heterogeneous woody species mix in Monks Wood, coupled with the relatively large size of Marsh Tit territories (i.e. most tree/shrub species occur in most 3- to 6-ha samples of the wood). Differences did emerge when trees were grouped by size, with the pseudo-territories having a higher incidence of small and medium-sized trees, particularly elm, Common Ash, European Aspen and Silver Birch (Table 3). These species were common in a relatively small number of transects, except for Common Ash, which was common in the majority of transects.

There was a clear predilection for territorial Marsh Tits to select areas of taller than average canopy height and to avoid extensive areas of relatively low canopy. This was consistent with the known preference of the species for mature woodland, and its absence from habitats such as hedgerows, low scrub and gardens (Cramp & Perrins 1993). The absolute difference in mean canopy height between breeding and non-breeding areas appears relatively small at 1.6 m, but this translates into a difference in canopy height of 13%. Canopy density increases with canopy height (Hinsley *et al.* 2002), influencing the availability of invertebrate prey, although a 1.6-m height increase equates to a density increase of only 6%. Canopy density is therefore unlikely to be a major consideration. Taller trees are generally older than shorter ones, however, so canopy height may act as a surrogate for various aspects of woodland maturity, such as structural heterogeneity or availability of dead and decaying wood for feeding, caching food and the provision of nest-sites. Although Marsh Tits typically nest close

to the ground (Wesolowski 1996) and the mean height of nests located in Monks Wood in 2004 and 2005 (3 m, $n = 30$) was consistent with this, 80% of these nests were situated in rot holes in mature or semi-mature trees (our pers. obs.).

There was little difference in the density of large trees between the pseudo-territories and the territories, although the density of medium-sized trees was almost twice as high in the former, and the density of small trees almost four times higher (Table 3). This implied that Marsh Tits were not selecting areas with more large trees in absolute terms. Instead, Marsh Tits appeared to be avoiding areas with higher densities of smaller immature trees and selecting areas with proportionately more large and mature trees, these accounting for 17% of the mean total of trees in territories compared with 6% for the pseudo-territories. It appeared that the lower canopies that were formed largely by young trees in new-growth or regenerating areas of the wood, which produced a lower mean canopy height, were not favoured. Canopy height may therefore act as a proxy for the vegetation stratification and nature of the understorey. Marsh Tits spend much of their time feeding in the middle and lower levels of the vertical vegetation spectrum (Perrins 1979) and, although the density of understorey shrubs was recorded, this too was found to be similar in both the territories and the pseudo-territories. However, the size and vigour of the shrubs and, hence, their ability to produce or support food for Marsh Tits in the form of fruits, seeds and insects, was not recorded. A greater density of young trees and saplings of, for example, Common Ash may inhibit the development of fruit-bearing understorey species such as Bramble and hawthorns through crowding and shading, thereby supplying less food for Marsh Tits during the winter months. This shading aspect may also affect the availability of food in the field layer, and these issues are currently under further investigation.

The relationships between plant species composition and vegetation structure in relation to territory selection by Marsh Tits need to be examined in more detail in both Monks Wood and elsewhere. In particular, the effect of a mature tree canopy coupled with a poor or largely absent shrub layer, a structure not found in Monks Wood, would be of interest. If Marsh Tits genuinely require habitat consisting of mature trees with a relatively open yet well-developed understorey dominated by shrubs, rather than dense stands of young trees, then one would expect them to be absent from areas with no such shrub layer. This is the observed

pattern in parts of Wytham Woods, Oxfordshire, where a dense tree canopy overlies little or no shrub layer; Marsh Tits are absent from these areas of the Woods but present in others (J. Carpenter & A. Gosler, pers. comm.). By adopting a niche that primarily utilizes the shrub layer, Marsh Tits may avoid competition with Great and Blue Tits, which are dominant in interspecific interactions over food or nest-sites, and are both socially and often numerically dominant in woodlands (Siriwardena 2001, Perrins 2003). The similar Willow Tit *P. montanus* is able to exist in scrub and bushy environments away from woodlands, possibly due to their ability to excavate their own nests, and thereby avoid direct competition in woodland habitats (Siriwardena 2004). Such scrub habitats rarely provide sufficient natural nest cavities for Marsh Tits, however, which may therefore utilize the scrub equivalent habitat in woodland, i.e. the shrub layer. In this environment, the availability of natural holes in mature trees provides the Marsh Tit with an advantage over the Willow Tit, which is dependent on laborious excavation of nest cavities during which it is susceptible to being usurped or predated (Perrins 2003, Siriwardena 2004). Marsh Tits may limit nest-site competition with other tit species by selecting crevices that are both small and close to the ground (Wesołowski 1996), and therefore relatively unattractive to, for example, Blue Tits. Such a pattern of niche separation would reinforce the importance of the shrub layer to Marsh Tits, with the greater canopy height of the overlying mature trees acting as a surrogate for such a structure. The potential to extract more information regarding the internal structure of deciduous woodland, such as the density of the shrub layer, from LiDAR data captured during the winter, when a lack of leaf canopy provides different penetration characteristics, is currently under investigation.

This study included territory data for several years, but only the 2004 data set was complete, i.e. identified all of the territories during that year. This meant that the characteristics of non-breeding areas could not be determined for any other year. However, the fact that the 2002 and 2003 territory data strongly supported the 2004 data, in terms of territory size and location characteristics, implied that the 2004 data set was not atypical. Indeed, some 15 of the 22 territories recorded in 2004 were occupied by at least one bird that had been present on the same territory the previous spring. Although territory boundaries may shift somewhat between breeding seasons, the overall location often remains the same (Southern & Morley 1950, Haftorn 1997). Much of the territory data

would therefore have been duplicated between years and given potentially similar results for 2003 and 2004.

Although *P. p. dresseri* is phenotypically distinct in terms of structure and plumage, the extent of behavioural or ecological differences between this race and other races of Marsh Tit is largely unknown. Although the population of Marsh Tits in southern and central Britain may have stabilized after the rapid decline of the 1960s and 1970s (Baillie *et al.* 2005), further research into the habitat preferences and spatial requirements of this distinct form in other locations is necessary, if informed woodland management is to benefit them.

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