WOODLAND BIRDS PROCEEDINGS

Habitat selection by Marsh Tits *Poecile palustris* in the UK

SHELLEY A. HINSLEY,[*1] JANE E. CARPENTER,[1,2] RICHARD K. BROUGHTON,[1] PAUL E. BELLAMY,[1] PETER ROTHERY,[1] ARJUN AMAR,[†3] CHRIS M. HEWSON[4] & ANDREW G. GOSLER[2]

[1]*Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, UK*
[2]*Edward Grey Institute of Field Ornithology, Department of Zoology, South Parks Road, University of Oxford, Oxford OX1 3PS, UK*
[3]*Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL, UK*
[4]*British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2 PU*

Running head: Habitat selection by Marsh Tits

*Corresponding author.
E-mail: sahi@ceh.ac.uk

†Current address: RSPB Scotland, Dunedin House,
25 Ravelston Terrace, Edinburgh, EH4 3TP, UK.

The Marsh Tit *Poecile palustris* is a small, hole-nesting woodland passerine whose national population in the UK has declined by more than 50% in the last 25 years. To investigate possible causes for the species long-term decline, we examined habitat selection by Marsh Tits at three scales. For individual foraging birds, winter time budgets and foraging behaviour, recorded using instantaneous sampling, differed little between Marsh and Blue Tits *Cyanistes caeruleus*, but Marsh Tits spent more time in the understorey and more time lower down in both the woodland canopy and understorey. At the scale of breeding territories, the characteristics (numbers by size class, vegetation density, species richness) of trees and shrubs were compared using 100 x 10 m sample transects of ten territories in each of four woods. The characteristics of the trees differed significantly between woods whilst those of the shrubs did not, suggesting that the characteristics of shrubs were more important in territory selection by Marsh Tits than were those of trees. Furthermore, in one of the four woods (Wytham Woods, Oxfordshire), Marsh Tits were largely absent from areas with dense tree canopy, but poor shrub cover. On a national scale, using data from 157 of the woodlands surveyed by the RSPB/BTO Repeat Woodland Bird Survey, Marsh Tit abundance in 2003/04 was found to be positively related to vegetation cover at heights corresponding to the shrub layer, especially at 2-4 m. These relationships were not apparent in data for the same woods for the 1980s, but shrub cover had increased substantially by 2003/04 and Marsh Tit abundance had increased in woods with the most cover in 2003/04. Thus factors damaging the shrub layer, such as over-grazing by deer, shading out by canopy closure and managed clearance of shrub cover, may reduce the suitability of woodland for Marsh Tits. Habitat use by a closely related species, Willow Tit *Poecile montanus*, is also discussed.

The Marsh Tit *Poecile palustris* is a small (body mass *c.* 10 g), hole nesting parid largely confined to mature deciduous woodland (Perrins 1979, Cramp & Perrins 1993). In the UK, unlike the more

familiar and widespread Great Tit *Parus major* and Blue Tit *Cyanistes caeruleus*, it does not breed in secondary habitats such as gardens and hedgerows. Pairs are sedentary and maintain large, year-round territories, probably as a consequence of their habit of storing food. When breeding, mean territory size is *c.* 4-5.5 ha (Broughton *et al.* 2006); winter ranges are larger, but based on the location of the breeding territory (Broughton, unpubl. data). Marsh Tits in the UK have undergone a population decline of more than 50% in the last 30 years and were added to the Red List of Birds of Conservation Concern in 2002 (Gregory *et al.* 2002 & 2003). More recently this trend has changed to show an increase of 33% from 1994-2005 (Eaton *et al.* 2006). Reasons for the decline are unknown, but may include changes in woodland structure, increased woodland fragmentation and isolation, changes in predator pressure and increased competition from other parids, especially Blue Tits, whose populations have increased (Perrins 2003, Siriwardena 2006). Factors affecting the structure of woodland include deer grazing/browsing, changes in management and natural processes associated with maturation and canopy closure (Fuller 2001, Fuller *et al.* 2005).

The ecology and behaviour of British Marsh Tits *Poecile palustris dresseri*, were reported in a number of largely descriptive studies in the late 1940s and the 1950s (e.g. Southern & Morley 1950, Hinde 1952, Morley 1953, Gibb 1954, Snow 1954), but there has been little work on the species in the UK over the last 50 years. This is probably due, at least in part, to the species reluctance to use nest boxes, its naturally low population density compared to Great and Blue Tits and its confinement to mature woodland. Several of these early studies (Colquhoun & Morley 1943, Hartley 1953, Gibb 1954, Betts 1955, Bevan 1959) noted that Marsh Tits tended to forage in the mid-layers of woodland, i.e. the shrub layer and the lower parts of trees, and also on the seeds of herbaceous plants. Although the earlier work identified the foraging niche of the British Marsh Tit as intermediate in height between that of the Blue Tit (in the top canopy) and the Great Tit (lower down and on the ground) (Lack, 1971), much has changed in British woodland, in terms of both habitat characteristics (Smith & Gilbert 2001) and bird populations (Fuller 1995, Mead 2000, Fuller

et al. 2005), since the 1950s. Given this, and the long-term decline in the UK national Marsh Tit population, it is timely to re-examine the species habitat requirements and how this relates to habitat use by other tits. In this paper, we present evidence for the importance of the shrub layer for Marsh Tits at three spatial scales: (i) at the level of the individual foraging bird, (ii) on the scale of whole territories in several different woods, and (iii) across woodland at a national scale.

METHODS

Individual foraging behaviour

The foraging behaviour and locations of Marsh Tits and Blue Tits were recorded in Monks Wood in the winter of 2004/05 as part of a larger study of the comparative foraging behaviour of these two species (Carpenter *et al.* unpubl. data). Monks Wood comprises 157 ha of mixed deciduous woodland in Cambridgeshire in eastern England (52º 24´ N, 0º 14´ W). The main tree species in order of abundance are Common Ash *Fraxinus excelsior*, English Oak *Quercus robur* and Field Maple *Acer campestre*, and the main shrub species are hawthorn *Crataegus* spp., Common Hazel *Corylus avellana*, Blackthorn *Prunus spinosa* and Honeysuckle *Lonicera periclymenum.* For more details see Hinsley *et al.* (2002) and Gardiner and Sparks (2005).

Bird locations and behaviour were recorded using an instantaneous sampling technique (e.g. Altmann 1974, Martin & Bateson 1993); the results are presented using the first observation only of each bird following detection. Location was recorded as either “canopy” or “understorey” and then vertical location and behaviour were assigned as follows:

Vertical location: i) top third, ii) middle third, iii) lower third, iv) ground.

Behaviour: i) foraging, ii) vigilance, iii) flight, iv) maintenance (e.g. preening, scratching), v) communication (e.g. calling, singing).

For foraging birds, the following activities were recorded: i) gleaning (rapid, repeated pecking) from trunks/branches/twigs, ii) gleaning from leaves, iii) searching without pecking, iv) foraging whilst hanging upside down, v) handling/eating food, vi) caching food.

Differences between the foraging locations and foraging behaviour of the two species were investigated using chi-square tests (untransformed data).

Territory characteristics across woods

The habitat structure of Marsh Tit breeding territories was investigated in five woods, Wytham Woods in Oxfordshire (51º 46'N, 01º 20'W), Monks Wood in Cambridgeshire, Swanton Novers in Norfolk (52º 51', 0º 59'E), Roudsea Wood in Cumbria (54º 14'N, 03º 02'W) and Treswell Wood in Nottinghamshire (53º 18'N, 0º51'W). These five woods were selected because their Marsh Tit populations were already colour-ringed or because colour-ringing of Marsh Tits could be incorporated into existing studies of other species or bird communities. Thus the locations of Marsh Tit breeding territories were determined during February to June using observations of individually colour-ringed birds (Broughton *et al.* 2006). Insufficient observations were obtained to define accurately territory boundaries, but the core area of each pair's breeding activity was identified.

For ten territories in each wood (except Treswell Wood where there were only three Marsh Tit territories in 2005), a 100 x 10 m transect was positioned in the centre of the core area. All the trees and shrubs within this transect were counted, separately for each species, using three size categories (referred to as small, medium and large) defined by diameter at breast height (dbh) for trees and by height for shrubs as follows:

Trees: i) small: dbh < 10 cm, ii) medium: dbh 10-30 cm, iii) large: dbh > 30 cm.

Shrubs: i) small: height < 2 m, ii) medium: height 2-4 m, iii) large: height > 4 m.

In addition, tree canopy density and shrub layer density were estimated using three 25 m radius sample circles located along each transect with their centres at 0, 50 and 100 m. Thus the edges of

the circles touched, but did not overlap. For the tree canopy and the shrub layer separately, and for each circle separately, the proportion of the circle attributable to each of five density scores was estimated. The five scores were 0, 1, 2, 3, and 4 where 0 was no tree canopy or shrub cover and 4 was dense, continuous cover (Hinsley *et al.* 1995, Hinsley *et al.* 2002). To obtain a single density index for each of the tree canopy and the shrub layer in each circle, the scores were multiplied by their proportions and the results summed. Thus for shrubs or trees in a sample circle with the following hypothetical scores and proportions: 0 = 0.10, 1 = 0.20, 2 = 0.00, 3 = 0.55, 4 = 0.15, the overall shrub or tree density index would be: 0 + 0.20 + 0 + 1.65 + 0.60 = 2.45. Other data concerning standing and fallen dead wood and species composition and percentage cover of the field layer were collected, but are not reported here.

Due to the small sample size for Treswell Wood (three territories) compared to the other four sites (ten territories each), it was omitted from the final analysis, but preliminary investigation indicated that including Treswell did not alter the conclusions of the analysis.

If the shrub layer within woodland constitutes the prime habitat of Marsh Tits, then we might expect that shrub characteristics within territories would be more crucial, and hence more critically selected and less variable, than those of the trees. We have therefore examined the variability of the shrub and tree characteristics of territories both within and between woods. Numbers of small, medium, large and large + medium trees and shrubs (the category of large + medium being used to represent the total amount of tree/shrub likely to be important for Marsh Tits) and tree and shrub density indices and species richness were compared across woods using one-way analysis of variance (ANOVA). Variation between woods (V_B) in the characteristics of the trees and shrubs, relative to the variation between territories within woods (V_W), was measured using the intraclass correlation, i.e. $r_I = V_B/(V_B + V_W)$, expressed as a percentage (Sokal & Rohlf 1981). This coefficient measures the similarity between individuals (i.e. territories) within groups (i.e. woods), relative to

the similarity between groups. A value of 100% would indicate that all the variance in the data was between woods, and hence that variance between territories within woods was zero.

Ideally, we would have liked to compare habitat characteristics within Marsh Tit territories with those in parts of the woods not used by Marsh Tits. However, Marsh Tits may be absent from habitat for reasons unrelated to suitability. For example, territories may remain vacant, or be vacated by single or widowed birds, if there are insufficient individuals to occupy all suitable space, and reoccupation of suitable habitat may be delayed by isolation effects. Despite these difficulties, some areas of Wytham Woods were thought by the resident research team to be generally devoid of Marsh Tits and therefore data were collected for six additional transects in these areas, separating transects by distances similar to those between territories. Territory and unoccupied area transects were compared using two-sample *t*-tests.

Habitat characteristics at a national scale

The Royal Society for the Protection of Birds (RSPB) and the British Trust for Ornithology (BTO) Repeat Woodland Bird Survey (RWBS) investigated trends in the breeding bird populations of British broadleaved and mixed woodland (Amar *et al.* 2006). Changes in bird populations since the 1980s (and for some sites since the 1960s and 1970s) were determined by repeat surveys in 2003 and 2004 and possible reasons for changes in bird abundance were investigated using a range of habitat and landscape data. A total of 406 sites were resurveyed. Of these, 153 had originally been surveyed by the BTO using territory mapping methods and 253 by the RSPB using point counts. When resurveyed, the same methodology as in the original survey was used for each site i.e. territory mapping for BTO sites and point counts for RSPB sites. Full details are given in Amar *et al.* (2006).

The RWBS collected a large number of habitat variables, and some data were also available from the earlier surveys. To avoid a general "data mining" approach, and to investigate the

hypothesis that the shrub layer within woodland is an important component of Marsh Tit habitat, habitat variables thought to most strongly represent the shrub layer were selected *a priori*. In addition, to examine the importance of shrubs versus trees, a variable describing tree canopy cover was also selected. Thus the following five variables were used, i) percentage vegetation cover at 0.5-2 m, ii) percentage vegetation cover at 2-4 m, iii) percentage vegetation cover at 4-10 m, iv) horizontal visibility, and v) percentage tree canopy cover. All these variables were collected for most sites resurveyed in 2003/04, but habitat data from the original surveys in the 1980s were only available for RSPB sites. The analysis used the 157 RSPB and 60 BTO sites at which Marsh Tits were recorded in either, or both, of the 1980s and 2003/04 surveys.

Each RSPB site was visited twice and five minute counts were made at a number of randomly selected points – usually 10 in each site, but occasionally more. For each site, Marsh Tit abundance was expressed as the mean of the maximum count for each point. BTO sites were recorded using territory mapping using data from a total of four visits in both the 1980s and 2003/04. Marsh Tit abundance was expressed as the number of territories per hectare. Habitat variables were averaged across measurements made in a 25 m radius circle centred on each point count location (RSPB sites), or across 10 points randomly distributed across the mapped area (BTO sites). Tree canopy cover was measured as percentage cover using a sighting frame focussing only on vegetation cover above 10 m. Measurements were averaged across four 5 m radius plots evenly spaced within the 25 m circles. Percentage vegetation cover in each of the three height bands was assessed for the whole of each 25 m circle. Horizontal visibility was estimated using the mean number of 10 cm sections of a 2.4 m pole placed at the centre of each 25 m radius circle which were at least 50% visible when viewed from four points, one in each cardinal direction (i.e. N, S, E and W), located 12.5 m from the centre of the 25 m circle. Essentially, the same habitat measurements were made at both RSPB and BTO sites in 2003/04. Full details are given in Amar *et al.* (2006).

Scatterplots with lowess lines to indicate trends were used initially to examine the relationships between Marsh Tit abundance and each of the vegetation variables in both survey periods for the RSPB sites and in 2003/04 for the BTO sites. The relationships were then tested and compared between survey periods after allowing for the effect of regional locality on Marsh Tit abundance (Amar *et al.* 2006). The statistical analysis used a general linear model (Minitab Release 13) with region (South Wales, Wales, West Midlands, East Midlands, South East and East) and survey period (1980s & 2003/4) as factors and vegetation cover as a covariate, and included a vegetation by survey period interaction effect.

RESULTS

Individual foraging behaviour

Both Marsh Tits and Blue Tits spent most of their time either foraging or being vigilant, 86% and 84% of records respectively being attributable to these two activities (Table 1). There were no significant differences between the two species in their overall time budgets. Foraging behaviour was also similar, the only significant difference being that Blue Tits spent more time feeding whilst hanging upside down than did Marsh Tits ($\chi^2_1 = 7.38$, $P = 0.007$) (Table 1). Marsh Tits spent more time handling/eating food items, which were usually seeds, but the difference was not quite significant ($\chi^2_1 = 3.24$, $P = 0.072$). If average handling/eating times were greater for seeds than for invertebrates, as seems likely, then Marsh Tits may have been eating more seeds than Blue Tits, but this was not tested.

Marsh Tits spent more time foraging in the understorey (60% of observations, $n = 119$) than did Blue Tits (44% of observations, $n = 128$) ($\chi^2_1 = 6.25$, $P = 0.012$), and hence concomitantly less time in the tree canopy (40%), than did Blue Tits (56 %). When foraging in the canopy, Marsh Tits spent less time in the top third than did Blue Tits (Table 2), but the difference was not significant ($\chi^2_1 = 2.82$, $P = 0.093$). When foraging in the understorey, Marsh Tits again spent less time in the top third

than did Blue Tits (Table 2) and this difference was significant ($\chi^2_1 = 5.83$, $P = 0.016$). Thus, overall, Marsh Tits spent more time foraging in the understorey and more time foraging lower down in shrubs than did Blue Tits.

Territory characteristics across woods

Characteristics (numbers by size class, vegetation density and species richness) of the trees and shrubs in Marsh Tit territories in the five study woods are summarised in Table 3. Overall, with the main exception of small trees and small shrubs, the characteristics of the trees varied significantly between woods whereas those of the shrubs did not (Table 3). Shrub species richness varied significantly, but the difference was less marked for shrubs ($F_{3,36} = 3.04$, $P = 0.041$) than for trees ($F_{3,36} = 11.56$, $P < 0.001$). Again with the exception of small trees and small shrubs, the intraclass correlation coefficients showed that the amount of variation in the characteristics of the trees due to differences between woods (as opposed to differences between transects within woods) was usually around 50%, whereas for shrubs the value was essentially zero or only a few percent. Thus the characteristics of the shrub layer within Marsh Tit territories were similar between woods, whereas those of the trees varied substantially, implying more critical selection of shrubs than trees. The difference in the results for small trees and shrubs is considered in the discussion.

In Wytham Woods, the main difference between areas occupied by Marsh Tits and those apparently not used was a lack of shrub cover in the unoccupied areas (Fig. 1). Occupied areas had more shrubs ($t_{12} = 3.52$, $P = 0.004$) and a larger shrub density index ($t_{12} = 5.93$, $P = 0.004$) than did unoccupied areas, but the numbers of trees did not differ ($t_{10} = -1.30$, $P = 0.224$). However, unoccupied areas had a larger tree canopy density index ($t_{10} = -4.48$, $P = 0.002$), suggesting that the lack of shrubs was at least in part due to a lack of light beneath the tree canopy.

Habitat characteristics at a national scale, using RWBS data

For the original survey in the 1980s, no relationships between Marsh Tit abundance and any of the four vegetation variables (the fifth variable, horizontal visibility, was not available for the 1980s) were apparent for the RSPB sites. However, in 2003/04, after accounting for the effect of region, Marsh Tit abundance at RSPB sites increased with increasing cover in all three of the height bands, the strongest relationship being with cover at 2-4 m (Fig. 2, Table 4). The relationships with cover at 0-2 m and 4-10 m are not shown because they were similar to that for 2-4 m (Fig. 2) with the regression lines crossing at *c.* 25% vegetation cover. Marsh Tit abundance was also significantly related to horizontal visibility, but in this case the relationship was negative, i.e. after accounting for the effect of region, abundance increased with decreasing visibility (Fig. 3, Table 4) which was consistent with the results for the height bands. There was no relationship with tree canopy cover. For all three height bands, the differences in the slopes of the relationships between the original 1980s survey and the resurvey in 2003/04 were significant, and remained so after accounting for the effect of regional locality (Table 4). However, there were no differences between survey periods in the vertical elevations of the lines. In 2003/04, the evidence for an effect of vegetation cover on Marsh Tit abundance was strongest for a height of 2-4 m ($P = 0.009$, Table 4), and cover at this height should correspond well with the location of the shrub layer. However, the individual relationship between abundance and horizontal visibility was stronger ($P = 0.002$, Table 4), and in a model using both variables, horizontal visibility remained significant ($F_{1,149} = 4.82$, $P = 0.03$) after accounting for the effect of cover at 2-4 m, whereas the reverse was not true (cover at 2-4 m, after horizontal visibility, $F_{1,149} = 2.06$, $P = 0.15$). In contrast to these results for the RSPB sites, for the BTO sites in 2003/04, there were no relationships between Marsh Tit abundance and any of the five vegetation variables.

DISCUSSION

At all three scales, from individual foraging behaviour to the nationally distributed RWBS woodlands, the shrub layer was found to be important for Marsh Tits. Although the details of foraging behaviour were largely similar between Marsh and Blue Tits, foraging location differed (Tables 1 & 2). As found in earlier studies (Colquhoun & Morley 1943, Hartley 1953, Gibb 1954, Betts 1955, Bevan 1959), Marsh Tits spent more time foraging in the understorey. When examining tree and shrub parameters within territories, the similarity across woods of shrub characteristics, compared to the variation between woods in those of the trees (Table 3), suggested that either shrubs were intrinsically less variable or that Marsh Tits were more selective about the shrub layer than about the tree canopy. The former seems unlikely, and the results from Wytham Woods concur with this. The areas of Wytham which lack a well developed shrub layer also lack Marsh Tits (Fig. 1), but are occupied by Great and Blue Tits (A. Gosler, pers. com.). The numbers of small trees and small shrubs did not follow the general pattern shown by the other parameters, probably because these size classes are not important in habitat selection by Marsh Tits. Many of the shrubs in the small category were single stems about one metre tall with little leaf cover. Small trees up to 10 cm dbh were more substantial and often several meters or more tall. However, in Monks Wood, it has been noted that areas less favoured by Marsh Tits are those dominated by stands of young trees (Broughton *et al.* 2006). This is discussed further below in the context of the habitat structure apparently selected by Marsh Tits.

The variables used in the analysis of the RWBS data were not specifically identified as the shrub layer, but vegetation at these heights, and especially that at 2-4 m where the strongest relationship with Marsh Tit abundance at RSPB sites was found (Fig. 2, Table 4), should correspond to the shrub layer. The negative relationship between Marsh Tit abundance and horizontal visibility (Fig. 3) was also consistent with the hypothesis that Marsh Tits favour a well developed shrub layer. However, it is more difficult to explain why there was no relationship between Marsh Tit abundance and vegetation cover in the original surveys of the RSPB sites in the

1980s. It is possible that these woodlands have become more suitable for Marsh Tits as they have matured over the *c.* 20 years between the two survey periods, allowing Marsh Tits to increase in the most suitable sites. Despite the long-term national decline in the UK Marsh Tit population, the RWBS analysis found that, for the RSPB sites used here, the species had increased by 27% (Hewson *et al.* this volume). Shrub cover, overall, in these woods had also increased substantially (Amar *et al.* 2006). The fact that the two regression lines cross, coupled with the 27% increase in Marsh Tits at these sites, suggested that woods with more cover had become more favourable for Marsh Tits, and that the suitability of those with less cover had either not changed or declined a little. There was no indication of a difference in elevation between the two regression lines (Fig. 2) which also suggested that the increase in Marsh Tit abundance had occurred in sites with more cover and not across all sites in general. If, as discussed below, Marsh Tit use of the shrub layer reduces competition with Great Tits and Blue Tits, then an overall increase in woodland shrub cover might buffer Marsh Tits against the effects of competition from these other species whose national populations have increased. Such an effect might have contributed to the increase in Marsh Tits in the RSPB sites recorded in 2003/04, and perhaps also to the recent increase in the national Marsh Tit population (Eaton *et al.* 2006).

A difference in response across sites was also apparent in the lack of any relationships between Marsh Tit abundance and the vegetation variables for the BTO sites in 2003/04. Overall, the BTO sites tended to be smaller than those of the RSPB; over 30% of BTO sites were less than 20 ha, whereas less than 10% of RSPB sites occurred in this size category (Amar *et al.* 2006). The RSPB sites tended to be large, mature woodland blocks, set in more wooded landscapes, and also had a greater representation in Scotland and the west. In contrast, the BTO sites were located in landscapes more dominated by intensive agriculture and urban/suburban development, 46% of sites being in the east and south east compared to 33% of RSPB sites (Amar *et al.* 2006). Marsh Tits are known to be sensitive to woodland area (Hinsley *et al.* 1996) and landscape-scale structure can

affect local extinction/colonisation characteristics and species composition within woodlands (Bellamy *et al.* 2003, Bennett *et al.* 2004). Overall, BTO sites had more shrub cover than those of the RSPB (e.g. BTO sites: mean cover at 2-4 m = 30 ± 12%, RSPB sites: 24 ± 16%), but Marsh Tit abundance at BTO sites showed an overall decrease of 27% between the two survey periods, compared to the 27% increase at RSPB sites. This also suggests that factors in addition to shrub cover may contribute to habitat suitability. More BTO sites may have been sub-optimal for Marsh Tits, at both local and landscape scales, and did not benefit from any positive effects of woodland maturation and/or increasing shrub cover.

In the literature (e.g. Perrins 1979, Cramp & Perrins 1993), Marsh Tit habitat is generally described as mature woodland, and the results reported here are consistent with this. Furthermore, these results suggest that the structure favoured by Marsh Tits comprises a tall tree canopy with a well developed shrub layer beneath it. In Wytham Woods, Marsh Tits also breed in areas of ancient hazel coppice where the shrub layer is unusually tall and, with the exception of a low density of large, mature oaks, forms much of the top canopy. Such a structure is broadly similar to that of scrub and raises the question of why a species that favours the shrub layer in woodland should be absent from structurally similar secondary habitats such as scrub and hedgerows.

The Willow Tit *Poecile montanus* is a closely related species with which Marsh Tit has frequently been confused; indeed the two were not recognised, or accepted, as separate species in the UK until the early 1900s (Kleinschmidt 1898, Simson 1966). Willow Tits in the UK have declined by more than 50% over the last 25 years and were added to the Red List of Birds of Conservation Concern in 2002 (Gregory *et al*. 2003). In the UK, they are generally thought of as woodland birds, but with a preference for wet, scrubby habitat (Perrins 1979, Cramp & Perrins, 1993) and recent work by the RSPB (Lewis *et al.*, this volume) has identified mature scrub, including derelict industrial sites and hedgerows, as the species current strongholds. Unlike all other British tits (except Crested Tit *Lophophanes cristatus* which in the UK occurs only in a restricted

area of Scotland) Willow Tits excavate their own nest holes and can utilise relatively small diameter stems for the purpose (Lewis, pers. com.). This ability may allow them to occupy scrub where the other species of tit are limited by the lack of nest holes. Within woodland, Willow Tits may in turn be limited by usurpation of their nest sites by other tits (Maxwell 2002, Lewis *et al.* this volume, but also see Siriwardena 2004). Marsh Tits reduce competition with Blue and Great Tits by concentrating their activity in the shrub layer, between Blue Tits in the top canopy and Great Tits lower down (Lack 1971), and may reduce competition for nest holes when necessary by nesting low down (Siriwardena 2006). In Wytham Woods, where the population density of Great and Blue Tits is relatively high (*c.* 2.4 x higher than in Monks Wood, Carpenter *et al.* unpubl. data), most Marsh Tits nest within a metre of the ground. Similarly, at Roudsea Wood, ten out of ten nest sites found when determining core areas of territories were within one metre of the ground. In Monks Wood, Marsh Tits use holes across a range of heights from ground level to *c.* 10 m, but they are often low (mean in 2004 = 3 m, $n = 30$; Broughton unpubl. data). Most of the nests are in Common Ash and this, as the dominant tree species in Monks Wood, appears to offer good numbers of suitable holes from ground level upwards. Common Ash also tends to have a relatively thin canopy and hence may be favourable for the maintenance of a good shrub layer.

Given the importance of the shrub layer to Marsh Tits, the reasons for the species national population decline may be linked to changes in woodland shrubs. Although woodland maturation may favour the development of a good quality shrub layer, this may be dependent, at least in part, on tree species composition, density and management. The development of a dense canopy, as may occur in species such as Common Beech *Fagus sylvatica* and Sycamore *Acer pseudoplantanus*, may shade out the shrub layer. Similarly, shrub layer growth and replacement may be damaged by excessive deer grazing (Fuller 2001, Perrins & Overall 2001) and management practices which clear the ground beneath the tree canopy. As food storers, seeds may be important for Marsh Tits and, as suggested by the observations of foraging behaviour, particularly so in winter. Thus

herbaceous, seed-bearing plants may also be important, but are equally, or more, vulnerable to the same factors likely to damage the shrub layer. It has been noted elsewhere (Perrins 1979) that the common English names of Marsh and Willow Tit seem rather inappropriate, and probably arose due to the confusion between the identities of the two species. Currently in the UK, the primary habitat of the Marsh Tit appears to be mature woodland shrub whilst that of the Willow Tit is mature scrub.

We would like to thank English Nature for permission to work in Monks Wood, Roudsea Wood, Swanton Novers and Treswell Wood, with particular thanks to Phil Grice, Ash Murray, Chris Gardiner and Rob Petley-Jones, and to Nigel Fisher, Conservator of Wytham Woods. We would also like to thank Robert Baker, Simon Butler, Laura Daniels, Chris du Feu and the South Nottinghamshire Ringing Group, Jim Fowler, Alex Lewis, Ken Smith and staff and students of the EGI, University of Oxford, for colour-ringing and/or recording Marsh Tits, and for assistance with habitat recording, and Alistair Dawson for Fig. 1. Special thanks also to Jim Fowler for accommodation and hospitality. Finally, thanks to two referees for improving the manuscript and especially for the suggestion that increasing shrub abundance might reduce competition from other tits.

REFERENCES

Altmann, J. 1974. Observational study of behaviour; sampling methods. *Behav.* **49:** 227-265.

Amar, A., Hewson, C.M., Thewlis, R.M., Smith, K.W., Fuller, R.J., Lindsell, J.A., Conway, G., Butler, S. & MacDonald, M. 2006. What's happening to our woodland birds? Long-term changes in the populations of woodland birds. RSPB Research Report no. 19 and BTO Research Report no. 169. Sandy, RSPB.

Bellamy, P.E., Rothery, P. & Hinsley, S.A. 2003. Synchrony of woodland bird populations: the effect of landscape structure. *Ecography* **26**: 338-348.

Bennett, A.F., Hinsley, S.A., Bellamy, P.E., Swetnam, R.D. & MacNally, R. 2004. Do regional gradients in land-use influence richness, composition and turnover of bird assemblages in small woods? *Biol. Cons.* **119**: 191-206.

Betts, M.M. 1955. The food of titmice in oak woodland. *J. Anim. Ecol.* **24**: 282-323.

Bevan, G. 1959. The feeding sites of birds in dense oakwood. *London Nat.* **38**: 64-73.

Broughton, R. K., Hinsley, S.A., Bellamy, P.E., Hill, R.A. & Rothery, P. 2006. Marsh Tit *Peocile palustris* territories in a British broadleaved wood. *Ibis* **148**: 744-752.

Colquhoun, M.K. & Morley, A. 1943. Vertical zonation in woodland bird communities. *J. Anim. Ecol*. **12**: 73-81.

Cramp, S. & Perrins, C.M. (eds) 1993. *The Birds of the Western Palearctic. Vol. 7: Flycatchers to Shrikes*. Oxford: Oxford University Press.

Eaton, M.A., Ausden, M., Burton, N., Grice, P.V., Hearn, R.D., Hewson, C.M., Hilton, G.M., Noble, D.G., Ratcliffe, N. & Rehfisch, M.M. 2006. *The state of the UK's birds 2005*. Sandy, Bedfordshire: RSPB, BTO, WWT, CCW, EN, EHS, and SNH.

Fuller, R.J. 1995. *Bird Life of Woodland and Forest*. Cambridge: Cambridge University Press.

Fuller, R.J. 2001. Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanisms. *Forestry* **74**: 289-298.

Fuller, R.J., Noble, D.G., Smith, K.W. & Vanhinsberg, D. 2005. Recent declines in populations of woodland birds in Britain: a review of possible causes. *Brit. Birds* **98**: 116-143.

Gardiner, C. & Sparks, T.H. (eds) 2005. *Ten years of change: woodland research at Monks Wood NNR, 1993-2003. Proceedings of the 50th Anniversary Symposium.* English Nature Research Report 613. Peterborough: English Nature.

Gibb, J. 1954. Feeding ecology of tits, with notes on Treecreeper and Goldcrest. *Ibis* **96**: 513-543.

Gregory, R.D., Wilkinson, N.I., Noble, D.G., Robinson, J.A., Brown, A.F., Hughes, J., Procter, D.A., Gibbons, D.W. & Galbraith, C.A. 2002. The population status of birds in the United

Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002-2007. *Brit. Birds* **95**: 410-450.

Gregory, R.D., Eaton, M.A., Noble, D.G., Robinson, J.A., Parsons, M., Baker, H., Austin, G. & Hilton, G.M. 2003. *The State of the UK's Birds 2002*. Sandy: The RSPB, BTO, WWT and JNCC.

Hartley, P.H.T. 1953. An ecological study of the feeding habits of the English titmice. *J. Anim. Ecol.* **22**: 261-288.

Hewson, C. & Amar, A. 2006. Recent changes in British woodland bird populations. *Ibis*, this volume.

Hinde, R.A. 1952. The behaviour of the Great Tit (*Parus major*) and some related species. *Behav. Suppl*. **2**: 1-201.

Hinsley, S.A., Bellamy, P.E., Newton, I. & Sparks, T.H. 1995. Habitat and landscape factors influencing the presence of individual breeding bird species in woodland fragments. *J. Avian Biol*. **26**: 94-104.

Hinsley, S.A., Bellamy, P.E., Newton, I. & Sparks, T.H. 1996. Influences of population size and woodland area on bird species distributions in small woods. *Oecologia* **105**: 100-106.

Hinsley, S.A., Hill, R.A., Gaveau, D.L.A. & Bellamy, P.E. 2002. Quantifying woodland structure and habitat quality for birds using airborne laser scanning. *Funct. Ecol.* **16**: 851-857.

Kleinschmidt, O. 1898. Weitere Notizen über Sumpfmeisen. *Orn. Monatsber*. **6**: 33-36.

Lack, D. 1971. *Ecological Isolation in Birds*. Oxford and Edinburgh: Blackwell Scientific Publications.

Lewis, A. 2006. Diagnosing the causes of the decline of British Willow Tits. *Ibis*, this volume.

Maxwell, J. 2002. Nest-site competition with blue tits and great tits as a possible cause of declines in willow tit numbers: observations in the Clyde area. *Glasgow Naturalist* **24**: 47-50.

Martin, P. & Bateson, P. 1993. *Measuring Behaviour*. 2nd Edition. Cambridge: Cambridge University Press.

Mead, C. 2000. *The State of the Nations Birds*. Suffolk: Whittet Books Ltd.

Morley, A. 1953. Field observations on the biology of the Marsh Tit. *Brit. Birds* **46**: 233-238, 273-287, 332-346.

Perrins, C.M. 1979. *British Tits*. London: Collins.

Perrins, C. 2003. The status of Marsh and Willow Tits in the UK. *Brit. Birds* **96**: 418-426.

Perrins, C.M. & Overall, R. 2001. Effect of increasing numbers of deer on bird populations in Wytham Woods, central England. *Forestry* **74**: 299-309.

Simson, C. 1966. *A Bird Overhead*. London: Witherby.

Siriwardena, G.M. 2004. Possible roles of habitat, competition and avian nest predation in the decline of the Willow Tit *Parus montanus* in Britain. *Bird Study* **51**: 193-202.

Siriwardena, G.M. 2006. Avian nest predation, competition and the decline of British Marsh Tits *Parus palustris*. *Ibis* **148**: 255-265

Smith, G. & Gilbert, J. 2001. *National Inventory of Woodland and Trees – England*. Edinburgh: Forestry Commission.

Snow, D.W. 1954. The habitats of Eurasian tits (*Parus* spp.). *Ibis* **96**: 565-585.

Sokal, R.R. & Rohlf, F.J. 1981. *Biometry*. 2nd Edition. New York: W.H. Freeman and Company.

Southern, H.N. & Morley, A. 1950. Marsh-Tit territories over six years. *Brit. Birds* **43**: 33-47.

Table 1. Comparison of overall time budgets and foraging behaviour of Marsh Tits and Blue Tits in winter in Monks Wood in 2004/05.

Overall time budget, % of records			**Foraging behaviour, % of records**		
Activity	Marsh Tit (*n* = 119)	Blue Tit (*n* = 128)	Behaviour	Marsh Tit (*n* =79)	Blue Tit (*n* = 91)
Foraging	65	69	Gleaning branches	32	38
Vigilance	23	16	Handling/eating	27	16
Flight	9	11	Searching, without pecking	22	17
Maintenance	2	3	Gleaning leaves	8	7
Calling	1	1	Hanging feeding	6	22
			Caching/retrieving	5	0

Table 2. Comparison of foraging locations within trees and shrubs of Marsh Tits and Blue Tits in winter in Monks Wood in 2004/05.

	In canopy, % of records		**In understorey, % of records**	
Location	Marsh Tit (*n* = 46)	Blue Tit (*n* = 70)	Marsh Tit (*n* = 71)	Blue Tit (*n* = 53)
Top third	38	53	42	64
Middle third	39	30	39	28
Bottom third	17	10	13	8
Ground (beneath tree or shrub)	6	7	6	0

Table 3. Comparison of the characteristics, and source of variation, of trees and shrubs in Marsh Tit territories in five different woods. Data are shown for Treswell Wood, but were not included in the analysis due to the small sample size. The *P* values (one-way ANOVA) refer to differences between woods in species richness, density indices and numbers of trees and shrubs. The intraclass correlation shows the variance in the data due to differences between woods (see text for more details).

	Mean (SD) values per transect (*n* =10 except for Treswell where *n* = 3)						Intraclass
	Wytham	Monks Wd	Swanton N	Roudsea	Treswell	*P*	correlation, %
TREES							
Tree species richness	3.4 (1.0)	4.6 (1.0)	5.0 (1.9)	6.9 (1.3)	2.7 (0.6)	< 0.001	51
Canopy density index	1.48 (0.32)	1.81 (0.13)	1.80 (0.40)	1.55 (0.34)	1.73 (0.08)	0.052	16
Nos. of large trees	10.6 (5.4)	6.7 (3.0)	12.1 (6.3)	20.4 (9.7)	17.3 (0.6)	< 0.001	40
Nos. of medium trees	10.0 (8.6)	37.7 (15.2)	18.6 (12.8)	33.9 (12.9)	14.3 (2.5)	< 0.001	48
Nos. of large + medium	20.6 (12.5)	44.4 (15.1)	30.7 (11.4)	54.3 (10.5)	31.7 (2.5)	< 0.001	57
Nos. of small trees	8.2 (10.6)	35.3 (43.0)	34.1 (31.6)	35.5 (30.3)	13.0 (8.0)	0.155	8
SHRUBS							
Shrub species richness	3.6 (1.1)	5.1 (1.0)	4.4 (1.9)	5.4 (1.6)	5.7 (1.5)	0.041	17
Shrub density index	1.94 (0.48)	1.89 (0.21)	1.94 (0.61)	2.07 (0.45)	2.47 (0.16)	0.851	0
Nos. of large shrubs	23.7 (16.3)	12.8 (6.0)	14.3 (11.9)	18.2 (17.0)	12.0 (2.7)	0.291	3
Nos. of medium shrubs	10.9 (5.7)	25.1 (7.3)	29.2 (32.4)	23.1 (19.1)	16.7 (4.9)	0.195	6

Nos. of large + medium	34.6 (20.8)	37.9 (10.7)	43.5 (38.0)	41.3 (33.8)	28.7 (3.5)	0.899	0
Nos. of small shrubs	2.8 (1.8)	9.1 (7.1)	63.4 (45.1)	39.9 (31.6)	14.0 (7.6)	< 0.001	48

Table 4. Summary of: **a)** fitted models of Marsh Tit abundance at 157 RSPB RWBS sites in 2003/04 and *F*-tests for the effects of vegetation cover at different heights and of horizontal visibility after allowing for the effects of regional locality ($n = 6$) and, **b)** *F*-tests for the differences in the slopes of the relationships between Marsh Tit abundance and vegetation cover at different heights in 2003/04 compared to the original surveys in the 1980s, after allowing for the effects of regional locality (for regional locality, $P < 0.001$ in all models). R^2 values are for the full models including region; data for horizontal visibility were not available for the 1980s.

Effect	R^2 (%)	*F*	*P*
a) Vegetation cover in 2003/04			
1. Cover at 0.5 – 2.0 m	16	4.56	0.034
2. Cover at 2.0 – 4.0 m	18	7.02	0.009
3. Cover at 4.0 – 10.0 m	16	4.50	0.036
4. Horizontal visibility	19	9.89	0.002
b) Differences in slopes between 1980s and 2003/04			
1. Cover at 0.5 – 2.0 m	14	10.63	0.001
2. Cover at 2.0 – 4.0 m	15	12.58	< 0.001
3. Cover at 4.0 – 10.0 m	15	11.97	0.001

Figure 1. Shrub and tree numbers (total number of shrubs ≥ 2 m and total number of trees with dbh ≥10 cm), and shrub and tree canopy density indices in transect samples of Wytham Woods, comparing areas occupied by Marsh Tits (unshaded bars, $n = 10$) with unoccupied areas (shaded bars, $n = 6$). Standard errors of the means shown by vertical bars.

Figure 2. Relationship between Marsh Tit abundance and vegetation cover corresponding to the shrub layer in 157 woods recorded by the RSPB during the 1980s (open circles and dashed line) and in the same woods by the RWBS in 2003/04 (crosses and solid line). Lines fitted using linear regression.

Figure 3. Relation between Marsh Tit abundance and horizontal visibility for 157 woods recorded by the RSPB during the RWBS in 2003/04. Line fitted using linear regression.

Fig. 1

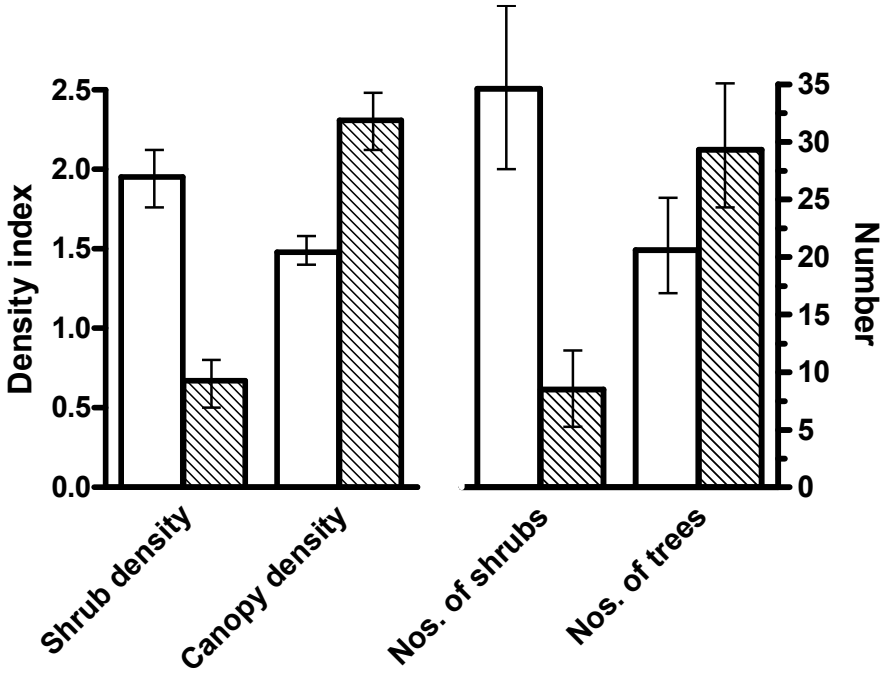

Density index
2.5
2.0
1.5
1.0
0.5
0.0
Number
35
30
25
20
15
10
5
0
Shrub density
Canopy density
Nos. of shrubs
Nos. of trees

Fig. 2

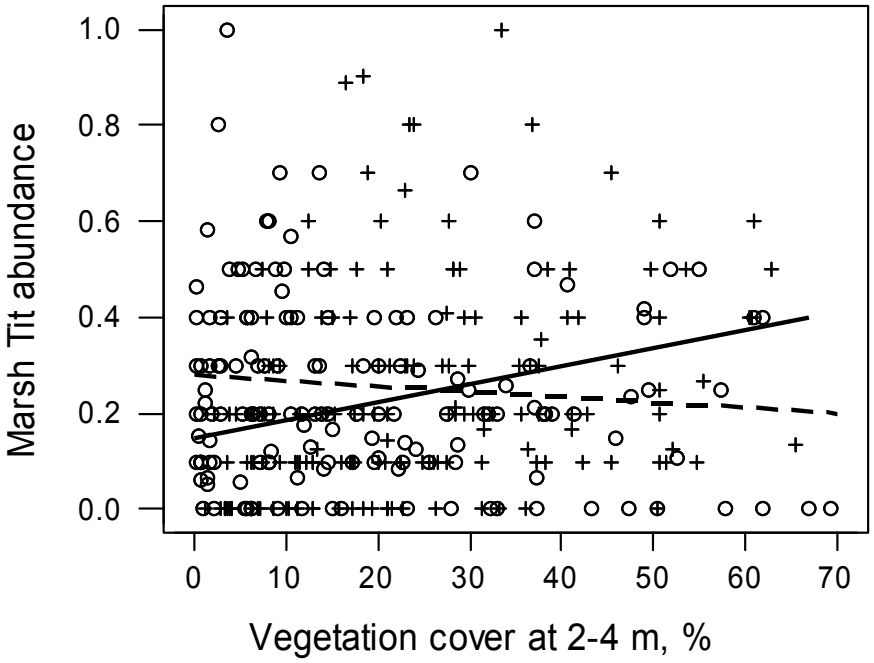
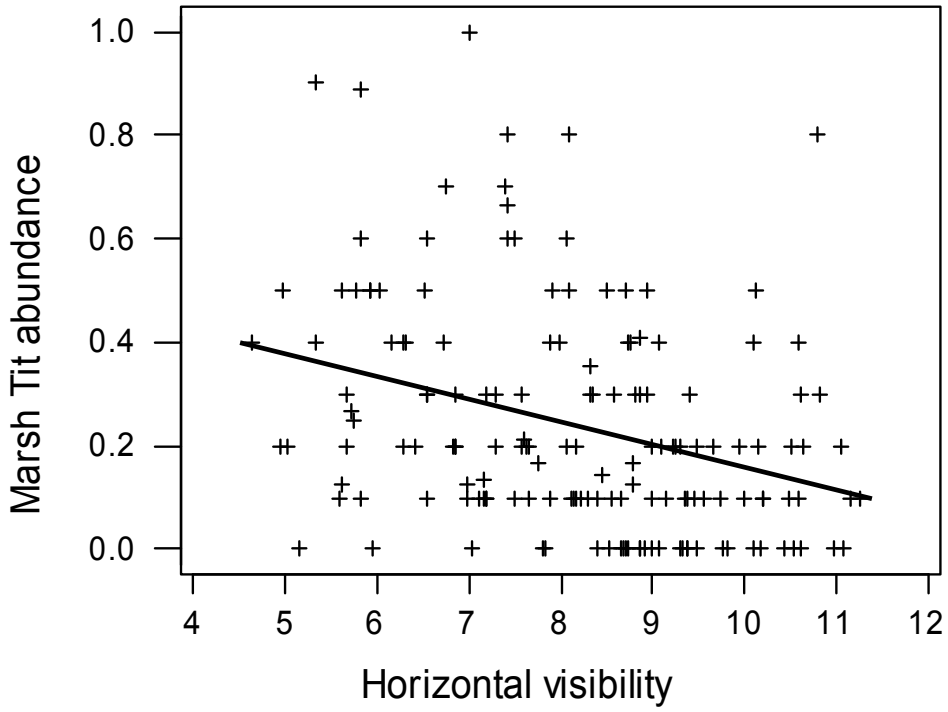

Marsh Tit abundance
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
60
70
Vegetation cover at 2-4 m, %

Fig. 3


Marsh Tit abundance
1.0
0.8
0.6
0.4
0.2
0.0
4
5
6
7
8
9
10
11
12
Horizontal visibility