# HABITAT MODELLING AND THE ECOLOGY OF THE MARSH TIT (*POECILE PALUSTRIS*)

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# ABSTRACT

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Among British birds, a number of woodland specialists have undergone a serious population decline in recent decades, for reasons that are poorly understood. The Marsh Tit is one such species, experiencing a 71% decline in abundance between 1967 and 2009, and a 17% range contraction between 1968 and 1991. The factors driving this decline are uncertain, but hypotheses include a reduction in breeding success and annual survival, increased inter-specific competition, and deteriorating habitat quality. Despite recent work investigating some of these elements, knowledge of the Marsh Tit's behaviour, landscape ecology and habitat selection remains incomplete, limiting the understanding of the species' decline.

This thesis provides additional key information on the ecology of the Marsh Tit with which to test and review leading hypotheses for the species' decline. Using novel analytical methods, comprehensive high-resolution models of woodland habitat derived from airborne remote sensing were combined with extensive datasets of Marsh Tit territory and nest-site locations to describe habitat selection in unprecedented detail. Further fieldwork established the causes and frequency of breeding failure at the local population scale, and dispersal distances and success were quantified. Information from these studies was used to inform national-scale spatial analyses of habitat distribution in relation to the pattern of range contraction for the Marsh Tit and two other woodland bird species.

The combined results indicate that Marsh Tits require extensive areas of mature woodland in order to accommodate large territories and short dispersal distances, with greatest selection for a woodland structure encompassing a tall, near-closed tree canopy and extensive understorey. The evidence suggests that nest-site competition, nest predation or deteriorating habitat quality have not driven the population decline. However, reduced connectivity between woodlands in the landscape, possibly due to hedgerow loss, may have interacted with increased mortality to precipitate population declines and local extinctions where habitat fragmentation was relatively high. The potential causes of increased mortality are discussed, along with priority areas for future research and the wider possible applications of remote sensing techniques in the field of woodland bird research.

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# PREFACE AND ACKNOWLEDGEMENTS

This study contained within this thesis began with fieldwork initiated at Monks Wood National Nature Reserve (NNR) in the 1990s by Dr Shelley Hinsley and Paul Bellamy, which involved the colour-ringing of Marsh Tits to determine the population size. In 2002 I was offered the opportunity to develop the project into a systematic study of the spatial ecology and behaviour of the Marsh Tit, which was and remains topical due to the national decline in the species' abundance. The availability of a large study population and extensive study area meant that high-quality investigations of the Marsh Tit's population and landscape ecology were possible. Furthermore, spatial habitat data derived from airborne remote sensing provided some of the most comprehensive woodland habitat datasets anywhere in the world. The opportunity to combine this with spatial data of the movements, territory extent and nest-site locations of Marsh Tits enabled the development of novel analyses with which to describe bird-habitat relationships in unprecedented detail. As such, there was great potential for a rewarding project that could inform the understanding of the Marsh Tit's decline, but also contribute to wider woodland bird research and conservation.

I am deeply indebted to my supervisory team of Dr Shelley Hinsley of the Centre for Ecology & Hydrology (CEH) and Dr Ross Hill of Bournemouth University (BU) for unwavering support and encouragement during the course of this work. I also thank CEH for support throughout the project and part-funding this thesis submission, and also BU for accepting me as a Visiting Research Fellow to enable this submission. I am very grateful to Dr Stephen Freeman and Dr Peter Rothery, respectively current and former colleagues at CEH, for statistical advice. Dr Ross Hill and colleagues processed and supplied the remote sensing data while at the Earth Observation Section at CEH Monks Wood. I also thank the British Trust for Ornithology for supplying national datasets of bird distribution. A number of students and colleagues contributed to fieldwork data collection during the study, and I thank Dr Jane Carpenter, Dr Daria Dadam, Deborah Marchant, and particularly Paul Bellamy and Dr Shelley Hinsley. I am also indebted to the landowners and managers for access to the woodland study sites, and particularly to Natural England for access to Monks Wood NNR. I am also especially grateful to Geoff Leach and Sarah Caesar for invaluable logistical support during fieldwork. Finally, I wish to thank the numerous reviewers and editors of the published and accepted journal papers contained within this thesis, for constructive criticism of the work.

# AUTHOR’S DECLARATION

As a submission for a PhD by publications, the published papers presented in this thesis have previously appeared in scientific journals as indicated. All papers in the main body of the thesis were multi-authored collaborations, with contributions from the supervisory team, colleagues and/or students at CEH. However, as lead author, the great majority of content in each paper was my own work, and the extent of each contribution is outlined and certified by co-authors in Appendix 2. I also declare that I was the sole author of the additional material comprising the thesis synthesis, including the Introduction, Methods and Discussion chapters, although valuable comments and suggestions were provided by the supervisory team. As such, and excepting where otherwise stated, this work can be considered as my own.

# 1 INTRODUCTION

## 1.1 Introduction to the thesis

Birds are perhaps the most obvious and accessible wild animals that people encounter throughout the world, excluding invertebrates. With numerous diurnal and nocturnal species present in almost every habitat from montane to pelagic, birds occur at nearly all latitudes and most people are liable to experience them on a daily basis. This familiarity, combined with the diversity and, often, intrinsic beauty of their form and vocalisations may explain why birds are deeply rooted in human cultures worldwide, as deity, myth, muse, currency, companion, quarry, livestock, exhibit, and scientific subject (Kear 1990; Greenoak 1997; Bircham 2007; Tidemann & Gosler 2010).

In the developed West, where economies and levels of disposable income facilitate extensive leisure and scientific activities, birds are by far the most popular of all wildlife for such pursuits. In the USA, for example, the conservation-oriented National Audubon Society has over 600,000 members (National Audubon Society 2012), and in the UK the Royal Society for the Protection of Birds (RSPB) has over a million members (RSPB 2012). In comparison, The Mammal Society has 2,000 members in the British Isles (The Mammal Society 2012), and the invertebrate conservation organisation Buglife has approximately 500 members (Buglife 2012).

It is evident, therefore, that birds are important to people, and there are strong arguments for conserving birds on utilitarian, scientific and cultural grounds (BirdLife International 2012a). As such, birds can act as flagship species for science and conservation in general, providing an accessible and familiar context for policy-makers and scientists to communicate ideas and issues, such as climate change, to the general public (IUCN 2009; Veríssimo et al. 2009).

### 1.1.1 The global biodiversity crisis

Biodiversity is defined as the total biotic variation in a given area, from the scale of genes to ecosystems (Purvis & Hector 2000), with a major constituent unit being the total number of species. There may be 14 million species on Earth (Purvis & Hector 2000), yet human activity has led to recent extinction rates that are up to 10,000 times above the background level, through degradation and destruction of habitats, hunting, and ecosystem disruption (Pimm et al. 1995). This has been termed a 'biodiversity crisis' and limited resources with which to address the problem have resulted in calls for prioritisation (Brooks et al. 2006). At the Rio 'Earth Summit' in 1992, the UK was the first signatory nation of the Convention on Biological Diversity to adopt a Biodiversity Action Plan (UK BAP), which was published in 1994 and contained targets to conserve habitats and reverse species declines (JNCC 2012). A joint strategic framework was published in 2007 which restated the aims of the devolved nations within the UK to tackle the loss of biodiversity (UK Biodiversity Partnership 2007). This was to be achieved via the identification of priority species and habitats, setting targets for their improvement, and ongoing monitoring. This monitoring involved a suite of 26 'biodiversity indicators', one of which was the population trends of selected bird species belonging to three habitat groupings: seabirds, farmland birds, and woodland birds (UK Biodiversity Partnership 2007).

### 1.1.2 Bird biodiversity indicators in the UK

The UK is notable in global terms for the long time series of bird monitoring data that have documented the changes in species distributions and abundance since the 1960s (Baillie et al. 2010). This allowed the development of the bird population indices for specific habitat types (Defra 2011), and also identified areas of biodiversity loss where remedial measures could be targeted.

The general index of 121 bird species in the UK showed a modest increase of 4% between 1970 and 2010 (Defra 2011), but within this was a more varied picture for species grouped by habitat. The seabird index of 19 species increased by 30% between 1970 and 2010, and the deep and long-term decline in the index of 19 species which constitute the farmland bird biodiversity indicator has received much attention in recent decades (Newton 2004; Defra 2011). The overall decline in abundance of many woodland birds has also been well documented (Fuller et al. 2005; Amar et al. 2006), and between 1970 and 2010 the population of 38 species in the UK woodland bird index fell by 19% (Defra 2011). Within this group, however, the 12 woodland generalist species increased by 12% during this period whilst the 26 woodland specialists declined by 32%.

### 1.1.3 Declines of woodland birds

Among the declining woodland specialists in the woodland bird index, seven species are listed on the Red List of ‘Birds of Conservation Concern’, having undergone a population decline of more than 50% over 25 years (Eaton et al. 2009). These are the Lesser Spotted Woodpecker (*Dendrocopos minor*), Tree Pipit (*Anthus trivialis*), Wood Warbler (*Phylloscopus sibiliatrix*), Spotted Flycatcher (*Muscicapa striata*), Willow Tit (*Poecile montanus*), Marsh Tit (*Poecile palustris*), and Capercaillie (*Tetrao urogallus*), although the latter is restricted to a small area of the Scottish uplands and is not considered further.

Fuller et al. (2005) reviewed possible causes of the declines of woodland birds, and proposed seven factors that may have had individual or combined effects: (1) pressures during migration or in the African wintering areas of migrant species, (2) effects of climate change on British woods, (3) a general reduction of invertebrate prey, (4) impacts of land-use change on woodland edges and hedgerows, (5) reduced management of woodlands, (6) increased browsing pressure on woodlands by deer, and (7) increased nest predation. However, studies attempting to link any of these factors directly to individual species declines have provided only limited supporting evidence. Charman et al. (2012a) suggested that the decline of the Lesser Spotted Woodpecker may be related to the contemporaneous decrease in canopy oak and increase in sub-canopy vegetation identified by Amar et al. (2010), while Charman et al. (2012b) speculated that a reduction in breeding productivity may be linked to a shortage of invertebrate prey, but these studies were not conclusive. Freeman & Crick (2003) identified mortality between fledging and breeding as the most likely driver of the population decline of the Spotted Flycatcher, rather than reduced nest success, and Mallord et al. (2012) detected no change in nest predation rates for the Wood Warbler. Lewis et al. (2007) and Siriwardena (2004) found no relationship between the incidence of Willow Tits and the frequency of nest competitors nor predators, with Lewis et al. (2009a) instead finding a preference for young, damp woodland, a habitat which may have become rarer (Hopkins & Kirby 2007). Such limited evidence means that the causes of the declines of these species remain largely speculative (Siriwardena 2004; Fuller et al. 2005; Lewis et al. 2009b; Smith & Charman 2012). Comparatively more information is available for the Marsh Tit regarding habitat preferences and ecology, and how these may relate to changes in woodlands, and this species will be the focus of the following sections.

## 1.2 The Marsh Tit

### 1.2.1 Classification and history of the Marsh Tit

The Marsh Tit is a 10-12 g bird of the Paridae family of Holarctic tits and chickadees that is associated with deciduous woodland habitat, nests in holes in trees, and feeds on seeds and insects, some of which it caches in autumn and winter (Cramp & Perrins 1993). The species is non-migratory and has a discontinuous distribution in the Palearctic, being present in Europe largely between latitudes of 40° and 60° north, and in east Asia between 30° and 55° north (BirdLife International 2012b).

The Marsh Tit was classified by Carl Linnaeus in 1758 as *Parus palustris*, in reference to a presumed fondness for damp woodland, although it has since been moved into the genus *Poecile* on the basis of genetic evidence (Gill et al. 2005). Thomas Pennant (*British Zoology,* 1776) and Gilbert White (*The Natural History and Antiquities of Selborne*, 1789) both mentioned the Marsh Tit in England as a year-round resident of woodlands. In 1897, however, examples of a previously undescribed sub-species of the Willow Tit (*Poecile montanus kleinschmidti*) were discovered among British Marsh Tit specimens in London's Natural History Museum. This had previously gone unnoticed due to the plumage similarity between the British races of the two species (see Appendix 1A). It became apparent that the Willow Tit was sympatric with the Marsh Tit in many parts of Britain (Rothschild 1907), and so previous references to the Marsh Tit's distribution and behaviour potentially involved both species. As such, the true status of the British Marsh Tit was essentially unknown at the beginning of the 20th Century.

### 1.2.2 Field studies of the Marsh Tit 1937-2002

The first detailed field study of the Marsh Tit was conducted by Henry Southern and Averil Morley at Bagley Wood, near Oxford, between 1937 and 1942, and involved colour-ringing Marsh Tits to enable territory-mapping and behavioural observations. Southern & Morley (1950) described an average territory size of 2.4 ha and mean survival from time of marking of 19.2 months for males and 13.3 for females. Morley (1953a) described the annual cycle of Marsh Tits, Morley (1953b) the songs, calls, territorial behaviour and visual displays, and Morley (1953c) the breeding and roosting behaviour. This series of papers was rich in detail and novel information, but was based on small samples of just 34 birds and 20 nests within 4-5 territories on a 20 ha plot of woodland. Information on habitat selection, dispersal or predation was still lacking, and no further detailed field study was to be undertaken on the British Marsh Tit for some 60 years.

Between 1947 and 1954, Fritz Amann studied Marsh Tit survival, dispersal and territoriality in Switzerland, using 303 colour-ringed birds over 70 ha. This work was not published until half a century later, however, reporting juvenile dispersal distances of 300 to 1,550 m, rapid pairing and settlement of juveniles, and basic qualitative habitat analyses (mature trees as optimal habitat) (Amann 1997). Schaub & Amann (2001) reported annual survival rates of 0.47 for adults and 0.19 for juveniles. Amann (2003) described territory sizes of 2.5-4.5 ha in oak-rich (*Quercus* spp.) habitat and up 17 ha in areas rich in Common Ash (*Fraxinus excelsior*) and clearings, with year-round territoriality and a high degree of mate fidelity between years.

Between 1967 and 1970, Fritz-Bernd Ludescher undertook a comparative study of the Marsh Tit and Willow Tit in Germany, colour-ringing 110 Marsh Tits and investigating territorial, nesting, and foraging behaviour (Ludescher 1973). Marsh Tits were again found to remain in pairs year-round, occupying territories averaging 5-6 ha which often coincided with those of the Willow Tit. Of the 29 nests examined, 69% were in cavities within dead wood and 55% were predated, mostly by Great Spotted Woodpeckers (*Dendrocopos major*). Ludescher (1973) detected no differences in foraging behaviour between Marsh and Willow Tits, with both species taking a wide variety of insects and seeds, caching many of the latter under bark.

Jan-Åke Nilsson studied Marsh Tits in southern Sweden during the 1980s, using *c*.350 nestboxes in a 64 km$^2$ study area of patchy habitat. Nilsson (1989) recorded maximum natal dispersal distances of 4.6 km for males and 7.3 km for females, with dispersal from the parental territory occurring 11-15 days after fledging (Nilsson & Smith 1985), and distances being positively influenced by population density (Nilsson 1989). In an elegant manipulation study using juveniles held in aviaries, Nilsson (1990) found that prior occupancy was the sole factor determining successful establishment, overriding size, hatching date, and previous social dominance. Males competed to disperse and settle in a vacant area before others, but prospecting females were tolerated to a greater extent than males by established birds, enabling females to be more selective in their choice of territory (Nilsson 1988).

Nilsson (1991) also manipulated food availability to show that females receiving extra nutrition produced an average of one more egg than unfed females, but ultimately clutch size appeared to be based on the declining value of offspring as the season progressed. Because early egg-laying and fledging largely determined the timing of juvenile dispersal, which is critical to successful settling, adults gained no advantage by increasing the size of their brood by laying more eggs if this ultimately delayed dispersal of their offspring and reduced their chance of recruitment into the breeding population.

During the 1980s and 1990s, Tomasz Wesołowski studied Marsh Tit nesting behaviour within 140 ha of the primeval Białowieża forest, Poland. Wesołowski (1996) found that nests were confined to deciduous stands of woodland, and were predominantly situated in small cavities within the live wood of a variety of tree species, at 0.5-27 m from the ground (mean 5.6 m). Wesołowski (2002) reported that 23% of nests failed, with predation accounting for 70% of these and being particularly heavy for the minority of nests in dead wood. The most significant predators were small rodents (*Rodentia*) and/or Common Weasel (*Mustela nivalis*). Supporting Nilsson (1991), Wesołowski (2000) found that female Marsh Tits that began laying eggs relatively late in the season reduced their clutch size and incubation period to compensate, so minimising the delay in juvenile dispersal.

These five major field studies revealed Marsh Tits to be sedentary, territorial, and socially monogamous, and tending to occur in pairs throughout the year or forming small winter flocks. Territories are large (typically 2.5-6 ha), breeding success and adult survival are high, juvenile dispersal is rapid and over relatively short distances, and successful establishment is determined by being the first occupant. In Britain, nesting begins in April when a tree cavity is lined with moss and fur and a typical clutch of 6-9 eggs is produced between mid April and early May (Cramp & Perrins 1993). Incubation is undertaken by the female for 13-16 days, and both adults feed the chicks for 18-21 days until they leave the nest. The young continue to be fed by the parents for up to a further 15 days before dispersing from the parental territory. Only one brood is produced each year, although it may be replaced if lost at an early stage. Breeding occurs at one year of age, and birds may live for up to 10 years (Robinson 2005). Prior to the work contained within the current thesis, little published information has been available in the British context for the causes of breeding failure, dispersal distances and success, or for the factors governing territory and nest placement.

### 1.2.3 Historical and current population status in Britain

Although the Marsh Tit is listed on the IUCN Red List as being of ‘Least Concern’, with an estimated global population of up to 72 million individuals (BirdLife International 2012b), a 36% decline was detected in Europe between 1982 and 2006 (PECBMS 2009). In Britain, national monitoring schemes indicated a 71% decline in abundance between 1967 and 2009 (Baillie et al. 2010), and a range contraction of 17% between 1968-72 and 1988-91 (Gibbons et al. 1993), particularly in northern England. The Marsh Tit remained most abundant in East Anglia, southern England and southern Wales, but is restricted to a small area of the Borders region in Scotland (Murray 2007). The total British population was estimated at 53,000 pairs in 2003 (Perrins 2003).

### 1.2.4 Proposed causes of the Marsh Tit’s decline

The reasons for the Marsh Tit’s decline in Britain were completely unknown in the early 2000s (Perrins 2003). Fuller et al. (2005) suggested potential factors including the effect of habitat fragmentation, a decline in habitat quality, locally increased predation by Great Spotted Woodpeckers, and nest-site competition from e.g. Blue Tit (*Cyanistes caeruleus*) and Eurasian Nuthatch (*Sitta europaea*). Siriwardena (2006) tested some of these hypotheses using datasets from national monitoring schemes but found no significant relationship between the abundance of Marsh Tits and selected nest predators (Great Spotted Woodpecker, Green Woodpecker (*Picus viridis*), and Jay (*Garrulus glandarius*)), nor competitors (Blue Tit, Great Tit (*Parus major*), and Eurasian Nuthatch). Siriwardena (2006) also noted that breeding success showed no decrease over time. Like Fuller et al. (2005), Siriwardena (2006) speculated that the most likely cause of the Marsh Tit’s decline was degradation of woodland habitat quality due to a lack of management and increased browsing pressure from deer. Siriwardena (2006) did not test this theory, however, and direct evidence was lacking.

Further evidence with which to test these hypotheses became available from the Repeat Woodland Bird Survey (RWBS: Amar et al. 2006) which examined gross changes in woodland habitat and bird populations between the 1980s and 2003-4 in 406 woods within 13 areas of Britain. Woodland structure was characterised in sample plots using 25 variables of vegetation height and coverage, based on visual estimates and direct measurements, and evidence of deer activity was also collected. Abundance of woodland birds was sampled using point counts and territory mapping (Amar et al. 2006). Despite the large number of variables tested, no meaningful correlates were identified between vegetation and Marsh Tit abundance. A more focussed re-analysis of the RWBS data was performed by Hinsley et al. (2007) using five variables of understorey and tree canopy, which found a significant positive relationship between Marsh Tit abundance and understorey cover, particularly in the 2-4 m height band, but only for woods surveyed by point counts.

### 1.2.5 Contemporary work on the Marsh Tit

Between 2005 and 2008, Jane Carpenter undertook research on Marsh Tit ecology and behaviour at Monks Wood National Nature Reserve (NNR) in Cambridgeshire and Wytham Woods in Oxfordshire for a DPhil thesis at the University of Oxford (Carpenter 2008), which was structured to investigate potential factors related to the population decline. Without testing, Carpenter (2008) discounted the hypotheses of reduced invertebrate prey and increased nest predation as unlikely, while habitat fragmentation and reduced annual survival were considered as potentially significant but also remained untested. Instead, Carpenter (2008) focussed investigations on the hypotheses of habitat change, increased inter-specific competition, and a deleterious effect of climate change.

In a comparative study of habitat associations of the Marsh Tit and Blue Tit using data from the RWBS, adopting a different modelling approach from that of Amar et al. (2006) and Hinsley et al. (2007), Carpenter et al. (2010) found a significant positive relationship between Marsh Tit presence and canopy cover, shrub species diversity, and the cover of understorey in the same 2-4 m height band identified by Hinsley et al. (2007). Marsh Tit abundance was positively correlated with increasing density of understorey vegetation and woodland cover in the landscape. Carpenter (2008) also conducted a small comparative study of breeding success using eight nests at each study site, quantifying the foraging behaviour and food provisioning rates of the adults, and sampling vegetation in the breeding territories. No differences were found between woods in the breeding success or food provisioning of young by their parents, and territories were of similar composition in both woods.

Comparing winter foraging, Carpenter (2008) recorded Marsh Tits more frequently in the understorey and lower canopy than Blue Tits, where the former spent less time in oak and more time being vigilant (and hence less foraging) than the latter. These differences were more pronounced at Wytham Woods, where Blue Tits (and Great Tits) were more abundant than at Monks Wood. In modelling future effects of climate change on the predicted range of the Marsh Tit, Carpenter (2008) estimated that much of England would become unsuitable by 2050, although expansion could be made into Scotland if suitable habitat were available.

In common with Fuller et al. (2005) and Siriwardena (2006), Carpenter (2008) ultimately concluded that declining habitat quality was likely to be the major factor driving the Marsh Tit's decline. This conclusion was based on the related hypothesis that woodland understorey had undergone a widespread decline or deterioration due to an abandonment of woodland management and increased browsing by deer. Work by Amar et al. (2010) indicates that this presumption is incorrect, however, and trends in the structural change of woodlands in England and Wales are explored in the following section.

## 1.3 Trends in the woodlands of England and Wales in the latter half of the 20th Century

### 1.3.1 Large-scale trends in broadleaved woodland habitat

Significant changes have taken place within English and Welsh woodlands during the period of the Marsh Tit's decline. In 1965, woodland of all types accounted for 7% of the area of England and Wales (Forestry Commission 1970), increasing to 8% by 1980 (Locke 1987) and 9% by 2000 (Forestry Commission 2001, 2002). While much of this increase was due to planting of coniferous plantations, the area of deciduous woodland also increased by 16% between 1965 and 2000 to 1.4 million ha (5% of land area). This increase incorporated a net decline of coppice management, from 9% (29,606 ha) of broadleaved woodland in 1965 to 3% (22,873 ha) in 2000. Coppicing is a traditional form of rotational cropping in which trees and shrubs are cut at the base and allowed to regenerate as multi-stemmed plants, with or without leaving isolated mature trees (standards). In essence, coppicing arrests woodland development at a dense, immature phase of shrubs and young trees, which are typically cropped at 15-30 year intervals and prevented from developing into mature woodland (Buckley 1992). Woodland which is not coppiced is termed ‘high forest’ if it has, or has the potential to attain, a tree cover of more than 20% (Forestry Commission 2002). In England and Wales, the area of broadleaved woodland classed as high forest increased by 34% between 1967 and 2000, ultimately accounting for 93% of the total (Forestry Commission 1970, 2001, 2002; Locke 1987).

### 1.3.2 Changes in woodland vegetation structure and composition

Using data from the RWBS, vegetation changes in 249 broadleaved woods across Britain between the 1980s and 2004 were reported by Amar et al. (2010). Vegetation was assessed using ground-based measurements in sample plots, and 11 of the 13 survey regions were within the Marsh Tit’s range in England and Wales. Results indicated that canopy cover (defined as vegetation taller than 10 m) increased or remained unchanged in eastern England and declined widely in southern England, the west and Wales (Table 1). Increasing woodland maturity and absence of management is predicted to increase canopy closure (Fuller et al. 2005), but these mixed results could be explained by self-thinning and wind-throw generating gaps in the canopy as some woods have matured.

Amar et al. (2010) also quantified changes in understorey vegetation cover within three height bands: 0.5 to 2 m, 2 to 4 m, and 4 to 10 m, and reported an overall increase in cover for each band between the sampling periods (Table 1). A second large-scale survey compared the structure of 103 woods across Britain between 1971 and 2001 (Kirby et al. 2005), and found a general trend of increasing maturity of lowland woods into a stem-exclusion phase. This was characterised by increased basal area of shrubs and trees, a reduction in the smallest size class of stems and a smaller increase in medium-sized stems, consistent with self-thinning (Kirby et al. 2005). Large trees remained rare, however, indicating that woods had not reached full maturity, with most stands of trees being less than 100 years old. There was a significant reduction in the frequency of open habitats within lowland woods, such as glades and rides, consistent with the increase in understorey shown by Amar et al. (2010). Kirby et al. (2005) found that some shrub species had declined in the decades between the two sampling periods, but Amar et al. (2010) detected no change in shrub species richness over time.

| Region and sub-region | Canopy | Understorey | | |
|---|---|---|---|---|
| | > 10 m | 0.5 – 2 m | 2 – 4 m | 4 – 10 m |
| **East** | | | | |
| Suffolk | ↑ | ↓ | ↔ | ↔ |
| Northamptonshire | ↔ | ↓ | ↑ | ↑ |
| **West** | | | | |
| Forest of Dean | ↓ | ↔ | ↑ | ↑ |
| Gloucestershire | ↓ | ↔ | ↑ | ↑ |
| Welsh Marches | ↓ | ↔ | ↑ | ↑ |
| Powys | No data | ↑ | ↑ | ↑ |
| Gwynedd | ↔ | ↑ | ↑ | ↑ |
| Devon/Somerset | No data | ↑ | ↑ | ↑ |
| **South** | | | | |
| Buckinghamshire | ↔ | ↔ | ↑ | ↑ |
| New Forest | ↓ | ↔ | ↔ | ↑ |

Table 1. Trends in estimated cover of canopy and understorey vegetation in given height bands between the 1980s and 2004, from Amar et al. (2010). Icons depict the direction of significant change: ↑ = significant increase, ↓ = significant decrease, ↔ = no significant change.

### 1.3.3 Impacts of deer

Perrins (2003) and Fuller et al. (2005) hypothesised that understorey vegetation may have suffered widespread damage due to increased browsing by expanding populations of deer. Dolman et al. (2010) reviewed the substantial evidence of impacts of deer browsing on field layer vegetation and low-growing woody plants, such as Bramble (*Rubus fruticosus*), and the survival of tree and shrub seedlings. However, most studies into the effect of deer on the understorey shrub layer have involved active coppice (Dolman et al. 2010), where the existing shrubs had been removed and hence all growth brought into the browsing range of deer. Studies into the effect of deer on established understorey vegetation, rather than regenerating coppice or seedlings, are rare. Gill & Fuller (2007) measured understorey density at 13 mature woods and found a negative relationship with deer density, but only below 1.5 m in height. Similarly, Cooke & Farrell (2001) reported severe browsing by Muntjac deer (*Muntiacus reevesi*) on low-growing Bramble and Privet (*Ligustrum vulgare*) and regenerating seedlings in Monks Wood NNR, but stated that browsing was of little consequence for established shrubs. The vast majority of lowland woods in England and Wales are presently approaching maturity and are not coppiced (Hopkins & Kirby 2007), and the evidence from Amar et al. (2010) and Kirby et al. (2005) suggests that there has been no widespread reduction in the cover of existing understorey despite an increase in observed signs of browsing by deer. Although Amar et al. (2010) found some regional variation in understorey change, with a significant decline in understorey cover at 0.5 to 2 m height in eastern England, where deer populations have expanded (Tables 1 and 2; Newson et al. 2012), understorey cover in this region actually increased or remained unchanged at taller height bands. Furthermore, understorey cover in all height bands increased or remained stable in every other sampled region, regardless of widespread expansion of deer populations and increases in abundance (Tables 1 and 2; Newson et al. 2012). In fact, surveyors in the Kirby et al. (2005) study considered that “only a few” British woods were “over-grazed” by deer in 2001. Therefore, the large-scale surveys do not support the hypothesis that an increase of woodland maturation and deer populations have resulted in the widespread decline in the coverage or species richness of understorey vegetation.

### 1.3.4 Trends in woodland fragmentation and isolation

While the area of broadleaved woodland has increased in England and Wales since the 1960s, changes also occurred in the wider landscape that may have reduced connectivity between woodlands. Following a trend that began in the 1940s (Barr & Gillespie 2000), estimates suggest that 12% of hedgerow length was lost in England and Wales between 1969 and 1985 (Hunting Surveys & Consultants 1986). A further 13% of hedgerows were removed in England and Wales between 1984 and 2003 (Barr & Gillespie 2000). There were also substantial reductions in the density of single and small groups of non-woodland trees in the landscape of England and Wales between 1980 and 1997/8, and a decline in the density of tree lines in Wales but an overall increase in England (Forestry Commission 2001, 2002). In 1997/8, 74% of English and Welsh woods were still less than 10 ha in size.

| Region and sub-region | Deer distribution | | | |
|---|---|---|---|---|
| | Muntjac | Roe | Fallow | Red |
| **East** | | | | |
| Suffolk | ↑ | ↑ | ↑ | ↑ |
| Northamptonshire | ↑ | ↑ | ↑ | ↑ |
| **West** | | | | |
| Forest of Dean | ↑ | ↑ | ↑ | |
| Gloucestershire | ↑ | ↑ | ↑ | |
| Welsh Marches | ↑ | ↑ | ↑ | |
| Powys | ↑ | ↑ | ↑ | |
| Gwynedd | | ↑ | ↑ | |
| Devon/Somerset | ↑ | ↑ | ↑ | ↑ |
| **South** | | | | |
| Buckinghamshire | ↑ | ↑ | ↑ | ↑ |
| New Forest | ↑ | ↔ | ↔ | ↑ |

Table 2. Qualitative estimates of changes in deer distribution by species between 1972 and 2007, based on distribution maps from Dolman et al. (2010). Icons depict the direction of significant change: ↑ = expansion of species, ↔ = no significant expansion of species apparent, blank cells = species absent.

### 1.3.5 Potential implications of habitat change for the Marsh Tit

A requirement for large territories suggests that woodland area and habitat fragmentation may be critical for Marsh Tits, as indicated by Hinsley et al. (1995, 1996). However, the fragmented distribution of woodland habitat in England and Wales may have been exacerbated during the 1960s-1990s by the substantial loss of connective hedgerows and farmland trees, leading to a possible increase in the ecological isolation of woodlands and their Marsh Tit populations, as intimated by Fuller et al. (2005).

Research to date indicates that the preferred habitat of the Marsh Tit is mature woodland, and that understorey density is an important element, particularly in the 2-4 m height band (Hinsley et al. 2007; Carpenter et al. 2010). Therefore, habitat quality for the Marsh Tit may have actually increased since the 1970s and 1980s due to the expansion and maturation of broadleaved woodland and increasing understorey cover identified by Kirby et al. (2005) and Amar et al. (2010), with no decline of shrub species richness (Amar et al. 2010). As such, the results of Kirby et al. (2005) and Amar et al. (2010) are evidence against the suggestion by Fuller et al. (2005), Siriwardena (2006) and Carpenter (2008) that the Marsh Tit decline is likely to have been driven by a deterioration of woodland habitat quality resulting from a loss of understorey cover or diversity.

Studies of habitat association rely upon the ability of sampling methods to describe the attributes of woodland habitat that are most relevant to a species. The paradox of apparently improving habitat yet a declining Marsh Tit population could indicate that key habitat requirements of the Marsh Tit have not been described in sufficient detail by previous studies. As such, it was unclear to what extent the woodland changes characterised by Kirby et al. (2005) and Amar et al. (2010) may have been beneficial or otherwise. Consequently, further study of the Marsh Tit's detailed habitat preferences and spatial requirements were required to fully understand the relative importance of canopy structure, tree species composition, and their relationship with understorey structure in Marsh Tit territories. The benefits and limitations of data collection methods are outlined in the following section.

## 1.4 Characterising woodland habitat

### 1.4.1 Field surveys

Assessment of woodland vegetation structure and composition in Britain has typically involved ground-based measurements and visual estimates in sample plots of ≤ 0.2 ha (Kirby et al. 2005; Amar et al. 2010). While ground-based sampling methods are the only practical option for the detailed quantification of ground flora and seedlings (Cooke 2006), they have significant limitations for the measurement of the complex three-dimensional structure of the woody understorey and tree canopy (Bradbury et al. 2005). For example, estimates of understorey coverage or tree canopy height from the ground can be hampered by dense sub-canopy vegetation and limited field of view, potentially resulting in data of a coarse spatial resolution and precision. As Marsh Tit territories typically contain several hectares of wooded habitat (section 1.2.1), ground-based sampling methods may fail to describe vegetation height, coverage and stratification in adequate detail over a sufficiently large area.

### 1.4.2 Remote sensing methods

Remote sensing methods have revolutionised the measurement of woodland habitat structure and composition in ecological studies (Lefsky et al. 2002; Vierling et al. 2008). Light detection and ranging (lidar) has the ability to describe the three-dimensional structure of woodland at high resolution (values in centimetres) and a large spatial scale (hundreds or thousands of hectares) (Bradbury et al. 2005). Lidar is an ‘active’ remote sensing technique whereby an airborne sensor emits high-density short-duration laser pulses over the ground and then records the time taken for a returning portion of the laser energy to be reflected from the target surface below. Full waveform systems record more returning data than discrete-return systems, and are able to provide more information on canopy density and sub-canopy structure (Lefsky et al. 2002). Both lidar systems can be used to quantify the height of the woodland tree canopy and also the understorey and tree snags (Hill & Broughton 2009; Martinuzzi et al. 2009). As such, lidar has the capability to quantify the height, cover, and structural complexity of woody vegetation across entire woodlands (and Marsh Tit territories) at a scale and detail far beyond the scope of field surveys.

The major limitation of lidar is the inability to distinguish between individual species of tree or shrub. However, optical imagery from remote sensing is capable of classifying vegetation based on the passive detection of electromagnetic wavebands emitted from foliage, using a multi-spectral or hyper-spectral sensor. Data from satellite-based instruments, such as the Landsat series (NASA 2012), typically have a coarse spatial resolution of tens of metres and are sufficient only for broad categorisations of tree species type (e.g. coniferous or deciduous) (Goetz et al. 2010). In contrast, airborne hyper-spectral instruments can provide data at a resolution of as little as 1-2 m and are capable of distinguishing between individual tree species in a woodland canopy (Hill et al. 2010). As yet, however, mapping the species composition of understorey trees and shrubs has been accomplished only with field surveys, and this method remains the most viable for determining the species present in this layer of woodland vegetation.

## 1.5 Origin and aims of the thesis

### 1.5.1 Origins of the research

In the 1990s, Shelley Hinsley and Paul Bellamy of the Institute of Terrestrial Ecology, later the Centre for Ecology & Hydrology (CEH), began a colour-ringing study of Marsh Tits at Monks Wood NNR in Cambridgeshire, attempting to determine the population size. In 2003, I developed the project into a long-term spatial analysis and population ecology study (hereafter ‘the Monks Wood study’), structured within a Geographical Information System (GIS). This included some of Carpenter’s (2008) study population and incorporated remote sensing data processed and provided by Ross Hill and the Earth Observation Section at CEH Monks Wood. The general objectives of the Monks Wood study were to provide additional information on the Marsh Tit’s habitat preferences and ecology, particularly spatial ecology, and use this information to help identify causes of the species’ decline. Where some overlap occurred with elements of the Carpenter (2008) study, such as breeding success and territory quality, there were substantial differences in emphasis, scale, and methodology. As such, Carpenter (2008) and the Monks Wood study can be considered as complementary.

### 1.5.2 Outline and specific objectives of the thesis

Within the wider framework of the Monks Wood study, the aim of this thesis was to address individual and inter-linked topics of Marsh Tit ecology in a series of peer-reviewed research papers. Specific objectives included the investigation of key hypotheses relating to the Marsh Tit’s decline, some of which were highlighted but untested by Carpenter (2008). These are structured within the chapters as follows:

- Chapter 2: Study area and data collection methods
  A general overview of the study area and methodologies used throughout. These are further described in detail in the papers within each chapter.

- Chapter 3: Characteristics and determinants of Marsh Tit territories and habitat selection
  The limitations of ground-based vegetation sampling for describing Marsh Tit habitat (section 1.4) highlighted the requirement for further research to address the hypothesis of deteriorating habitat quality. This chapter contains

novel analyses of Marsh Tit habitat selection using high-resolution data of woodland vegetation structure derived from airborne remote sensing, combined with Marsh Tit territory data based upon presence/absence (Broughton et al. 2006: Paper I) and a time-series of occupation (Broughton et al. in press: Paper II). The results are discussed with reference to national changes in woodland habitat (section 1.3).

- Chapter 4: Factors determining nest-site selection
  A further objective of the habitat analyses was to investigate nest-site selection at the territory scale, to inform the assessment of habitat selection by Marsh Tits and also address the wider behavioural question of the relative roles of habitat and social cues in nest placement by birds (Mennill et al. 2004). Paper III (Broughton et al. 2012) uses habitat data derived from remote sensing, and territory boundary and nest-site data derived from field surveys, to address these questions in unprecedented detail.

- Chapter 5: Nest-sites and breeding success
  Paper IV (Broughton et al. 2011) tests the hypothesis that reduced breeding success of Marsh Tits has contributed to the species’ decline (Siriwardena 2006; Carpenter 2008). Broughton et al. (2011) investigates the fine-scale location of nest cavities and provides the first test of the additional hypothesis that the availability of nest-sites may be limiting in British woods (Fuller et al. 2005; Siriwardena 2006). Broughton et al. (2011) also quantifies the frequency and causes of breeding failure at the local scale. The results are compared to national trends from less detailed datasets (Siriwardena 2006) to assess the likely overall contribution of nest-site competition and predation to the decline of the Marsh Tit.

- Chapter 6: Patterns of dispersal and ranging behaviour
  A major aim of the research was to assess the role of habitat fragmentation in the Marsh Tit’s decline, a subject that was highlighted by Carpenter (2008) but not investigated. Paper V (Broughton et al. 2010) describes the dispersal behaviour of Marsh Tits in the fragmented landscape of the study area, quantifying dispersal distances and identifying potential barriers to success. This represents the first systematic study of natal and breeding dispersal in

British Marsh Tits, the subsequent ranging behaviour of birds after settling, and the causes of further dispersal by such birds.

- Chapter 7: Patterns of distribution change and habitat fragmentation
  Paper VI (Broughton et al. in review) further addresses the hypothesis of habitat fragmentation as a factor in the Marsh Tit decline. Although Paper VI has not yet been accepted for publication in a scientific journal, it is included here as an important broadening of the research perspective to the national scale and additional woodland bird species that are in decline. Broughton et al. (in review) provides the first spatial analysis of distributional change in the Marsh Tit in relation to habitat coverage. The study uses information from previous chapters to consider the effects of dispersal capabilities and territory requirements on the species' landscape ecology, and how landscape change may have contributed to the Marsh Tit's decline. The results for the Marsh Tit are then compared with those from similar analyses of the Willow Tit and Lesser Spotted Woodpecker, for which patterns of distributional change were previously unstudied and information on territory size and dispersal distances are mostly lacking in Britain.

- Chapter 8: Discussion
  An overall discussion that considers the individual effects and potential interactions between the aspects of Marsh Tit ecology, habitat and landscape characteristics featured in this thesis. The relative contributions of such effects or interactions to the decline of the Marsh Tit are discussed in the context of other work, and future research requirements are highlighted.

- Chapter 9: Conclusions
  The most likely factors contributing to the decline of the Marsh Tit are identified, and management recommendations are presented that may aid the species' conservation and recovery.

# 2 STUDY AREA AND DATA COLLECTION METHODS

## 2.1 Study Area

The Monks Wood study was conducted in 505 ha of woodland comprised of 16 patches set within 50 km$^2$ of arable landscape in Cambridgeshire, UK, centred on Monks Wood NNR (hereafter 'Monks Wood') at 52° 24'N, 0° 14'W (Figure 1). Monks Wood contains the largest number of Marsh Tit pairs within the metapopulation (Table 3) and is an ancient semi-natural woodland (ASNW) (Goldberg et al. 2007). The tree canopy is dominated by Common Ash (43% by area), English Oak (*Quercus robur*, 16%), and Field Maple (*Acer campestre*, 12%), with smaller amounts (< 6% each) of Silver Birch (*Betula pendula*), European Aspen (*Populus tremula*), and elm (*Ulmus* spp.). The understorey is dominated by hawthorn (*Crataegus* spp.), Blackthorn (*Prunus spinosa*), and Common Hazel (*Corylus avellana*) (Gardiner & Sparks 2005). Monks Wood was historically managed as coppice but was largely clear-felled around 1918, and the majority of the wood has since regenerated and matured naturally. Coppicing was reintroduced to 9% of the wood in 1961, predominantly in one 7.5 ha block (Steele & Welch 1973). The remainder of the wood has received little or no active management besides the maintenance of rides and glades. Consequently, the overstorey consists of mature or semi-mature trees up to 25 m tall, with a 7 ha block of younger woodland that has self-seeded on adjoining arable land since the 1960s (Gardiner & Sparks 2005).

Twelve other woods in the study area are also classified as ASNW (Table 3, Figure 1), having a similar tree composition and historical management regime to Monks Wood, including small areas of relatively recent coppice, felling or planting (comprising < 10% of their respective areas). The remaining three woods are planted ancient woodland sites (PAWS), where most of the ASNW vegetation was felled in the 1940s-1960s and re-planted with Norway Spruce (*Picea abies*), pine (*Pinus* spp.), European Beech (*Fagus sylvatica*), and some Lawson Cypress (*Chamaecyparis lawsoniana*). Active management effectively ceased in the PAWS woods in the 1980s, with dead or wind-thrown trees remaining *in situ*, and native hardwood species regenerating among the exotics. Muntjac and small numbers of Roe Deer (*Capreolus capreolus*) are present in all woods (see Cooke 2006), although annual or year-round culling of deer occurs in eight of the ASNWs and one of the PAWS. The arable matrix surrounding the woods is dominated by wintersown cereal and oil-seed rape crops, with managed hedgerows, shrubs and trees bordering many fields and highways.

Figure 1. The study area in northwest Cambridgeshire, UK, centred upon Monks Wood National Nature Reserve (labelled 1). The four ‘inner woods’ representing the core study area are coloured black, the seven ‘outer woods’ are coloured dark grey, and the five ‘peripheral woods’ are outlined black (see text). Numbers can be cross-referenced with Table 3 for the name and type of woodland. Polygons shaded light grey represent areas of trees and shrubs that were not occupied by Marsh Tits. The dotted line depicts the A1(M) motorway and the dot-dashed line the East Coast Mainline railway.

## 2.2 Marsh Tit data collection

### 2.2.1 Core and peripheral study areas

Data collection was most intensive in Monks Wood, including the marking (colour-ringing) of virtually all full-grown Marsh Tits and a varying number of nestlings each year between 2003 and 2012, and the detailed mapping of breeding territories between 2003 and 2011. Colour-ringing of adults and nestlings, territory mapping and nest-finding also was undertaken in Odd Quarter Wood, Upton Wood and Bevill’s Wood between 2005 and 2010. Together with Monks Wood, these made up the four ‘inner woods’ (Table 3, Figure 1). A further seven woods, further from Monks Wood, were termed the ‘outer woods’ and the remaining five woods comprised the ‘peripheral woods’, where data collection was less comprehensive than in the inner woods.

| Wood | Number on Fig. 1 | Wooded area (ha) | Type | Maximum territories |
|---|---|---|---|---|
| Monks | 1 | 147 | ASNW | 22 |
| Odd Quarter | 2 | 13 | ASNW | 4 |
| Upton | 3 | 28 | PAWS | 7 |
| Bevill’s | 4 | 31 | PAWS | 3 |
| Hill | 5 | 16 | ASNW | 3 |
| Holland | 6 | 27 | ASNW | 9 |
| Wennington | 7 | 70 | ASNW | 13 |
| Aversley | 8 | 58 | ASNW | 10 |
| Archers | 9 | 18 | ASNW | 3 |
| Coppingford | 10 | 31 | PAWS | 4 |
| Hermitage | 11 | 12 | ASNW | 3 |
| Riddy | 12 | 8 | ASNW | 2 |
| Gamsey | 13 | 4 | ASNW | 1 |
| Little Less & Boulton’s Hunch | 14 | 29 | ASNW | 3 |
| Lady’s | 15 | 7 | ASNW | 1 |
| Raveley | 16 | 6 | ASNW | 2 |
| Total | - | 505 | - | 90 |

Table 3. Woods in the study area and their spatial area, classification type, and maximum number of Marsh Tit territories during the study period 2003-2011. See Figure 1 for relative location of each wood using numbered labels.

### 2.2.2 Methods of capture and marking

Marsh Tits were captured using two methods. During the breeding season (May), chicks were extracted from nests in natural tree cavities using a small noose at 8-14 days of age, when they could be marked with an individual combination of colour-rings and a standard BTO alloy ring before being returned to the nest. In total, 626 nestlings from 74 natural nest-sites and 13 nestboxes were colour-ringed between 2004 and 2011, mostly in the inner woods.

During the same period, portable cage traps (40 x 15 x 15 cm) were used to make 874 captures of 411 full-grown birds in the non-breeding season (predominantly August-October). Traps were baited with sunflower seeds and the trap-door locked open until birds began entering freely. During a trapping session the operator could manually release the trap-door on a target bird by pulling a nylon line attached to the trap. Captured birds were marked as per nestlings. Biometric data collected included wing length, tail length, weight, fat and muscle score, moult score, and age class.

Reliably identifying, ageing and sexing Marsh Tits has long posed problems for British ornithologists due to the similarity of the Willow Tit and also the similarity of age and sex classes (Perrins 1964; Gosler & King 1989). Broughton et al. (2009) provided a comprehensive review of identification criteria (Appendix 1A), incorporating new information on the near-diagnostic bill pattern reported in Broughton et al. (2008a), and was largely based upon the sample of Marsh Tits from the Monks Wood study population. Building upon earlier work on ageing and sexing by Gosler & King (1989) and King & Muddemann (1995), Broughton et al. (2008b) established criteria for assigning captured Marsh Tits to age and sex classes with a high degree of reliability, based upon wing length and moult (Appendix 1B). These methods were applied to all birds captured during the study.

### 2.2.3 Recording of movements and nest-sites

Territorial birds were located in spring with the aid of playback of recorded song and calls, using the mp3 facility of a mobile phone, during thorough searches of each site between February and April. The location and behaviour of birds sighted were recorded on large-scale maps of each wood, and then digitised within a Geographical Information System (ArcView 3.2 and ArcInfo 9.1, ESRI, Redlands, CA, USA) at a spatial resolution and estimated accuracy of 30 m prior to 2004 and 15 m thereafter. Playback was also used to locate dispersed juveniles in late June to August.

Territory mapping was achieved by following birds for periods of up to four hours on at least four visits during March-May, and generating maps of the maximum defended area based on the locations of observations and territorial behaviour towards other Marsh Tits and playback (Bibby et al. 2000). It was inappropriate to use automated methods of territory delineation, such as kernel estimation, because of the inherent bias imposed by the difficulties of observing birds in dense vegetation, poor light, or periods of inactivity. The use of kernel estimation or minimum convex polygons (MCP) relies upon the systematic collection of objective data using methods such as telemetry (Kenward 2001), and also lacks intuitive consideration of behavioural observations or sharp habitat boundaries. As a result, Marsh Tit territory boundaries were delineated using a method based on standard territory mapping techniques (Bibby et al. 2000), which was effectively a ‘subjective MCP’, where behaviours such as boundary skirmishes or song-duels were used to define the boundary location within the confines of the wooded habitat. This method has been used to define the territory boundaries of the related Black-capped Chickadee (*P. atricapillus*) (Mennill et al. 2004).

Marsh Tit nests were located by intensive searching of each territory during April and May and following birds back to the nest-site. The coordinates of each nest-site were collected at an estimated accuracy of 5-12 m using a hand-held geographical positioning system (GPS) unit. An endoscope was used to inspect the contents of all nests less than 7 m from the ground. Other data collected for nest-sites included the origin of the nest-hole (e.g. rot hole, broken stem, split), tree/shrub species and diameter at breast height (dbh) of the stem, compass orientation of the nest entrance and its height from the ground, which adults were attending at the beginning and end of the observed nesting period, and whether nests were successful or not in fledging at least one chick. Nests were judged to be successful if the adults were subsequently seen feeding fledged young, and/or if nest inspection revealed no sign of predation or other failure (e.g. chick remains) from the 15th day after hatching. In total, 180 nests were located in 2003-2011, 136 of these in Monks Wood.

### 2.3 Vegetation data from field survey

Ground-based sampling of vegetation in Monks Wood was carried out in 2004 using 35 transects, with 22 positioned through the centre of each Marsh Tit breeding territory in that year and 13 transects in areas of non-territory (Broughton et al. 2006). Transects were 100 m long and 10 m wide, and counts were made of each tree and shrub to species where these were over 1 m tall. Trees were classified according to the diameter at breast height (dbh) of the largest stem as small (< 5 cm), medium (5-30 cm), or large (> 30 cm).

### 2.4 Vegetation data from remote sensing

#### 2.4.1 Woodland canopy height models

Airborne remote sensing data were acquired that characterised the structure of the entire woodland canopy and understorey at high resolution, circumventing some of the potential limitations of scale and precision inherent in ground-based sampling (section 1.4). A digital canopy height model (DCHM) of Monks Wood was derived from lidar data acquired in June 2000 using a discrete-return instrument (Optech ALTM-1210, Optech Inc., Toronto, Canada). The lidar data were captured during a series of parallel flight lines over the study area and the data processed to generate the DCHM at a spatial resolution of 1 m and height precision of 0.01 m (Hinsley et al. 2002; Gaveau & Hill 2003). Airborne lidar data of greater detail were acquired in June 2005 using an Optech ALTM-3033 instrument, which were used to generate DCHMs at a spatial resolution of 0.5 m for the following woods: Monks, Bevill’s, Holland, Wennington, Riddy, Gamsey, Raveley, and Lady’s. Full details of this data acquisition and processing are given in Hill & Broughton (2009). Within the lidar DCHMs for Monks Wood, field observations and frequency distributions of lidar vegetation heights suggested that values of < 1 m in the model could be classified as field layer vegetation, values of 1-8 m as the understorey layer of sub-dominant trees and shrubs, and values of > 8 m as the overstorey layer of mature tree crowns (Hill & Broughton 2009). These models allowed the calculation of the frequency of canopy height values, mean canopy height and overstorey canopy closure for each wood in its entirety, and also every Marsh Tit territory and area of non-territory therein, permitting analyses of territory composition in unprecedented detail.

### 2.4.2 Woodland understorey height model

The DCHMs derived from the lidar data collected in summer 2005 (‘leaf-on’ tree condition) contained information on the understorey only where it was exposed by gaps in the overstorey of the mature tree canopy. However, further lidar data of 0.5 m resolution were acquired in April 2003, when understorey shrubs were in leaf but the overstorey trees were not (‘leaf-off’ tree condition). This provided information on understorey shrubs which were otherwise obscured beneath the overstorey when the trees were in full leaf (Hill & Broughton 2009). By combining this understorey height model with understorey data from the DCHM where all height values were 1-8 m, it was possible to create a model of the complete understorey vegetation. This allowed calculation of the height and coverage values for understorey vegetation in any chosen area of woodland, such as Marsh Tit territories or nest-sites. Full details of lidar data acquisition and processing to create the understorey model are also given in Hill & Broughton (2009).

### 2.4.3 Tree species digital map

In additional to the high resolution data of the structure of the woodland canopy and understorey, a 1 m resolution raster map of the six dominant tree species comprising the Monks Wood overstorey was also available (Hill et al. 2010). The map was produced from a per-pixel supervised classification of time-series Airborne Thematic Mapper (ATM) data acquired in 2003, using the difference in the timing of leaf growth, tinting, and eventual fall during the spring-autumn cycle to discriminate between individual species (Hill et al. 2010). Each 1 m grid cell in the overstorey was assigned to a tree species (excluding a minority that were unclassified), and the resulting digital map had a surveyed overall accuracy of 88%. This dataset allowed the quantification of tree species composition within Marsh Tit territories, non-territory areas, and around nest-sites, which could be used to test for the selection or avoidance of individual tree species by Marsh Tits.

# 3 MARSH TIT TERRITORIES AND HABITAT SELECTION

This chapter is concerned with the spatial extent and vegetation composition of Marsh Tit territories, and comprises two papers. Paper I, Broughton et al. (2006), used territory mapping methods to delineate 32 Marsh Tit territories with a mean area of 4.1 ha, which was almost double that found in the previous British study (section 1.2). Broughton et al. (2006) also used a combination of lidar remote sensing data and vegetation sample plots (sections 2.3 and 2.4.1) to compare tree canopy height and tree/shrub species composition between breeding territories and uninhabited areas of woodland in a single year. The use of remote sensing data to calculate canopy heights across entire territories was a novel development in the characterisation of Marsh Tit habitat, which has typically involved measurements and estimates from ground-based sample plots only (Amar et al. 2006; Hinsley et al. 2007; Carpenter et al. 2010). Broughton et al. (2006) showed that the canopy height was significantly taller in Marsh Tit territories compared with unoccupied areas, and was the first study to indicate selection for a taller tree canopy. A limitation of the lidar data used in Paper I was the inability to describe the density or species composition of shrubs below the tree canopy, leaving ground-based sampling as the only option for characterising this vegetation. This sampling showed no differences in understorey between areas occupied by Marsh Tits and areas that were unoccupied. This finding disagreed with the results of Hinsley et al. (2007) and Carpenter at al. (2010), which may have been a consequence of site-specific characteristics and the coarse resolution of ground-based vegetation survey techniques used in all studies. Due to the large size of Marsh Tit territories, sample plots may be unrepresentative of the overall composition (section 1.4).

To better understand the relationship between Marsh Tit occupation and woodland structure, a second study was devised using more comprehensive datasets. Paper II, Broughton et al. (2012a), used 5 years of Marsh Tit territory data and high resolution models of the complete woodland understorey and overstorey layers, derived from airborne lidar data, and an overstorey tree species map derived from optical remote sensing (section 2.4.3). Broughton et al. (2012a) overlaid annual territories to score areas of the wood by Marsh Tit occupation frequency, which was used as the predictor variable in the analyses to compare the vegetation within. While this approach was somewhat counter-intuitive, in that vegetation obviously determines Marsh Tit settling rather than vice versa, the explicit aim of the analysis was to compare vegetation between discontinuous areas of woodland that differed in the frequency of Marsh Tit occupation over time. Because the boundaries of these areas were set on an *a priori* basis, vegetation variables became the random continuous variables which varied in response to the way in which the wood was partitioned for comparison. The occupation frequency of a given area of woodland was not a random variable because it had no sampling distribution, and was therefore unsuitable as a response variable. An alternative approach, e.g. using individual territories as sampling units for the vegetation in models containing repeated measures and annual effects, would be problematic due to the high degree of non-independence and small annual samples (41% to 55% of individual birds were present in the 22-23 annual territories in consecutive years). Crucially, such an approach would also preclude the fine-scale spatio-temporal overlay that simultaneously and parsimoniously compared vegetation and occupation across the entire study site using all available data.

Adopting this methodology, Broughton et al. (2012a) found significant positive relationships between Marsh Tit occupation and overstorey height, tree canopy closure, and the coverage of understorey vegetation below the overstorey. The results also identified significant correlations between these structural variables. There was no selection by Marsh Tits for any particular tree species, but the study identified a negative influence of woodland edge on Marsh Tit occupation. These results clarified and confirmed that Marsh Tit occupation was related to vegetation structure throughout the full vertical profile of woodland habitat, and clearly defined the preferred habitat as mature woodland. The results were also notable in showing that an extensive understorey shrub layer could exist below a maturing, unmanaged, near-closed tree canopy in this study area.

The results of Broughton et al. (2006) and Broughton et al. (2012a), within the context of trends identified by national surveys (Kirby et al. 2005; Amar et al. 2010; section 1.3), indicate that widespread changes in woodland structure resulting from a lack of management or increased deer browsing are unlikely to be responsible for the decline of the British Marsh Tit. Furthermore, Broughton et al. (2012a) also indicates that reintroduction of active management, such as extensive coppicing, could be detrimental to remaining populations. The papers in this chapter represent the evolution of a new approach to integrating data from bird territory mapping and remote sensing that enabled detailed analyses of bird-habitat relationships. Such methods have the potential for much wider application in the field of habitat analysis for woodland birds, and possibly other habitats and taxa.

3.1 Paper I:

*Ibis* (2006), **148**, 744–752

# 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/km$^2$ 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, Wesołowski 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, Goławski & 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).

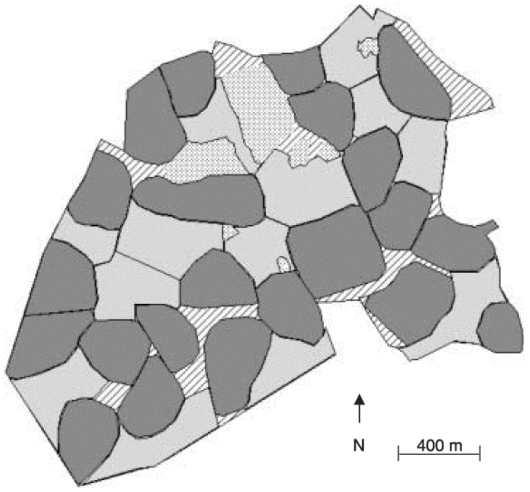

**Figure 1.** Location of 2004 territories (dark grey) and pseudo-territories (light grey) in Monks Wood. Stippled areas are open fields, hatched areas are unsampled woodland.

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 $m^2$ 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-$m^2$ 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

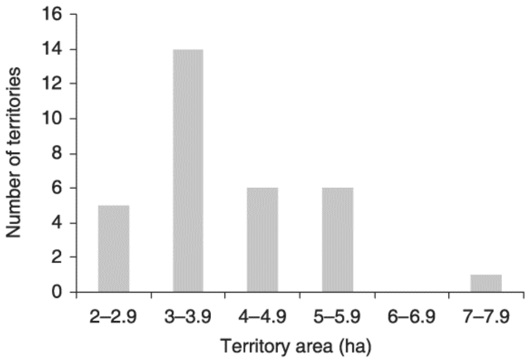

**Figure 2.** Frequency of occupied territory areas 2002–04 ($n = 32$).

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 ± 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 ± 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/km$^2$). 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 ± 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 | *n* |
|---|---|---|---|---|---|
| 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 |

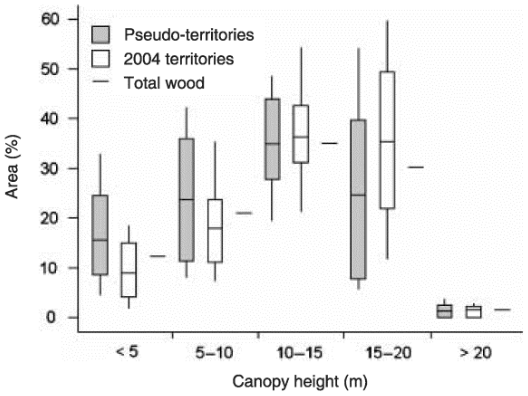

**Figure 3.** Mean area proportions in categories of canopy height for the unoccupied pseudo-territories (*n* = 13), the occupied 2004 territories (*n* = 22) and the whole wood. The data show the interquartile range (box), mean (bar) and data extent (whiskers) for the percentage of area in each height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

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

| | Territories | Pseudo-territories | *t* | *P* |
|---|---|---|---|---|
| Tree species | 3.9 ± 0.9 | 3.7 ± 0.8 | 0.78 | 1.00 |
| Shrub species | 5.5 ± 1.3 | 5.5 ± 1.3 | 0.08 | 1.00 |
| Shrub + Tree species | 9.5 ± 1.9 | 9.2 ± 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 | *n* | Pseudo-territories | sd | *n* | *t* | *P* |
|---|---|---|---|---|---|---|---|---|
| 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/km$^2$ (and again in 2005, our pers. obs.), was low in comparison with the 22–28 pairs/km$^2$ found elsewhere in England (Bagley Wood, Oxfordshire) by Southern and Morley (1950). Glue (1973), however, found just 2.3 pairs/km$^2$ 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 & Wesołowski 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 (Wesołowski 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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3.2 Paper II:

# DESCRIBING HABITAT OCCUPATION BY WOODLAND BIRDS USING TERRITORY MAPPING AND REMOTE SENSING DATA: AN EXAMPLE USING THE MARSH TIT (*POECILE PALUSTRIS*)

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## ABSTRACT

Changes in the structure of woodlands and forests, caused by shifts in management, stand maturity and composition, have been implicated in the population decline of some bird species in Europe and North America. One such species is the Marsh Tit (*Poecile palustris*). We investigated relationships between Marsh Tit occupation (derived from territory mapping) and vegetation structure, tree species composition, and proximity to woodland edge in a British woodland, using a combination of five years of occupation data and high-resolution (0.5 and 1 m), large-scale (155 ha) habitat models derived from remote sensing. The results demonstrated that Marsh Tit occupation was linked to vegetation characteristics throughout the woodland's full vertical profile, showing significant positive relationships with overstorey height, tree canopy closure, and the coverage of understorey vegetation below the overstorey. Marsh Tit occupation was lower within 50 m of the woodland perimeter, where habitat structure was less favourable than in the woodland interior. No preference was shown for areas rich in any particular prevalent tree species. Our results suggest that widespread changes in woodland structure resulting from abandonment by managers are unlikely to be responsible for the decline of the British Marsh Tit, and that reintroduction of active management that prevents woodland maturation could be detrimental to remaining populations. The study demonstrates a novel approach to integrating territory maps and remote sensing data to permit highly detailed analyses of bird-habitat interactions, and has wider possible implications for woodland management and related bird species.

## INTRODUCTION

Habitat selection is a hierarchical process of behavioral responses that results in the disproportionate use of resources relative to their availability, influencing the fitness and survival of individuals (Jones 2001). The study of occupation patterns is a common approach to identify variation in habitat quality for birds (Johnson 2007), and typically involves the measurement or classification of vegetation structure or composition (e.g. Wilson et al. 2005, Arriero et al. 2006). Characterizing forest or woodland vegetation can be problematic, however, due to the strongly heterogeneous and three-dimensional environment (Hinsley et al. 2002, 2006). Data collection methods for describing woodland habitats are often restricted to ground-based techniques of limited spatial extent (e.g. sample plots: Barg et al. 2006, Amar et al. 2010), or broad categorizations of tree species or age composition (Mazur et al. 1998, van Oort and Otter 2005), rather than the use of fine-grained, three-dimensional datasets at the landscape scale. In complex environments such as woodland, extrapolation of localized sampling and use of broad-scale categorization may not adequately describe habitat at a spatial resolution relevant to the individual birds or population concerned, and preclude detailed investigations of structural heterogeneity (Hinsley et al. 2008).

The use of remote sensing methods, such as light detection and ranging (LiDAR), can overcome some of these difficulties by providing landscape-scale data (> 10 ha, Bradbury et al. 2005) at high spatial resolution (Vierling et al. 2008). LiDAR is particularly suitable for the detailed spatial modelling of woodland habitats, with the capacity to quantify the canopy surface and also the understorey beneath (Hill and Broughton 2009, Martinuzzi et al. 2009). Optical imagery, derived from satellite or airborne multispectral scanners, has also been used to characterise broad-scale vegetation types (Laurent et al. 2005), yet there have been few attempts to integrate different sources of remote sensing data for analyses of bird habitat (Goetz et al. 2010).

Populations of many forest and woodland bird species have declined throughout the temperate and boreal regions of Europe and North America, which has been linked to habitat changes resulting from forest management (Holmes and Sherry 2001, Imbeau et al. 2001, Amar et al. 2006). Several species of forest-dwelling parid in the *Poecile* genus are included in this group, namely the Gray-headed Chickadee (*P. cinctus*), Willow Tit (*P. montanus*), and Boreal Chickadee (*P. hudsonicus*), which have shown a negative response to management activities such as logging and thinning (Virkkala 1990, Siffczyk et al. 2003, Hadley and Desrochers 2008). The Marsh Tit (*P. palustris*) has also declined throughout much of its European range, although the reasons for this are poorly understood (Burfield and van Bommel 2004, Fuller et al. 2005).

The Marsh Tit is a 10-12 g cavity-nesting passerine of deciduous woodland, feeding on seeds and invertebrates largely gleaned from trees and shrubs. Pairs are socially monogamous and sedentary within a home-range throughout the year, defending a large (average 4-6 ha) and exclusive breeding territory during spring that is selected by males (Gosler and Clement 2007, Broughton et al. in press). In Britain, where Marsh Tit abundance fell by 71% between 1967 and 2008 (Baillie et al. 2010), widespread abandonment of woodland management has been suggested as a possible factor in the species' decline, by allowing unfavorable changes in habitat structure through woodland maturation (Fuller 2005, Amar et al. 2006). Although the decline of the British Marsh Tit coincided with a reduction in woodland management (Mason 2007), previous work has variously identified increased woodland canopy height, canopy cover, and understorey density as important factors influencing Marsh Tit occupation (Broughton et al. 2006, Hinsley et al. 2007, Carpenter et al. 2010), and some of these elements may have actually increased as a result of maturation (Mason 2007). However, previous studies were inconsistent with regard to which habitat features were identified as being important to Marsh Tits, whether features of understorey (Hinsley et al. 2007), tree canopy (Broughton et al. 2006), or both (Carpenter et al. 2010). This inconsistency may have resulted from limited spatial and/or temporal resolution, present in all studies, which lacked sufficient detail when describing occupation patterns and the structural complexity of habitat. Such uncertainty has implications for habitat management, because if Marsh Tits select for understorey attributes rather than tree canopy, then active management of woodlands that arrests maturation through cropping or thinning of the tree canopy may benefit both understorey vegetation and Marsh Tits (Fuller et al. 2005). Conversely, if Marsh Tits have an overriding preference for a mature tree canopy then such interventions may be counterproductive. Marsh Tits may also be sensitive to the proximity of woodland edge (Hewson and Fuller 2006), yet no study has attempted to investigate the combined roles of woodland canopy and understorey structure, and edge effects in relation to Marsh Tit occupation.

In this study, we use a novel combination of fine-scale, airborne LiDAR-derived models of an entire woodland canopy, overstorey, and understorey layers (Hill and

Broughton 2009), airborne multi-spectral classification of overstorey tree species composition (Hill et al. 2010), and five years of Marsh Tit occupation data, derived from territory mapping. Employing these comprehensive, high resolution datasets, we aim to improve the understanding of Marsh Tit habitat preferences, inform conservation policy, and aid interpretation of the species' decline. The combined application of such detailed, long–term, landscape-scale occupation and vegetation datasets is unprecedented in woodland bird research, and acts as a case-study for the analysis of species and habitat spatial data.

## METHODS

### Study area

The study site was 155 ha of woodland at the Monks Wood National Nature Reserve in Cambridgeshire, UK (52° 24'N, 0° 14'W, hereafter 'Monks Wood'). Monks Wood is a discrete patch of lowland semi-natural woodland, dominated by Common Ash (*Fraxinus excelsior*), English Oak (*Quercus robur*), and Field Maple (*Acer campestre*) in the overstorey tree layer, with smaller amounts of Silver Birch (*Betula pendula*), European Aspen (*Populus tremula*), and elm (*Ulmus* spp.). The understorey layer is largely composed of hawthorn (*Crataegus* spp.), Blackthorn (*Prunus spinosa*), and Common Hazel (*Corylus avellana*) (Gardiner and Sparks 2005). Monks Wood was historically managed as coppice, a traditional form of rotational cropping in which trees and shrubs are cut at the base and allowed to regenerate as multi-stemmed plants, leaving isolated mature trees (standards). This activity arrests woodland development at a dense, immature phase of shrubs and young tree stems, preventing development of a mature overstorey (Fuller and Green 1998). Much of Monks Wood was clear-felled around 1918 and has been undergoing natural regeneration and maturation since that time (Steele and Welch 1973), but coppicing was reintroduced to 9% of the wood in 1961 on a 15-20 year rotation, predominantly in one 7.5 ha block (Fig 1a). The remainder of the woodland has received little or no management and consists of an overstorey of mature or semi-mature trees (up to 25 m tall), with abundant standing deadwood, frequent tree falls, and open or scrubby glades, with an extensive understorey throughout (Broughton et al. 2006, Broughton et al. 2011). Approximately 7 ha consists of younger woodland that has regenerated on adjoining arable land since the 1960s.

### Marsh Tit occupation

The majority of Marsh Tits in Monks Wood were individually marked with coloured leg bands each year: 83% banded in 2004, and 95-98% in 2005-2008. All 22-23 annual spring territories were delineated each year. Banded birds were followed at least weekly for periods of up to four hours during March-May, and territory maps of the maximum defended area were generated based on observations of movements and territorial behaviour (for detailed description see Broughton et al. 2006, 2010). Occupation was defined as defence of, or presence within, a territory for least two weeks or until the bird was presumed killed. Territories were occupied by pairs or unpaired males (Broughton et al. 2011), the latter (0-5 per year) varying in annual location and not considered to represent a differing selection process from paired males. Approximately 2-3% of birds relocated territory areas between years (Broughton et al. 2010), and 45-59% of all birds were replaced annually due to mortality. Territory extent of surviving birds differed from the previous year by a mean of 26% (SD = 20%, *n* = 44), and 10-41% of the study area remained vacant each year (Broughton et al. 2006, and our unpublished data). This demonstrated a high turnover of birds, the ability of individuals to relocate territories, vacant woodland available should they choose to select a new area, and variation in territory extent of those birds that did not relocate between years.

Territory polygons were digitised in a Geographical Information System (GIS; ArcGIS version 9.3.1, ESRI 2009) and converted to grid-based raster representations (0.5 × 0.5 m resolution grid cells). In order to use all territory information while minimising potential effects of philopatry, due to territory placement by the same individuals in consecutive years which introduces non-independence, territories were not used as sampling units. Instead, each territory grid cell was given a value of 1 and non-territory grid cells a value of 0. Annual territory maps for 2004-8 were overlaid cumulatively, so that a grid cell which was part of a territory in all five years accrued a value of 5 and a grid cell that was never occupied had a value of 0. The cumulative territory map therefore depicted differential categories of Marsh Tit occupation across the study site over the five-year period (Fig. 1a). These occupation categories were given a score $Z$ on a scale of $Z = 0$ (never occupied) to $Z = 5$ (maximum occupation). Grid cells with the same occupation score within the cumulative territory map were used to group vegetation in corresponding areas into each of the six categories of Marsh Tit occupation. The structure and composition of vegetation could then be compared between areas with a different Marsh Tit occupation score.

### Models of woodland structure

Airborne LiDAR data were acquired in summer (June) 2005, when trees and shrubs were in full leaf, and used to generate a 0.5 m resolution raster canopy-height model of Monks Wood (Hill and Broughton 2009). This model described the detailed structure of the full woodland canopy surface, providing height values (to 1 cm) for the tallest vegetation present in each 0.5 m grid cell. Based on field observations and frequency distributions of LiDAR vegetation heights for Monks Wood (Hill and Broughton 2009, Hill et al. 2010), values of < 1 m in the model were classified as field layer vegetation, values of 1-8 m as the understorey layer of sub-dominant trees and shrubs, and values of > 8 m as the overstorey layer of mature tree crowns (Fig. 1b). We calculated mean overstorey height and tree canopy closure (defined as the percentage cover of overstorey) for each area categorized by Marsh Tit occupation score ($Z$ = 0-5), using a GIS.

The summer LiDAR data contained information on the understorey only where it was exposed by gaps in the overstorey. To address this, additional LiDAR data of 0.5 m resolution were acquired in spring (April) 2003 (Hill and Broughton 2009), when understorey shrubs were in leaf but the overstorey trees were not. This provided information on understorey shrubs which was not present in the LiDAR data acquired during summer, due to their being ‘shaded’ beneath overstorey trees in full leaf. This spring model of ‘shaded’ understorey shrubs was combined with the summer model of ‘exposed’ understorey vegetation to create a ‘total’ understorey height model (Fig. 1c), representing all vegetation in the height range of 1-8 m. As with overstorey, the mean height of vegetation in the three understorey models (i.e. shaded, exposed, total), and the percentage of area covered by each, were determined for each area categorized by Marsh Tit occupation score ($Z$ = 0-5). Full details of LiDAR data acquisition and processing are given in Hill and Broughton (2009). Previous analyses have indicated that no significant dynamic change in the vegetation structure of Monks Wood was apparent during the study period (Broughton et al. in press), permitting the use of LiDAR and territory data acquired in different years.

We calculated the frequency of height values for all vegetation within each Marsh Tit occupation category by summing the cell counts of the overstorey and total understorey height models in one-metre height thresholds, or ‘bins’, between 1 m and the maximum woodland canopy height value (25.4 m). A grid cell at a single geographical location would, therefore, contribute to two separate height bins if it contained both overstorey and understorey vegetation. This additive approach demonstrated the height distribution of tree and shrub vegetation throughout each Marsh Tit occupation category.

## Overstorey tree species model

A 1 m resolution raster map of the six tree species comprising the overstorey was produced from a supervised classification of time-series Airborne Thematic Mapper (ATM) data acquired in 2003 (Hill et al. 2010). The tree species model (Fig. 1d) had a surveyed overall accuracy of 88%, and the cover of each tree species in each category of Marsh Tit occupation was calculated as the proportion of overstorey area.

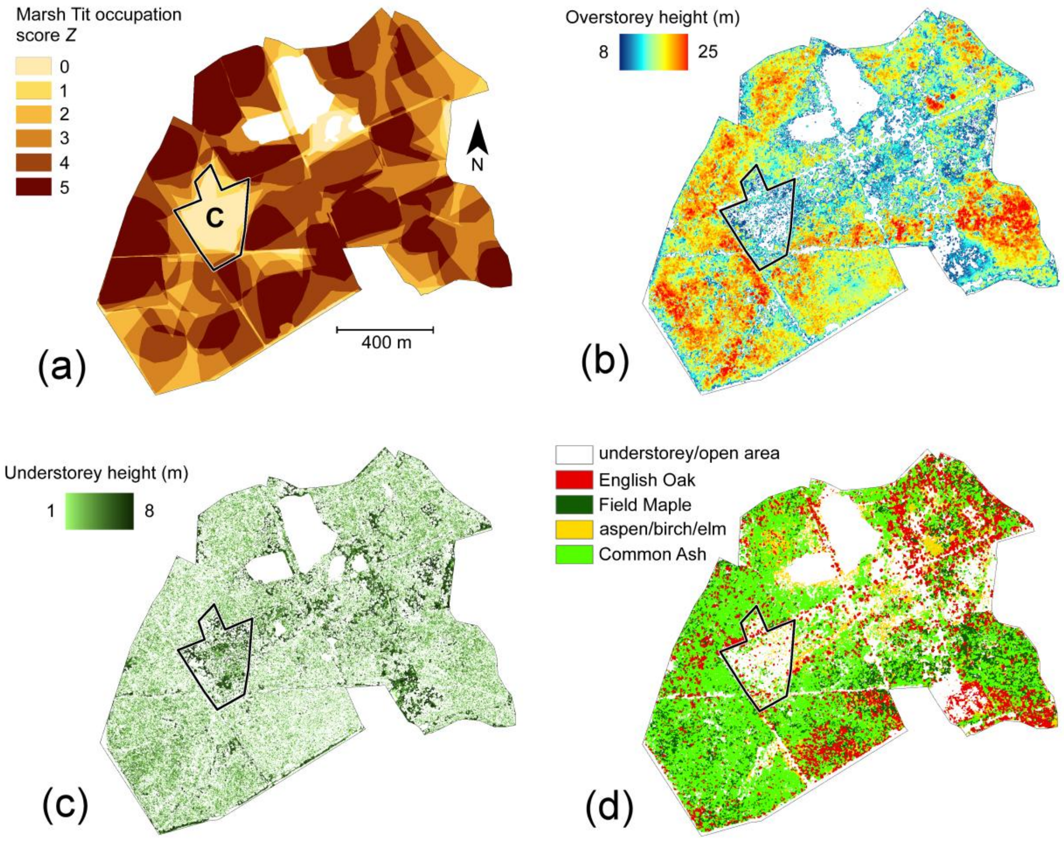

Figure 1. Marsh Tit occupation and vegetation models for Monks Wood: (a) Cumulative territory map of Marsh Tit occupation, where score *Z* corresponds to the number of breeding seasons (out of 5) that Marsh Tits occupied a given area. Four open fields enclosed within the wood appear in white, and the outlined polygon marked ‘C’ denotes a 7.5 ha coppice block. (b) LiDAR model showing vegetation heights of the woodland overstorey, at 0.5 m cell resolution. (c) LiDAR model showing vegetation heights of the total understorey, at 0.5 m cell resolution. (d) Map of tree species distribution in the overstorey, derived from optical imagery, at 1 m resolution. The coppice block denoted in (a) is also outlined in black in (b) to (d).

### Woodland edge effects

We looked for an edge-effect on patterns of Marsh Tit occupation by delineating buffers of 50 m and 100 m inside the perimeter of Monks Wood and around the internal field areas depicted in Fig. 1a, giving two measures of sensitivity for ‘edge’ and ‘interior’ habitat (Hewson and Fuller 2006). Edge avoidance was assessed by calculating and comparing the percentage of each buffer and corresponding interior that was occupied by Marsh Tits in most or all years ($Z$ = 3-5). The 50 m and 100 m delineations of woodland edge and interior were also used to subdivide the overstorey and understorey models, for comparison of structural variables.

### Statistical analyses

Because areas of Monks Wood with the same frequency of Marsh Tit occupation were delineated according to the pre-defined scoring method (Fig. 1a), the occupation score within each scored area was, by definition, fixed. As such, occupation score was used as a predictor of known, fixed value, and vegetation characteristics as random, continuous variables varying between such areas. The aim of this approach was to compare vegetation between areas defined by differing levels of Marsh Tit occupation.

Linear regression was used to estimate overstorey and understorey characteristics as a function of Marsh Tit occupation score ($Z$), and inter-relationships between occupation score and woodland structural variables were also investigated using Spearman’s rank order correlation. We tested the suggestion that Marsh Tits settled preferentially in areas rich in oak trees (Amann 2003), or any other tree species, by determining whether the proportion of any tree in the overstorey of successive Marsh Tit occupation categories increased along with occupation at a greater rate than that of other species. The proportions of each tree species within the overstorey of each occupation category were not independent, however, due to the mutually exclusive and exhaustive relationship between them. We therefore divided the proportion $P_{SZ}$ of each tree species $S$ by that of unclassified vegetation $U_Z$ in the corresponding occupation category of score $Z$, denoting these standardised proportions by the ratios $Q_{SZ} = P_{SZ} / U_Z$. This reduces the dimensionality of the data by one, in the manner of a compositional analysis (Aitchison 1986). Taking the natural logarithm of each ratio leaves the expected values unbounded above or below, and allows the fitting of standard linear models by least squares. We initially fitted a model in which both intercepts $\alpha_S$ and slopes $\beta_S$ representing the relationship with occupation score $Z$ varied between the six tree species:

Equation 1. $E(\log(Q_{SZ})) = \alpha_S + \beta_S Z, \quad S = 1,2, \dots 6; \quad Z = 0,1, \dots 5.$

The intercepts $\alpha_S$ accommodate differences in the overall abundance of each species within the overstorey. Additional models were then fitted with various constraints imposed upon the slopes $\beta_S$ and standard regression theory was used to compare and select between them. Obtaining estimates $\hat{\alpha}_S, \hat{\beta}_S$ of the coefficients in the selected model allows transformation to estimates $\hat{P}_{SZ}$ and $\hat{U}_Z$ of the original proportions, which sums to unity for each category as the lack of independence requires. All statistical tests were carried out in R version 2.9.1 (The R Foundation for Statistical Computing, 2009).

## RESULTS

### Woodland structural composition

Mean height of the overstorey increased significantly with Marsh Tit occupation score $Z$ (overstorey mean height = $11.9 + 0.9Z$, $r^2 = 0.86$, $P = 0.008$, $n = 6$), as did tree canopy closure (% tree canopy closure = $50.8 + 9.1Z$, $r^2 = 0.87$, $P = 0.007$, $n = 6$), which was almost complete where Marsh Tit occupation was greatest (Table 1). The mean height and percentage cover of total understorey declined significantly as Marsh Tit occupation increased (total understorey mean height = $4.7 - 0.3Z$, $r^2 = 0.90$, $P = 0.004$, $n = 6$; % total understorey coverage = $45.3 – 0.8Z$, $r^2 = 0.91$, $P = 0.003$, $n = 6$), but the overall change in cover was relatively minor (Fig. 2). Breaking down total understorey into its constituent parts, the mean height of shaded understorey also changed little with Marsh Tit occupation (shaded understorey mean height = $2.5 + 0.04Z$, $r^2 = 0.39$, $P = 0.19$, $n = 6$), and exposed understorey showed a small increase (exposed understorey mean height = $5.2 + 0.1Z$, $r^2 = 0.83$, $P = 0.01$, $n = 6$). However, in terms of coverage, the proportions of each component changed substantially as Marsh Tit occupation increased (% exposed understorey coverage = $36.0 – 6.2Z$, $r^2 = 0.88$, $P = 0.006$, $n = 6$; % shaded understorey coverage = $9.3 + 5.4Z$, $r^2 = 0.85$, $P = 0.009$, $n = 6$), so that the majority of total understorey was exposed where occupation was low ($Z = 0\text{-}1$) and shaded where occupation was higher ($Z = 2\text{-}5$) (Fig. 2).

| Occupation score *Z* | Area (ha) | Overstorey mean height (SD) (m) | Tree canopy closure (%) | Shaded understorey mean height (SD) (m) | Exposed understorey mean height (SD) (m) | Total understorey[a] mean height (SD) (m) |
|---|---|---|---|---|---|---|
| 0 | 8.2 | 11.6 (2.6) | 51.2 | 2.4 (1.0) | 5.2 (2.0) | 4.8 (2.1) |
| 1 | 5.1 | 12.1 (2.9) | 50.1 | 2.5 (1.0) | 5.3 (2.0) | 4.6 (2.1) |
| 2 | 13.1 | 14.6 (3.6) | 77.3 | 2.7 (1.2) | 5.3 (1.9) | 3.7 (2.0) |
| 3 | 34.3 | 15.1 (3.6) | 83.3 | 2.7 (1.2) | 5.6 (1.9) | 3.6 (2.0) |
| 4 | 44.9 | 15.2 (3.4) | 87.3 | 2.6 (1.1) | 5.6 (1.8) | 3.5 (1.9) |
| 5 | 49.8 | 15.7 (3.1) | 91.1 | 2.6 (1.1) | 5.5 (1.8) | 3.2 (1.7) |

[a] Total understorey is a combination of shaded and exposes understorey (see text).

Table 1. Mean heights and standard deviations of overstorey and understorey vegetation, and the percentage of tree canopy closure in areas categorized by Marsh Tit occupation score *Z*. Models were of 0.5 m spatial resolution.

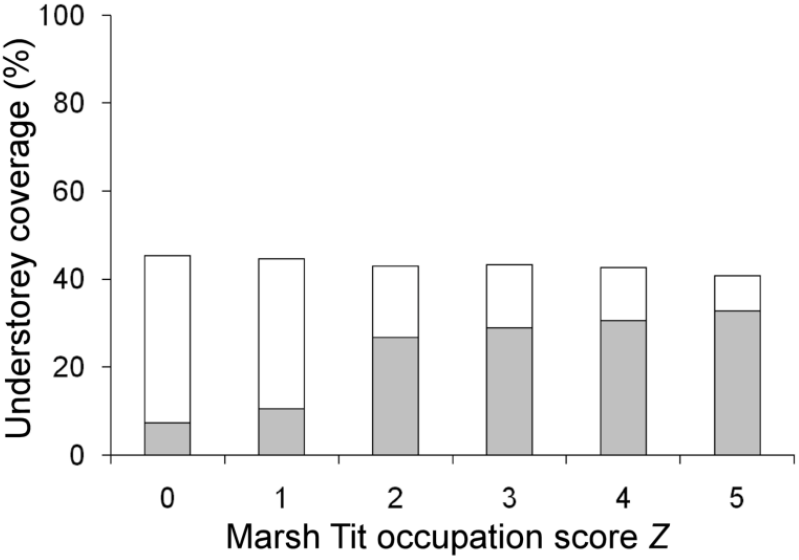

Figure 2. Relationship between Marsh Tit occupation score *Z* and understorey vegetation cover (as a percentage of the area of occupation score *Z*). Total understorey is represented by the stacked column of its constituent parts (shaded and exposed understorey).

Significant correlation between overstorey and understorey variables indicated that they were inter-related in describing woodland structural maturity (Table 2), leading to difficulty in identifying which individual variable (if any) was most critical in territory selection. Tree canopy closure and overstorey mean height were very strongly and positively correlated with each other and Marsh Tit occupation score, as was the coverage of shaded understorey, but all were negatively correlated with the mean height and coverage of total understorey (Table 2).

The vertical distribution of height values in the overstorey and total understorey models revealed a contrasting pattern between areas of low ($Z$ = 0-1) and higher ($Z$ = 2-5) Marsh Tit occupation (Fig. 3). Areas of higher Marsh Tit occupation were dominated by understorey vegetation in height bins of 1-3 m and overstorey vegetation in height bins of 14-18 m, this effect being amplified as Marsh Tit occupation increased. Areas of low occupation were largely dominated by vegetation below 13 m, particularly at height bins of 7-8 m at the interface of the understorey and overstorey layers.

Over the entire study area, 8.2 ha of woodland remained unoccupied throughout the study period (occupation category $Z$ = 0, Table 1). Compared to the other occupation categories, vegetation in these unoccupied areas had the shortest overstorey height, almost the lowest percentages of tree canopy closure, the tallest total understorey, but least cover of shaded understorey (Table 1, Fig. 2). The majority of unoccupied area (64%) was located in the 7.5 ha coppice block (Fig. 1a), which was largely avoided by Marsh Tits with 70% of the block never being occupied in the five years of study.

### Overstorey tree species composition

Common Ash and English Oak were the dominant tree species in the overstorey of each Marsh Tit occupation category (Fig. 4a). Field Maple was the third most extensive species, except for where Marsh Tit occupation was low ($Z$ = 0-1). The individual contributions of European Aspen, Silver Birch, and elm to each category of Marsh Tit occupation were low (Fig. 4b). Fitting the regression model (Equation 1), imposing a constant slope and then isolating and testing the slope of each tree species in turn, gave a final selected model that had separate slopes each for elm and Silver Birch, with the other four tree species sharing an identical slope. The fit of this final model (Fig. 4a and 4b) deteriorated significantly when the slope for Silver Birch ($F_{1,27}$ = 4.7, $P$ = 0.04) or elm ($F_{1,27}$ = 21.6, $P$ = 0.004) was set equal to that of the four remaining species. Addition of a separate slope for other species did not improve this reduced model, indicating that Marsh Tits were not preferentially selecting an overstorey rich in any particular tree species (disregarding the negligible coverage of elm).

| | Marsh Tit occupation score *Z* | Overstorey mean height | Tree canopy closure | Total understorey[a] mean height | Shaded understorey mean height | Exposed understorey mean height | Total understorey[a] coverage | Shaded understorey coverage |
|---|---|---|---|---|---|---|---|---|
| Overstorey mean height (m) | 1.00* | | | | | | | |
| Tree canopy closure (%) | 0.94* | 0.94* | | | | | | |
| Total understorey[b] mean height (m) | -1.00* | -1.00* | -0.94* | | | | | |
| Shaded understorey mean height (m) | 0.43 | 0.43 | 0.37 | -0.43 | | | | |
| Exposed understorey mean height (m) | 1.00* | 1.00* | 0.94* | -1.00* | 0.43 | | | |
| Total understorey[b] coverage (%) | -0.94* | -0.94* | -0.87* | 0.94* | -0.49 | -0.94* | | |
| Shaded understorey coverage (%) | 1.00* | 1.00* | 0.94* | -1.00* | 0.43 | 1.00* | -0.94* | |
| Exposed understorey coverage (%) | -1.00* | -1.00* | -0.94* | 1.00* | -0.43 | -1.00* | 0.94* | -1.00* |

*Denotes a statistical significance of $P < 0.05$

[a] Total understorey is a combination of shaded and exposed understorey (see text).

Table 2. Correlation matrix of variables derived from overstorey and understorey LiDAR models of Monks Wood. Values are Spearman's rank order correlation statistic ($r_s$) where $n = 6$. Units of measurement for each variable are given on the vertical labels only.

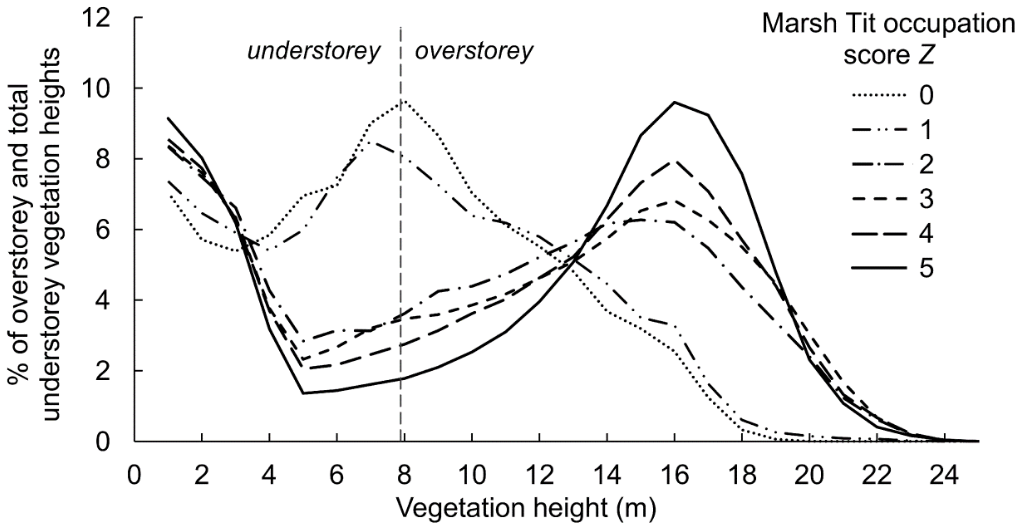

Figure 3. Distribution of vegetation height surfaces in relation to areas defined by Marsh Tit occupation score *Z*. Vegetation surfaces are represented as a percentage of pooled total understorey and overstorey height values.

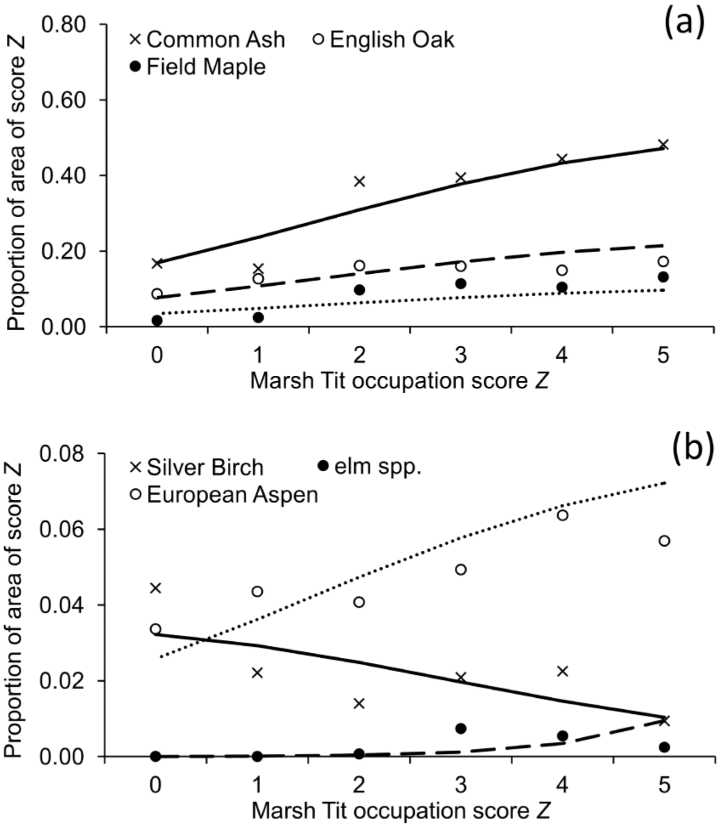

Figure 4. Proportion of the area categorized by each Marsh Tit occupation score *Z* that was occupied by each overstorey tree species. Lines estimated using regression of log ratios, where the model allowed individual slopes for Silver Birch and elm spp. while grouping remaining species in a constant ratio to one another. Plot (a): Common Ash (solid line), English Oak (dashed line), Field Maple (dotted line). Plot (b): Silver Birch (solid line), elm spp. (dashed line), European Aspen (dotted line). Note the differing vertical scales on the *y* axes.

| | 50 m edge buffer | | 100 m edge buffer | |
|---|---|---|---|---|
| | Edge | Interior | Edge | Interior |
| Percentage where Marsh Tit occupation score (*Z*) = 3-5 | 70.6 | 87.5 | 81.3 | 87.7 |
| Overstorey mean height (SD) (m) | 14.3 (3.2) | 15.4 (3.4) | 15.1 (3.4) | 15.2 (3.5) |
| Shaded understorey mean height (SD) (m) | 2.6 (1.1) | 2.6 (1.1) | 2.6 (1.1) | 2.6 (1.1) |
| Exposed understorey mean height (SD) (m) | 5.4 (1.9) | 5.5 (1.9) | 5.4 (1.9) | 5.5 (1.9) |
| Total understorey[a] mean height (SD) (m) | 3.8 (2.0) | 3.5 (1.9) | 3.5 (1.9) | 3.5 (1.9) |
| Tree canopy closure (%) | 76.1 | 86.3 | 82.2 | 84.3 |
| Area coverage of shaded understorey (%) | 25.7 | 31.1 | 29.8 | 29.6 |
| Area coverage of exposed understorey (%) | 17.9 | 12.2 | 13.8 | 13.5 |
| Area coverage of total understorey[a] (%) | 43.6 | 43.3 | 43.6 | 43.1 |

[a] Total understorey is a combination of exposed and shaded understorey (see text)

Table 3. Comparison of overstorey and understorey heights and coverage, and tree canopy closure, between edge and interior habitats in Monks Wood, using 50 m and 100 m buffers to define woodland edge.

### Woodland edge effects

Edge effects were more pronounced between the 50 m buffer of woodland edge and the interior when compared to the 100 m edge delineation. The percentage area of high Marsh Tit occupation score (*Z* = 3-5) was 17% lower in the 50 m edge buffer than in the interior, but the difference between the 100 m edge buffer and its corresponding interior was only 4% (Table 3). This larger disparity in the 50 m delineation was also reflected in the vegetation; compared to the interior, vegetation within the 50 m edge buffer had a lower overstorey mean height, less tree canopy closure, more coverage of exposed understorey but less of shaded understorey, and these differences were much greater than those between the 100 m edge buffer and its interior (Table 3).

## DISCUSSION

The approach of combining high resolution remote-sensing data with cumulative overlays of annual bird territories gave novel insights into the relationship between a woodland bird species and its habitat. Previous studies of Marsh Tit habitat associations have been inconsistent; Hinsley et al. (2009) found a positive relationship between Marsh Tit occupation and tree canopy height, as did Broughton et al. (2006) using a subset of territories from the current study, but no association was found with understorey characteristics. Hinsley et al. (2007), however, found that understorey characteristics, rather than tree canopy, were the most consistent variables in Marsh Tit territories between sites. Carpenter et al. (2010), meanwhile, found significant associations between Marsh Tit presence and features of both the tree canopy and understorey layers at sites across England and Wales. Yet, all of these studies employed Marsh Tit territory or presence data from a single year only, or small-scale, ground-based vegetation sample plots. By using comprehensive, high-resolution vegetation datasets for the entire study area, and complete Marsh Tit territory data over five years, the current analyses integrate and develop the findings of previous studies by showing that Marsh Tit occupation is strongly linked to woodland structure throughout the full vertical profile. The prominence of understorey vegetation in the height bin range of 1-3 m at the highest levels of Marsh Tit occupation underlines the importance of understorey at the 2-4 m level identified by Hinsley et al. (2007) and Carpenter et al. (2010). The relationships between Marsh Tit occupation, overstorey height, and tree canopy closure in our results also reinforce the findings of Broughton et al. (2006) and Hinsley et al. (2009).

Our results also show that a substantial understorey can persist under a mature, near-closed tree canopy, which is important in demonstrating that the two structures are not necessarily incompatible in unmanaged woodland, as has been hypothesized elsewhere (Fuller et al. 2005). Coppice management is therefore not always a pre-requisite for maintaining a substantial woodland understorey. Indeed, Marsh Tits largely avoided the large (7.5 ha) block of coppice management in our study area, which accounted for the majority of the area of Monks Wood that was permanently unoccupied. These unoccupied areas were characterised by less tree canopy cover and a shorter overstorey than the rest of the wood. Such a structure may be avoided by Marsh Tits because it constricts them within a shorter vertical layer of vegetation, reducing the diversity of feeding opportunities that would otherwise be available in a wider range of vegetation strata. It may also heighten inter-specific competition by increasing spatial proximity between birds, and increase foraging pressure within a more limited spatial zone (Hartley 1953).

There were structural differences between woodland interior and woodland edge habitats within a 50 m buffer of the perimeter. The buffer had relatively less tree canopy closure, lower overstorey height, and more exposed understorey vegetation, all features avoided by Marsh Tits in the study area, and indicative of a lower, shrubbier habitat than that found in the interior. Marsh Tit occupation was correspondingly lower in the 50 m edge buffer than the woodland interior, although the effect became minor as the buffer increased to 100 m from the woodland edge, indicating the limit of influence. Although vegetation structure was likely to be a significant driver of the observed edge avoidance, greater exposure to predators, such as Sparrowhawks (*Accipiter nisus*), or inclement weather (Hadley and Desrochers 2008) may also have contributed, although we had no specific information on this.

Based on our results and the conclusions of previous studies (Broughton et al. 2006, Hinsley et al. 2007, Carpenter et al. 2010), it is possible to identify woodland policy objectives aimed at providing high quality habitat for breeding Marsh Tits. Woodland stand maturity should be promoted, with a mean overstorey height in excess of 15 m, tree canopy closure of at least 80%, and a minimum of 40% of the ground area covered by understorey. Marsh Tits demonstrate a clear affinity with understorey present in the 1-4 m height range, specifically located beneath a mature overstorey layer rather than as exposed shrubs and young trees in e.g. an active coppice regime. Due to edge avoidance, providing a single pair of Marsh Tits with the minimum 1.5 ha territory (Broughton et al. in press) of high-quality breeding habitat would require a circular woodland area of 4.5 ha to accommodate a 50 m buffer against the edge environment. Patch shape and core to edge ratio may partially explain why the probability of occupation is only *circa* 20% for woods of this size in Britain (Hinsley et al. 1996), as long, narrow woodland patches less than 100 m wide will contain no interior that is buffered from edge effects.

We were unable to detect any selection for English Oak in the woodland overstorey, or for other tree species (disregarding negligible amounts of elm), suggesting that tree species composition may be less important than structural variables (MacArthur and MacArthur 1961), at least for the species complement of Monks Wood. Similar results have been obtained for the closely-related Willow Tit in Britain, which showed a preference for young deciduous woodland rather than tree species composition (Lewis et al. 2007, 2009). These differences between the Marsh Tit and Willow Tit in structural habitat selection may reflect niche separation in Britain.

The decline of the Marsh Tit throughout the latter third of the 20th Century is puzzling, as the condition of British woodlands appears to have changed to their advantage during that time. The area of broadleaved woodland older than 50 years doubled between 1965 and 2000, while the area of active coppice management declined (Mason et al. 2007). There has been an increase in the numbers and range of deer in England, which may damage woodland vegetation, but Newson et al. (2011) found no relationship with Marsh Tit abundance. Furthermore, maturation of woodland coincided with a widespread and substantial increase in understorey vegetation cover in the preferred 2-4 m height range (and 4-10 m range) between the 1980s and early 2000s (Amar et al. 2010). We have shown that increased woodland maturation, understorey coverage and absence of coppice management can all have a positive influence on Marsh Tit occupation, yet the species' abundance fell by more than a third in Britain during the period in which these habitat changes were taking place (Baillie et al. 2010).

If results from our study site can be extrapolated to other areas of lowland Britain, the implication is that widespread abandonment of woodland management and associated changes in vegetation structure have not contributed to the Marsh Tit's decline. The UK Government's target to increase woodfuel production significantly (Forestry Commission England 2007) could, therefore, have a detrimental effect on remaining Marsh Tit populations by preventing or reversing maturation of woodlands. Forest management and commercial exploitation have been shown to have negative impacts on other forest-dwelling, cavity-nesting *Poecile* species in the Holarctic, such as the Gray-headed Chickadee (Siberian Tit) and Boreal Chickadee in the mature conifer forests of Finland and Quebec, Canada, respectively (Virkkala 1990, Hadley and Desrochers 2008), and also the Willow Tit in a mosaic of mixed forest habitats in Finland (Siffczyk et al. 2003). The Black-capped Chickadee (*P. atricapillus*), however, showed little response to localised logging or natural succession in north-eastern USA (Loery and Nicholls 1985, Holmes and Sherry 2001). The Chestnut-backed Chickadee (*P. rufescens*) also adjusted to partial felling of mature forest stands in the Pacific Northwest of North America (Mahon et al. 2007), and may have even benefitted from commercial forestry (Brennan and Morrison 1991). These varied responses within a single genus underline the importance of accurately defining detailed habitat associations for woodland/forest bird species before conservation or commercial policies are implemented, in order to determine the implications of management regimes.

As high-resolution LiDAR and multispectral data become increasingly available and affordable (Vierling et al. 2008), alongside enhanced technologies for mapping bird movements and distribution at greater spatial resolution (Fiedler 2009), analytical methods are increasingly required that can exploit the information produced. Our work provides a novel case-study of how the integration of detailed spatial datasets of habitat and territory maps is an effective manner of achieving this aim, which can have a broad application in the fields of population ecology and species conservation.

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# 4 FACTORS DETERMINING NEST-SITE SELECTION

This chapter continues the habitat selection analyses, concentrating on the role of habitat in nest placement by Marsh Tits. The drivers of nest-site selection by birds are poorly understood, with the competing hypotheses of habitat-driven cues, social factors such as conspecific attraction, and previous nesting experience of females (Ramsay et al. 1999; Mennill et al. 2004; Bentzen et al. 2009; Melles et al. 2009). Few studies have addressed these questions with explicit reference to the territory boundaries of the birds concerned, which represent the spatial limits of the available area for nest placement. The most detailed studies involve a North American close-relative of the Marsh Tit, the Black-capped Chickadee (*Poecile atricapillus*), conducted by Ramsay et al. (1999) and Mennill et al. (2004). This work discounted an effect of habitat, food availability and previous experience of female chickadees on nest placement (Ramsay et al. 1999), instead concluding that females situated nests closer to the territory borders of neighbouring high-ranking males. This intriguing finding was predicted to facilitate extra-pair young being fathered by these socially-dominant males, but genetic analyses showed that this was not the case and the reason for the spatial patterning of nest placement remained unclear (Mennill et al. 2004). However, the spatial analyses failed to consider the greater probability of a nest being located closer to the territory boundary than the centre due to chance, as geometry determines that the area of an ovoid polygon that is closer to the outer edge is greater than that which is closer to the central point. Such underlying probabilities may have contributed to the pattern of nest placement observed by Ramsay et al. (1999) and Mennill et al. (2004), potentially undermining the conclusion of conspecific attraction.

In this chapter, Broughton et al. (2012) (Paper III) aimed to explore similar questions to Ramsay et al. (1999) and Mennill et al. (2004) regarding the relative roles of social and habitat factors in nest placement by the Marsh Tit, a species with a broadly similar ecology to the Black-capped Chickadee (Gosler & Clement 2007). The study gave special consideration to the probability of nest placement within different parts of the territory, using randomisation tests. Habitat structure and composition in the nest vicinity were compared to the remainder of the territory using comprehensive datasets derived from remote sensing, and the effect of female experience and age class were also investigated. Data were lacking for social hierarchies among males, but Mennill's et al. (2004) test of nest placement relative to male dominance was approximated using male age as an indicator of social status.

The results of Broughton et al. (2012) found no evidence for an effect of previous experience or conspecific attraction on nest placement by female Marsh Tits, with the nests of first-year birds being sited randomly within the territory and those of older females concentrated towards the territory core. In contrast to Ramsay et al. (1999) and Mennill et al. (2004), and results for the Hooded Warbler (*Wilsonia citrina*) by Melles et al. (2009), the only factor to have a significant relationship with nest placement was habitat; female Marsh Tits of all ages placed nests in areas of the territory where vegetation structure was relatively more mature and contained more Common Ash than elsewhere. However, a satisfactory answer could not be found for the differential nest placement within the territories of first-year and older Marsh Tits, suggesting that other factors were operating. Nevertheless, Broughton et al. (2012) represents the first study to highlight the importance of probability and territory geometry in spatial analyses of nest placement, and is a novel application of remotely sensed habitat data in the investigation of nest-sites relative to territory boundaries.

## 4.1 Paper III: **PATTERNS OF NEST PLACEMENT IN A POPULATION OF MARSH TITS *POECILE PALUSTRIS***

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### ABSTRACT

The factors influencing nest placement by territorial birds are not fully understood, 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. The core area of each breeding territory was centred on a region of comparatively taller overstorey and less understorey than other parts of the territory. Nest-sites were situated in localised areas of a similar structure, although absolute differences between selected and non-selected areas of the territory were not substantial. Both female age groups nested in areas of the territory where the overstorey contained relatively more Common Ash (*Fraxinus excelsior*) and Field Maple (*Acer campestre*), which may have been related to tree height, but there was no selection for English Oak (*Quercus robur*). We found no significant habitat differences between the territories of FY and AFY females that explained their differing patterns of nest placement.

## INTRODUCTION

The causes and consequences of nest-site selection are recurrent themes in ornithological research. Studies have commonly investigated the influence of habitat and/or previous experience on nest placement, often within the context of resource availability, reproductive success and nest predation (Nilsson 1984; Marzluff 1988; Martin 1993; Muller et al. 1997; Sockman 2000). There is also growing interest in nest placement with regard to the spatial arrangement of conspecifics, with attempts to understand the relative importance of social and physical determinants of nest-site selection (e.g. Ramsay et al. 1999; Melles et al. 2009; Bayard and Elphick 2010), including their impact on the incidence of extra-pair paternity (Mennill et al. 2004; Westneat and Mays 2005).

For territorial species, nest placement decisions can be constrained by the distribution of specific resources within the territory, such as the availability of snags for primary cavity-nesters like the Black-backed Woodpecker (*Picoides arcticus*) (Bonnot et al. 2009). The limited availability of nest resources may even suppress the breeding density of secondary cavity-nesters, as in the Great Tit (*Parus major*) (Mänd et al. 2009), while nest placement by Crested Tits (*Lophophanes cristatus*) appears tied to a particular habitat structure (Summers et al 1992; Atiénzar et al 2009). Male Cerulean Warblers (*Dendroica cerulea*) can alleviate such constraints on female nest placement by defending territories containing multiple patches of potential nesting habitat (Jones and Robertson 2001). Nest placement by female Hooded Warblers (*Wilsonia citrina*) was random with regard to habitat variables, however, and was instead clustered among conspecifics (Melles et al. 2009). Similarly, Ramsay et al. (1999) found that Black-capped Chickadees (*Poecile atricapillus*) placed nests close to their territory boundary, discounting habitat, food availability and female previous experience as significant factors in nest-site selection at the territory scale. Mennill et al. (2004) concluded that this pattern of nest placement was driven by conspecific attraction among Black-capped Chickadees, 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. Similar work on Red-winged Blackbirds (*Agelaius phoeniceus*) has also failed to show a significant relationship between the location of a female’s nest within the territory and the incidence of extra-pair paternity by neighbouring males (Weatherhead et al. 1994; Westneat and Mays 2005). As such, the relative importance of social and habitat cues to nest placement within the territory, and the function of observed patterns of conspecific attraction, remain unclear (Mennill et al. 2004; Melles et al. 2009).

Characterising complex vegetation at the territory level can be problematic, however, as localised ground-based sample plots may not adequately describe available habitat at an appropriate spatial extent or resolution (e.g. Jones and Robertson 2001). 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 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).

The Marsh Tit (*P. palustris*) is a Eurasian 10-12 g sedentary woodland species which adopts a similar breeding strategy to the closely-related Black-capped Chickadee, whereby socially monogamous pairs occupy exclusive spring territories and nest-sites are selected by the female (Morley 1953; Broughton et al. 2006). Marsh Tits are obligate users of secondary cavities, primarily derived from natural decay processes in the stems of trees and shrubs, but rarely use the abandoned cavities of primary cavity-nesting birds (Wesołowski 1996; Broughton et al. 2011). There have been no investigations into the social and habitat factors that may govern nest placement within the territories of this species.

In this study we aimed to investigate the roles of habitat, female experience of previous nest locations, and conspecific attraction on Marsh Tit nest placement, using seven years of territory, bird and nest-site data. The application of high-resolution models of canopy and understorey vegetation, derived from airborne remote sensing, enabled the spatial analyses of nest-sites, territory composition and habitat structure in exceptional detail. Studies of nest placement by cavity-nesting birds within the context of territory configuration and social organisation remain rare. This work on the Marsh Tit provides the first investigation into such patterns for an additional species, and permits comparison with results from the congeneric Black-capped Chickadee (Ramsay et al. 1999; Mennill et al. 2004).

## METHODS

### Territory and nest data

The study was conducted in 153 ha of woodland in the Monks Wood National Nature Reserve in Cambridgeshire, UK ($52^o$ 24'N, $0^o$ 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 and the Eastern Woods are fragments of 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 variable amounts of Silver Birch (*Betula pendula*), European Aspen (*Populus tremula*) and elm (*Ulmus* spp.). The understorey layers are dominated by hawthorn (*Crataegus* spp.), Blackthorn (*Prunus spinosa*) and Common Hazel (*Corylus avellana*) (Broughton et al. 2006). The study sites are mature woodland and broadly correspond to the 'old-growth' stage of development (Quine et al. 2007), with little visual change in vegetation structure between years. The four smallest Eastern Woods each held a single Marsh Tit territory during the study, the two larger woods held 6 and 10 territories, and Monks Wood held 21-23 territories each year.

Almost the entire breeding population of Marsh Tits in Monks Wood (96%) 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 territories in Monks Wood were identified during a minimum of six visits to each territory between February and May. Territory occupants were followed for 1-4 hours on each visit, and movements were plotted on 1:10,000-scale geo-referenced maps (Broughton et al. 2006, 2010). Particular attention was paid to territorial behaviour such as boundary disputes and singing, in order to identify territory boundaries, and playback of recorded song was also employed to elicit behavioural responses. The mapped bird registrations were digitised in a Geographical Information System (GIS) and territories were delineated as non-overlapping maximum defended areas based on standard territory-mapping techniques (Bibby et al. 2000), using the behavioural attribute data of bird registrations for interpretation (see Broughton et al. 2006 for further detail).

A total of 117 nest locations (112 in natural cavities, five in nest-boxes) were identified in Monks Wood during survey visits to each territory in April and May of 2004-2010 (14-21 nests per year, with 36-72% belonging to FY females). 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). Although Marsh Tits are secondary cavity-nesters, and thus reliant on pre-existing tree holes, we have previously shown that there is a very low rate of cavity re-use which indicates that nest-sites were abundant throughout Monks Wood (Broughton et al. 2011). On this basis, we were able to exclude the possibility that female choice of nest placement was significantly constrained by nest-site availability.

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 as per Monks Wood. 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 due to the birds not being marked. The locations of nests within these territories were digitised as per Monks Wood, with 14 nests located in 2010 (6 and 4 nests in the two larger woods, one nest each in three of the four smaller woods) and one in 2008 (in the fourth small wood), all belonging to different females of unknown age.

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 parts of the territory 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. As such, the distribution of the nests of FY females was essentially acting as a ‘random’ comparison with that of AFY females. We were unable to test for any effect of unsuccessful nesting on subsequent nest placement by the same female, as the nest failure rate was low (16.4%) (Broughton et al. 2011) and only three females survived to breed in the study area in the year following nest loss.

### 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 all woods was generated during leaf-on conditions from airborne lidar data acquired in June 2005 (data for all woods processed as described in 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). Lidar data has been shown to be capable of representing the height of deciduous woodland vegetation with a high degree of accuracy (Lefsky et al. 2002; Lim et al. 2003), including the Monks Wood study site (Hill et al. 2002), so we did not attempt to validate data in the field. However, field observations in Monks Wood were used to ascribe height values of > 8 m to the overstorey layer of mature tree crowns (Hill et al. 2010), which 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 for comparison, and also to compare overstorey height between the territory cores and margins. Data acquisition and processing for the Eastern Woods followed the methodology used for Monks Wood, which we justified based on the similar woody species present, age-structure and management. The results from the limited single-year dataset from the Eastern Woods were used to assess the wider applicability of the comprehensive multiple-year territory data from Monks Woods. As the Eastern Woods data involved unique females and territory locations for each nest, issues of pseudo-replication and bias were minimised, and the data were considered to be a representative snap-shot of the woods in one year.

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

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.

Mean overstorey height, understorey height and understorey coverage were treated as paired data for comparison of nest buffers and their corresponding territories, and for territory cores and their corresponding margins. We applied angular transformation to proportional understorey coverage data, with non-parametric tests being employed where normalisation of data could not be achieved by transformation, and Spearman’s rank order correlation was used to test for inter-variable correlations. All tests were two-tailed. As the vegetation structure in the study sites was predominantly mature we expected little dynamic change over the study period (2004-2010). As we were comparing relative values of vegetation height and coverage between the nest buffers and remainder of the territories, and the territory cores and margins, absolute changes in the vegetation structure after the 2003 and 2005 lidar data acquisition would only be problematic if they occurred unevenly within territories. If such uneven change had occurred over the timeframe of the study, we reasoned that any significant patterns of vegetation structure relating to nest placement that were evident in the early years of the study would become less distinct or unapparent in the later years, as the time between acquisition of the lidar and bird data increased. We tested for this effect by comparing the pattern of results of the nest buffer and territory analyses of structure (overstorey and understorey height, and understorey coverage) for the early years of study (2004-6 combined) and the later years (2008-10).

To test whether the proportion of any tree species in the overstorey differed between the nest buffers and territories, the proportional values required transformation to address the problem of non-independence when some or all were considered together, 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. To overcome this, the proportions of each tree species within the overstorey of each territory area (nest buffer, territory remainder, core or margin) were divided by that of the unclassified vegetation category in the same defined area. This reduced the dimensionality of the data by one, in the manner of a compositional analysis (Elston et al. 1996). Taking the natural logarithm of each ratio left the transformed values unbounded above or below and closer to a normal distribution, allowing each to be treated as an independent variable in comparative analyses.

## RESULTS

### Nest placement within the territory

Of the 117 nests located in Monks Wood, 95 nest cavities were unique, and no territorial pairs that were present during a breeding period failed to acquire a nest cavity. 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 each combination of territory boundary, nest-site and the arrangement of neighbours between and within years was unique. In addition, we found no evidence of an effect of previous female site-selection on 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).

| | Observed number of nests in territory core (%) | Median (range) of random points in territory cores | *P* |
|---|---|---|---|
| All females ( *n* = 117) | 44 (37.6) | 29 (27) | < 0.01 |
| FY females (*n* = 58) | 14 (24.6) | 14 (20) | 0.13 |
| AFY females (*n* = 59) | 30 (50.9) | 15 (24) | < 0.01 |

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.

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: $t = 0.40$, $P = 0.69$).

| | Nest buffers | Territories | Test statistic | *P* |
|---|---|---|---|---|
| **Overstorey mean height (m) (mean (SD))** | | | | |
| 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) (median (range))** | | | | |
| MW: all females | 2.87 (4.48) | 3.28 (1.75) | $W = 855.00$ | < 0.01 |
| MW: FY females | 2.97 (2.13) | 3.34 (1.69) | $W = 149.00$ | < 0.01 |
| MW: AFY | 2.78 (4.40) | 3.26 (1.67) | $W = 305.00$ | < 0.01 |
| EW: all females | 2.95 (1.41) | 3.34 (1.33) | $W = 168.00$ | < 0.01 |
| **Understorey mean coverage (proportion) (mean (SD))** | | | | |
| 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 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.

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 6.4%, but 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: $t = 0.62$, $P = 0.54$). When comparing the observed pattern of the results for understorey height, coverage and overstorey height for nest buffers and corresponding territories during the early years of study (2004-6) and later years (2008-10) there was little difference in the pattern between time periods (Table 3), or between each period and the full duration of study (Table 2, Table 3). The only discrepancy was the near-significant result for overstorey mean height in 2004-6, but this was considered a minor inconsistency. The results in Table 3 indicated that the lidar data was equally valid in assessing relative within-territory variables throughout the study period.

| | Nest buffers | Territories | Test statistic | *P* |
|---|---|---|---|---|
| **Overstorey mean height (m) (mean (SD))** | | | | |
| 2004-6 | 15.87 (2.11) | 15.44 (1.34) | $t = 2.01$ | 0.07 |
| 2008-10 | 16.20 (2.31) | 15.31 (1.27) | $t = 2.02$ | < 0.01 |
| **Understorey mean height (m) (median (range))** | | | | |
| 2004-6 | 2.95 (1.94) | 3.30 (1.75) | $W = 1378.00$ | < 0.01 |
| 2008-10 | 2.91 (4.47) | 3.44 (1.63) | $W = 990.00$ | < 0.01 |
| **Understorey mean coverage (proportion) (mean (SD))** | | | | |
| 2004-6 | 0.38 (0.06) | 0.43 (0.08) | $t = 4.67$ | < 0.01 |
| 2008-10 | 0.40 (0.09) | 0.43 (0.05) | $t = 2.09$ | 0.04 |

Table 3. Mean habitat variables in the nest buffer and remainder of the territory for breeding territories in Monks Wood during the early years of study (2004-6, $n = 52$) and the later years of study (2008-10, $n = 44$) for females of all ages. Comparisons performed using paired *t*-tests and Wilcoxon Signed Rank *W*-tests, with angular transformation being applied to proportion data before testing.

Table 4 shows that 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 analyses. Of the remaining tree species, a significantly greater coverage of Common Ash and Field Maple were present in the nest buffers compared to the territories, although the absolute difference for Field Maple was only 3%. There was no difference between FY and AFY females in the proportions of Common Ash in the nest buffers (two-sample *t*-test: $t = 0.93$, $P = 0.36$), nor of Field Maple (two-sample *t*-test: $t = 1.13$, $P = 0.26$). There was less coverage of English Oak in the nest buffers than the territories of both female groups, but the difference was not statistically significant (Table 4).

| | Mean (SD) proportion in nest buffers | Mean (SD) proportion in territories | Wilcoxon Signed Rank *W* statistic | *P* | Proportion of MW | Mean (SD) height in MW (m) |
|---|---|---|---|---|---|---|
| Common Ash | 0.54 (0.22) | 0.45 (0.16) | 5760.0 | < 0.01 | 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) | 5302.0 | < 0.01 | 0.12 | 15.93 (3.30) |
| English Oak | 0.11 (0.12) | 0.15 (0.08) | 3892.0 | 0.23 | 0.18 | 14.88 (2.87) |
| Unclassified vegetation | 0.13 (0.15) | 0.20 (0.10) | - | - | 0.15 | 11.95 (2.52) |

Table 4. 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. Wilcoxon Signed Rank *W*-tests were performed on transformed data (see text) for common species only.

Significant negative correlations were apparent between the ranked values of overstorey and understorey mean heights in the nest buffers and corresponding territories of FY and AFY females in Monks Wood, these being moderate relationships in the nest buffers but strong relationships in the territories (Table 5).

This indicated that the vertical structure of the overstorey and understorey was more diverse in the nest buffers compared to the territory remainders, which was also indicated by the larger standard deviations of the means and ranges around the medians for nest buffer overstorey and understorey mean height in Table 2. There were only weak or insignificant relationships between understorey height and coverage, but overstorey mean height was positively and significantly correlated with the coverage of Common Ash for both female age classes. A positive relationship between overstorey mean height and Field Maple was also apparent, being stronger for AFY females.

| | **FY females** | | | | **AFY females** | | | |
|---|---|---|---|---|---|---|---|---|
| | Overstorey mean height | | Understorey mean height | | Overstorey mean height | | Understorey mean height | |
| | **B** | **T** | **B** | **T** | **B** | **T** | **B** | **T** |
| Understorey mean height | -0.42$^{**}$ | -0.82$^{**}$ | - | - | -0.43$^{**}$ | -0.87$^{**}$ | - | - |
| Understorey coverage | -0.06 | 0.08 | 0.29$^{**}$ | 0.03 | -0.43 | 0.17 | 0.24 | -0.04 |
| Common Ash coverage | 0.37$^{**}$ | 0.37$^{**}$ | - | - | 0.44$^{**}$ | 0.35$^{**}$ | - | - |
| Field Maple coverage | 0.27 | 0.26 | - | - | 0.44$^{**}$ | 0.47$^{**}$ | - | - |
| English Oak coverage | -0.06 | -0.10 | - | - | -0.01 | -0.06 | - | - |
| | **C** | **M** | **C** | **M** | **C** | **M** | **C** | **M** |
| Understorey mean height | -0.61$^{**}$ | -0.79$^{**}$ | - | - | -0.67$^{**}$ | -0.87$^{**}$ | - | - |
| Understorey coverage | 0.34$^{**}$ | 0.00 | 0.09 | 0.29$^{**}$ | 0.20 | -0.28$^{**}$ | 0.23 | 0.49$^{**}$ |
| Common Ash coverage | 0.59$^{**}$ | 0.65$^{**}$ | - | - | 0.62$^{**}$ | 0.71$^{**}$ | - | - |
| Field Maple coverage | 0.24 | 0.43$^{**}$ | - | - | 0.33$^{**}$ | 0.62$^{**}$ | - | - |
| English Oak coverage | -0.36$^{**}$ | -0.16 | - | - | -0.11 | -0.09 | - | - |

Table 5. Correlations between habitat variables in Marsh Tit nest buffers (B) and their corresponding territory remainders (T), and territory cores (C) and their corresponding margins (M), for first-year (FY, $n = 58$) and after first-year (AFY, $n = 59$) females in Monks Wood. Values are Spearman's rank order correlation statistic $r_s$. Superscript * denotes a statistical significance of $P < 0.05$, and ** of $P < 0.01$.

### Habitat in the territory cores and territory margins

Although AFY females nested disproportionately within the territory cores, compared to random nest placement by 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 of Monks Wood 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. For females of both age groups, territory cores contained significantly taller overstorey and shorter understorey than the corresponding margins, with greater coverage of all three tree species and less coverage by understorey (Table 6). There was no statistically significant difference for any variable between the territory cores of FY and AFY females (results of two-sample *t*-tests not presented).

Moderate or strong negative correlations were found between overstorey and understorey mean heights in the territory cores and margins of both female age groups, with positive associations between overstorey height and Common Ash coverage (Table 5). There was a weak yet significant correlation between understorey coverage and understorey mean height in the margins of FY females, with a stronger relationship for AFY females. Positive correlations were also apparent between overstorey height and Field Maple coverage, again being stronger for AFY than FY females. There were weak or insignificant negative correlations between overstorey mean height and the coverage of English Oak for both female age groups.

## DISCUSSION

The results confirmed that nest-site availability was unlikely to have influenced nest placement by Marsh Tits in Monks Wood, as the frequency of cavity re-use was lower than that recorded for this species in the primeval conditions of Białowieża forest, Poland, where holes were super-abundant (Wesołowski 2006, Broughton et al. 2011). We also 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 differed from the work by Ramsay et al. (1999) and 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 by 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 account for this effect. 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, but the purpose of any such behaviour remains elusive. We did not investigate extra-pair paternity in this study, but evidence from the Black-capped Chickadee (Mennill et al. 2004), and also the Red-winged Blackbird (Weatherhead et al. 1994; Westneat and Mays 2005), suggested that access to extra-pair copulations had little bearing on nest placement within the territory.

Our results further disagree with those for the Black-capped Chickadee (Ramsay et al. 1999; Mennill et al. 2004), and also the Hooded Warbler (Melles et al. 2009), in finding that nest placement by Marsh Tits was related to habitat variables. We identified statistically-significant differences in habitat structure between the nest buffers and the remainder of the Marsh Tit territories, and the results supported the previous finding that Marsh Tit occupation was associated with taller canopy height at our Monks Wood study site (Broughton et al. 2006). The nest buffers of both female age groups in Monks Wood had a significantly taller overstorey than other areas of the Marsh Tit territories, and the trend was replicated in the nest buffers of the smaller single-year dataset for the Eastern Woods, and also the territory cores of Monks Wood. Additionally, understorey height and coverage were significantly lower in the nest buffers compared to the remainder of the territories, and also in the territory cores compared to the margins. The mean height of the overstorey was negatively correlated with that of the understorey but there appeared to be no strong or consistent relationship between understorey coverage and other structural variables, and no selection for greater understorey height or coverage by Marsh Tits.

The results for understorey conflicted with Hinsley et al. (2007) and Carpenter et al. (2010), who concluded that Marsh Tit occupation and abundance was positively associated with the density and coverage of this vegetation layer. The failure to detect this trend around nest sites in our study suggests that selection for understorey might not be directly related to nesting behaviour or nest-site selection; it is possible that greater visibility around nest-sites confers some advantage in relation to predator detection and avoidance. As there was no substantial change in the relationships between nest placement and vegetation structure between the early and late years of the study period (Table 3), we were confident that these results were not compromised by the lidar data becoming invalid over the time span of the study due to changes in vegetation structure. Any such changes were likely to have been relatively homogeneous or insignificant by the latter years of bird data collection.

Carpenter (2008) found that Common Ash and Field Maple were the tree species most frequently used for foraging in Monks Wood when Marsh Tits were provisioning young, and we detected a significantly higher proportion of these species in the overstorey of the nest buffers compared to the rest of the territories, and in the territory cores compared to the margins. As Common Ash was the tallest tree species in Monks Wood, however, followed by Field Maple, it was unclear whether selection by Marsh Tits was operating on the basis of tree species or tree height. There were significant positive correlations between overstorey height and the coverage of Common Ash and Field Maple, and these relationships were apparent in almost all subdivisions of the territories. In contrast, English Oak was the shortest tree species and showed a weak or very weak negative correlation with overstorey height in all territory areas. Yet English Oak was also more common in the territory cores than the margins, particularly for FY females, but not in the nest buffers compared to the rest of the territories. The territories of both female age groups were, therefore, centred on core areas containing relatively less understorey and a taller overstorey containing greater amounts of all three tree species, compared to the margins. Nest-sites, meanwhile, were centred on more localised areas of the territory that were likewise dominated by a modest understorey and relatively tall overstorey, but the trees were composed of Common Ash and Field Maple in preference to English Oak. This suggested a possible selection process driven by tree height at the scale of the territory core, but with additional selection based on tree species at the smaller scale of the nest buffer. Such a selection is supported by Carpenter’s (2008) finding that Common Ash and Field Maple were preferred over English Oak by foraging Marsh Tits when breeding.

Why Common Ash and Field Maple may be selected over English Oak around nest-sites is unclear. We have no information on food availability on the various tree species within the study site, although Carpenter (2008) suggested that Marsh Tits may have been competitively excluded from foraging areas by other tit species. As such, Marsh Tits may not select for Common Ash and Field Maple *per se*, but instead be avoiding competition with more dominant species in areas rich in English Oak, which offers high quality habitat for Great Tits (Wilkin et al. 2009) and Blue Tits (*Cyanistes caeruleus*) (Stenning 2008). The potential for inter-specific avoidance or attraction is rarely considered in nest placement studies (though see Burger 1987), but is worthy of further investigation for the Marsh Tit due to the potential contribution of competitor species to its negative conservation status (Carpenter et al. 2010; Broughton et al. 2011).

It was logical to surmise that AFY females preferentially nested in the territory cores because these areas contained a concentration of the same habitat structural characteristics as those found in the nest buffers, namely a tall overstorey with a comparatively modest understorey. The territory cores of FY females contained a similar concentration of these attributes, however, so it was unclear why the nests of FY females were randomly placed throughout the territory. Some aspects of habitat selection may have been based on variables not examined in our analyses, perhaps involving other attributes of tree quality, which may account for this finding and also some of the subtle or non-significant differences in our results. As FY females tended to be paired to younger, and presumably lower-ranking, males than the breeding partners of AFY females, these sub-dominant males may have been less able to acquire and centre their territories upon large areas of high-quality habitat, which we may have been unable to detect. Alternatively, although FY females appeared capable of assessing habitat quality at the scale of the nest buffer, they may have been less able to assess habitat quality at the larger scale of the whole territory, perhaps due to less familiarity with their environment than older females, or lack of previous breeding experience.

While we were unable to identify the underlying basis for the random pattern of nest location observed among FY females, we found no evidence to support the hypothesis that Marsh Tit nest placement was significantly influenced by conspecific attraction or a female’s previous breeding location. Instead, nest placement appeared to be related to habitat variables within the foraging distance around the nest site and, for AFY females at least, habitat characteristics in the territory core compared to the margin. Although many studies have reported a relationship between localised habitat characteristics and nest placement in other territorial species (Jones and Robertson 2001; Oppel 2004; Atiénzar et al. 2009), few have addressed this within the context of explicit territory boundaries and the arrangement of neighbouring conspecifics. Where this has been undertaken, conspecific attraction has appeared to be more influential than within-territory habitat variation in determining nest placement (Ramsay et al. 1999). To date, however, the resolution or spatial extent of habitat data in such studies has been much lower than that of the bird data, which may obscure fine-scale patterns of habitat selection. Our study appears to be the first to combine data for nest-sites, territory boundaries and population structure with high-resolution lidar data and optical imagery in the spatial analysis of nest placement. Due to the complex nature of vegetation in the spatially extensive territories of many bird species, remote-sensing may offer the best opportunity of obtaining habitat data of sufficient detail with which to investigate nest placement at the territory scale.

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# 5 NEST-SITES AND BREEDING SUCCESS

This chapter narrows the focus of Paper III from nest placement within the territory to consider the physical characteristics of nest-sites within tree and shrub cavities, and the influence of these variables on nest-site availability and nest failure. Broughton et al. (2011), which is presented as Paper IV, also considers other factors preventing Marsh Tit territories from producing young.

Studies of the natural nest-sites and breeding success of cavity-nesting woodland birds are uncommon in Europe, as nestboxes tend to provide a more convenient and standardised method of monitoring breeding activity. However, this could lead to methodological bias (Møller 1989), as nestboxes could offer greater protection than natural cavities, which may be more vulnerable to predation if composed of soft, dead wood or situated close to the ground (Nilsson 1984; Wesołowski 2002).

Fuller et al. (2005) hypothesized that British Marsh Tits may have suffered increased nest predation by Great Spotted Woodpeckers and greater nest-site competition from Great Tits and Blue Tits, and these possibilities were priorities for research. Ludescher (1973) and Wesołowski (2002) undertook detailed studies of Marsh Tit nest-sites and breeding success in Germany and Poland respectively, but such information is not directly applicable to the British situation due to the differing densities and composition of predators and competitors. Siriwardena (2006) tackled the questions posed by Fuller et al. (2005) in the British context by analysing the large, but non-standardised, dataset from the BTO Nest Record Scheme, finding no relationships between the abundance of Marsh Tits and their potential avian nest predators and competitors. Siriwardena (2006) also found no increase in failure rates of Marsh Tit nests over time, although the BTO data contained a majority of nestbox records which was a potential source of bias.

In an attempt to describe the selection of natural nest-sites by Marsh Tits in Britain and the influence of nest-site availability, competition and nest predation, and to quantify breeding failure, Broughton et al. (2011) documented the fate of 153 breeding territories and 134 nests in the Monks Wood study area. The results showed that Marsh Tits were flexible in their choice of nest-site and this was unlikely to be a limiting factor for the species in British woods; nests were primarily sited in knotholes in immature live Common Ash, a resource that is generally common throughout England and Wales (Amar et al. 2010), and nest-site competition from other species appeared insignificant. Notably, the rate of nest failure in the study population was comparable to that found by Siriwardena (2006) in the national dataset from the BTO, providing validation of those results regardless of the high proportion of nestboxes involved. Furthermore, at 18% the failure rate was one of the lowest recorded for this species in Europe (Cramp & Perrins 1993; Wesołowski 2002). Overall, therefore, the evidence suggested that nest failure had not been a major factor in the decline of the British Marsh Tit.

Broughton et al. (2011) extended the scope of the study beyond typical analyses of breeding success to quantify the number of occupied spring territories that failed to reach the nesting stage at all. In addition to the territories where nests failed, a further 12% did not produce a nest due to predation of adults and a lack of female recruits prior to nesting. This highlighted a reduction in the productivity of Marsh Tits that would not be detected by nest monitoring, nor be present in the dataset analysed by Siriwardena (2006). An increase in predation of adults and a reduction in recruitment ability, perhaps through impaired dispersal (section 1.3 and chapters 7 and 8), could, therefore, represent an additional pressure on Marsh Tit populations that may have contributed to their decline.

Consequently, Broughton et al. (2011) is an important contribution to Marsh Tit research by confirming the results of Siriwardena (2006) and allowing the nest failure hypothesis for the Marsh Tit decline to be discounted. The work is also a rare example of research into the breeding success of a British woodland passerine in natural cavities, and points to further causes of reduced productivity that occur before the nesting period and are rarely considered for any species.

## 5.1 Paper IV:

*Bird Study* (2011) **58**, 229-237

# Nest-sites, breeding failure, and causes of non-breeding in a population of British Marsh Tits *Poecile palustris*

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**Capsule** Choice of nest-site appeared flexible and the rate of breeding failure was low, but some birds did not reach the nesting stage.

**Aims** To analyse nest-site selection and its effect on nest predation and establish the rate of breeding failure.

**Methods** We used vegetation sample plots to assess the nest-site resource and established the fate of birds in 153 territories and 134 nests over seven years. The fate of 30 nests from neighbouring woods was also determined.

**Results** Most nests were situated 0–4 m high in knotholes in live, medium-sized Common Ash trees. Overall, birds in 12.4% of occupied spring territories did not reach the nesting stage, primarily because of an absence of females, and 16.4% of nests in the same population were not successful. The nest failure rate was 18.4% across a wider population, which included neighbouring woods, primarily because of nest predation.

**Conclusion** Marsh Tits were flexible in their choice of nest-site with low rates of nest competition and predation. Nest failure is unlikely to be a significant factor in the decline of British Marsh Tits but failure to reach the nesting stage may be an additional pressure.

There is a growing body of literature on the natural nest-sites used by cavity-nesting species (Alatalo *et al.* 1988, Wesolowski 1989, Denny & Summers 1996, Mitrus & Soćko 2004, Walankiewicz *et al.* 2007), including the influence of structural variables on nest predation, such as nest height (Nilsson 1984, Albano 1992), cavity wall thickness or hardness (Albano 1992, Christman & Dhondt 1997), and cavity dimensions (Wesolowski 2002). For Marsh Tits *Poecile palustris*, a 10–12 g secondary cavity-nesting species of Eurasian woodlands, the most comprehensive data for nest-site selection and breeding success come from secondary forest in Sweden (Nilsson 1984) and primeval conditions in the Bialowieza forest of Poland (Wesolowski 1996, 2002). There is little comparable information from the highly modified woodlands of northwest Europe where Marsh Tits have undergone a significant decline in abundance (Burfield & van Bommel 2004), and particularly from Britain where the population fell by 66% between 1969 and 2006 (Eaton *et al.* 2009). One of the hypothesized drivers of this population decline is breeding failure owing to high levels of predation by, for example, increasing numbers of Great Spotted Woodpeckers *Dendrocopos major*, or competition for nest-sites from the socially dominant Great Tit *Parus major* or Blue Tit *Cyanistes caeruleus*. Siriwardena (2006) tested this hypothesis by analysing 730 records from the British Trust for Ornithology's Nest Record Scheme, but found no evidence of a decline in nest success across Britain. Siriwardena's (2006) study included a majority of nestbox data, however, and such sites may influence predation levels (although see Nilsson (1984)). Systematic studies of Marsh Tit nests in natural cavities elsewhere in Europe have shown much higher rates of failure (Ludescher 1973, Nilsson 1984, Wesolowski 2002).

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The aims of the current study were to identify the preferred size and type of tree or shrub used for nesting by Marsh Tits in a British population and the rate and causes of nest failure, comparing breeding results with the broad-scale findings of Siriwardena (2006) and with other regions of the species' range (reviewed in Cramp & Perrins (1993); also see Wesolowski (2002)). We also wished to examine whether suitable nest-cavities may be limiting for Marsh Tits and whether nest-site competition from more dominant tit species could be a significant problem.

## METHODS

### Study area

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'), which represented our core population, and among 15 neighbouring patches of woodland that lie wholly within a 7-km radius of Monks Wood (hereafter the 'outlying woods'), which represented the wider population. The size of the outlying woods ranged from 4.1 to 70.0 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 some 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, 2010). Monks Wood was clear-felled around 1918 and has regenerated naturally since that time, with 90% of the wood being unmanaged. The outlying woods are predominantly composed of mature English Oak, Common Ash and Field Maple, and three woods are composed of about 60-year-old plantations of pine *Pinus* spp., Norway Spruce *Pinea abies*, English Oak and Common Ash (see Broughton *et al.* (2010) for further details of the study area).

### Territory and nest data

Almost the entire population of Marsh Tits in Monks Wood were individually marked with colour-rings between 2003 and 2010 (Broughton *et al.* 2010). Birds were sexed and aged as first-years or older according to Broughton *et al.* (2008). Six female spring immigrants that could not be aged before the post-breeding moult were assumed to be first-years, this age group forming 92% of the female immigrants of known age (Broughton *et al.* 2010). Each spring, the boundaries of all 21–23 Marsh Tit territories in Monks Wood were delineated and digitized in a geographical information system (GIS), based on observations of territorial behaviour between late February and May (Broughton *et al.* 2006, 2010). Birds in this population typically began nest-building in early April (Broughton *et al.* unpubl. data), and a total of 117 nest locations were identified during intensive surveying of each Monks Wood territory every 1–7 days in April and May of 2004–10, to monitor the survival and breeding status of each bird. The following variables were recorded for all nests: tree species; situated in live or dead wood; dbh of the stem in which the cavity was located (categories of small: <10 cm, medium: 10–30 cm, and large: >30 cm); and height of nest entrance rendered into height bins of 1 m. A further variable of 'cavity type' was based on the classification of Wesolowski (1996): knothole cavity (formed at the site where a branching stem has detached from a trunk/limb); rotten sapwood (behind live or dead bark); chimney (formed in the top of a broken stem), woodpecker hole; or split (fissure in stem). Nestboxes were available at a maximum density of only one per 2 ha in Monks Wood, and nests in these were excluded from analyses of cavity type where appropriate.

Searches of varying intensity each year were conducted in the outlying woods between 2005 and 2010 in order to locate additional nests belonging to ringed and unringed Marsh Tits (Broughton *et al.* 2010). A total of 30 nests were discovered in 10 woods, and were recorded as per Monks Wood, although comprehensive breeding data for the entire population of each wood were not available. The majority of nests below 7 m in elevation in all woods were inspected at least weekly using an endoscopic camera, with clutch size being determined for nests found before the eggs hatched. Nests above this height, and some below, could not be inspected practically or safely. The number of young fledged was estimated by counting chicks after day 15 post-hatching (about 3–5 days before fledging), at which point they were large and fully feathered, and then checking nests after fledging for signs of corpses. Nests that fledged at least one chick were considered successful, this being determined by observation of empty and undamaged nests, dependent fledglings being attended by the adults, or subsequent sightings of ringed chicks after independence. Causes of nest failure were deduced from field signs, such as flooding, usurping by another species, damage to the cavity, remains of nest contents, disappearance of parents, or predator bill, tooth or claw marks.

For 17 Monks Wood territories where the nest could not be located, and the 15 nests which could not be inspected, the progression of breeding was estimated based on adult behaviour (Morley 1949, 1953). A breeding attempt was assumed to have commenced in a territory once a female was heard food-soliciting from a male (Morley 1949, Nilsson & Smith 1988), and successful nesting was confirmed by observation of adults feeding dependent fledglings in the territory. Breeding failure was deduced by absence or premature cessation of breeding activity, or the disappearance of adults, this being confirmed for ringed birds by searching for or following individuals for approximately 1 hour on a minimum of two occasions several days apart, and for unringed birds by searching the territory area to locate individuals or pairs. Potential or known predators of nests and breeding adults present within the study area are listed in the Appendix.

### Nest-cavity resource

In order to estimate the potential nest-cavity resource available at Monks Wood, 34 vegetation sample plots measuring 100 m × 10 m were positioned across the wood (Marchant 2006). For trees, the same categories of dbh and species were recorded as for nest-sites, along with snags and large, standing dead limbs (Hinsley *et al.* 2007). Shrubs were recorded to species and those of >4 m in overall height were considered large enough to accommodate nest-cavities and were included as an available resource. Each Monks Wood Marsh Tit territory in all years coincided with at least one sample plot, and results from all plots were summarized for the whole wood and compared with the frequency of variables across all nests sites. The disproportionate use of particular tree or shrub species, dbh class, and live or dead wood for nesting was tested by comparing the situation of nests to the availability of the resource across Monks Wood, using the frequency of stem types in the sample plots to generate expected values. Potential nest-cavities were presumed to be proportionately distributed across stem types.

### Data analysis

As the Monks Wood vegetation sample plots provided expected values of nest-site variables that were not derived from the nest data itself, we used the G-test of independence and associated Williams correction factor to compare proportions with the observed frequencies. A Fisher exact test was used when expected values were small in a test of two nominal variables, otherwise we employed standard chi-square tests. All tests were two-tailed. Only nests from a pair's initial breeding attempt were included in analyses, and problems of replication in analyses of cavity-type selection, owing to the same nest-cavity being used in successive years, were avoided by considering only unique nest-sites. All nests were included in analyses of predation, however, including multiple records across years from the same nest-cavity, because each annual nesting attempt was considered a unique exposure to predation or other failure.

The calculation of the nest failure rate can be biased by the duration of nest observation, as nest mortality is a function of time, and this requires a correction in order to obtain an appropriate estimate of success for a population (Mayfield 1975). As we could determine the total number of Marsh Tit territories that were occupied in the Monks Wood population at the beginning of the spring and the overall number of these territories that reached the nesting stage and eventually fledged at least one chick, we were able to calculate the overall rate of nest failure for the population without recourse to correction methods. Additionally, we could determine the number of spring territories that were occupied by at least one bird but did not reach the nesting stage. For the outlying woods, however, nest searches and territory monitoring were neither systematic nor comprehensive. As such, the rate of overall nest failure was calculated according to the Mayfield method (Mayfield 1975), taking 6 days as the laying period, 14 days as the incubation period and 19 days as the nestling period (Robinson 2005, Broughton *et al.* unpubl. data). When calculating nest exposure days, timing of nest loss was estimated from the age of chick remains or was assumed to have occurred midway between the two observations spanning the event.

## RESULTS

### Territories that failed to reach the nesting stage

Of 153 spring territories in Monks Wood, 12.4% failed to reach the nesting stage despite being occupied by at least one potential breeding bird from early March. Of these territories, most (57.9%) failed to progress to nesting because they were occupied by lone males (no female present), 26.3% because of the disappearance of one or both members of a pair during March or early

April (that was not replaced subsequently), 10.5% because of divorce (females moving to another male's territory), and 5.3% because of being occupied by a lone female. These figures indicated a shortage of females during the spring period, while the disappearances were attributed to predation as these birds could not be relocated within the wider meta-population (Broughton *et al.* 2010). We did not observe any pairs that did not attempt to nest if they survived beyond early April, but detected two cases of polygyny in Monks Wood (Broughton 2006) and a further two cases in the outlying woods.

## Nest-cavity selection

Of the 95 individual natural nest-cavities recorded in Monks Wood, 17.9% were used more than once during the course of the study, with 12.6% used in two consecutive years and 5.2% used more than twice. The majority of the 130 individual nest-sites (including seven nestboxes) located in all woods, i.e. Monks Wood and the outlying woods, were positioned at a height of 0–4 m from the ground (mean = 3.0 m ± 0.22 sd; Fig. 1.) in natural knothole cavities (63.8%). The distribution of nests among other cavity types was: 18.5% in rotten sapwood; 8.5% in chimneys; 5.4% in nestboxes; 2.3% in splits; and 1.5% in woodpecker holes. Shrub species were rarely used for nesting in Monks Wood, accounting for just 9.0% of natural nests despite representing 30.4% of available stems, with the most frequently used species being hawthorn. Small trees were abundant in Monks Wood, accounting for 51.9% of tree stems but only 10.5% of Marsh Tit nests in trees. As only the larger stems in this size category were used, and many small stems were probably too small to accommodate a suitable nest-cavity, this size category was excluded from subsequent analyses. The majority of Monks Wood natural nests (89.5%) were in large and medium-sized trees, which were used at the frequency expected from their availability (Table 1). Common Ash was used for nesting disproportionately to its abundance throughout Monks Wood, while English Oak and Field Maple were under-represented among nests, and the combined category of Silver Birch, European Aspen and elm was used at the approximate frequency at which it occurred (Table 1). While the 28 natural nests in the outlying woods were distributed differently among tree species, being most commonly located in Common Ash (42.9%), elm (17.9%) and Field Maple (10.1%), the proportions in live wood (82.1%) and medium stems (75.0%) were similar to those in Monks Wood.

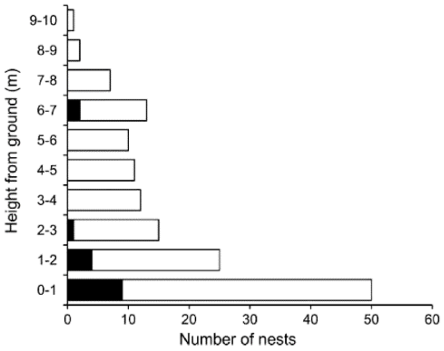

**Figure 1.** Height distribution of 147 Marsh Tit nests (130 individual cavities), and the incidence of predation (in black). Note that two nests at 0–1 m and five nests at 1–2 m were in nestboxes, one of the latter being predated.

## Nest failure

Of the 134 territories in Monks Wood that reached the nesting stage and the nests were located ($n = 117$) or nests were not found but were estimated to have reached at least the stage of nest-building by observation of adult behaviour ($n = 17$), 16.4% failed to produce young. Excluding the five nests in nestboxes, of which one was predated by a Common Weasel *Mustela nivalis*, the percentage of natural nests that failed was very similar at 15.5%. For the sample of 30 nests in the outlying woods, an overall nest failure rate of 27.0% was derived using the Mayfield method (Mayfield 1975), with the loss of four nests over 497 days of observation giving a daily mortality rate of 0.008. Combining the failure rate of Monks Wood and the estimated failure rate for the outlying woods, applied proportionately to the sample sizes, the overall failure rate for 164 nesting attempts across all woods was 18.4%, or 17.6% for 157 natural nest-cavities only. With three to five nests failing each year, sample sizes were too small to test for an annual effect.

Of all 26 nests that failed and the cause was known, 14 (53.9%) showed signs of attack by a predator (Table 2), of which 71.4% could be attributed to mammals (mostly small mustelids and rodents) and the remainder to Great Spotted Woodpeckers. Overall, 28.6% of predated nests were attacked at the egg stage and 71.4% at the chick stage. Of the mammalian nest predators, Common Weasel appeared to be the most important, this being

**Table 1.** Location of natural Marsh Tit nest cavities in Monks Wood in relation to availability of resources as derived from vegetation sampling to provide expected values for the *G*-tests (applying Williams correction).

| Variable | % of nests (*n*) | % of available resource (*n*) | *G*-test statistic | df | *P* |
|---|---|---|---|---|---|
| Dead wood (snags/standing limbs) | 14 (13) | 6.18 (272) | 6.99 | 1 | <0.01 |
| Live wood | 86 (82) | 93.82 (4126) | | | |
| **Tree species** | | | | | |
| Common Ash | 77 (65) | 54.09 (668) | 26.58 | 3 | <0.01 |
| English Oak | 2 (2) | 11.74 (145) | | | |
| Field Maple | 7 (6) | 20.73 (256) | | | |
| Silver Birch + European Aspen + elm spp. | 14 (12) | 13.44 (166) | | | |
| **Tree age** | | | | | |
| Medium trees (dbh = 10–30 cm) | 65 (62) | 65.49 (987) | 2.12 | 1 | 0.14 |
| Large trees (dbh > 30 cm) | 35 (23) | 34.51 (520) | | | |

Small trees (dbh < 10 cm) were excluded from analyses, as many were considered too small to accommodate a nest.

**Table 2.** Causes of Marsh Tit nest failure (first broods only), deduced from field signs.

| Cause of nest failure | % of failed nests ($n = 26$) | Number of failures at nest-building/egg/chick stage |
|---|---|---|
| Great Spotted Woodpecker | 15.4 | 0/0/4 |
| Eurasian Badger | 3.9 | 0/0/1 |
| Common Weasel | 23.1 | 0/2/4 |
| Grey Squirrel | 7.7 | 0/1/1 |
| Wood Mouse | 3.9 | 0/1/0 |
| Flooding | 7.7 | 0/1/1 |
| Usurping by Blue Tit or Great Tit | 7.7 | 0/2/0 |
| Female disappeared | 19.2 | 3/0/2 |
| Unknown | 11.5 | ?/?/0 |

Two nests were in nextboxes: one predated by a Common Weasel, and one usurped by a Blue Tit.

deduced from the remains of nest contents, scats in the cavity, and the small entrance hole of predated nests apparently excluding other mustelids. Common Weasels were also the only predator responsible for killing females on the nest, this occurring in 66.7% of all weasel attacks, and 28.6% of all predated nests. One nest, at the base of a rotten Silver Birch snag, was predated two days after hatching by a presumed Eurasian Badger *Meles meles*, which was able to open the entire nest-cavity.

The modal value of all natural nest heights was 0–1 m (Fig. 1), and nests at this lowest height were predated more frequently than those positioned higher (Fisher exact test, $P = 0.02$), although nests situated at 0–2 m elevation (encompassing the height range of predated nests observed by Nilsson (1984)) were not predated more often than higher nests (Fisher exact test, $P = 0.14$). Nests in dead wood were not predated more frequently than nests in live wood (Fisher exact test, $P = 0.06$). Of the two nests in old woodpecker holes, one in a Great Spotted Woodpecker cavity succeeded, and one in a Lesser Spotted Woodpecker *D. minor* cavity was predated by a Great Spotted Woodpecker over two days. In two located nests, all chicks died owing to females disappearing within several days of hatching. As only females brood the young in this species (Morley 1953, pers. obs.), the unfeathered chicks quickly perished despite observation of continued food provisioning by the male. Disappearance of these females was attributed to probable predation away from the nest. One nest failed because of usurping by a pair of Great Tits during the laying stage, while Blue Tits were observed attempting to commandeer four natural nest-cavities and one nestbox. The natural cavities were aggressively and successfully defended by the Marsh Tits, but the nestbox was lost and the Marsh Tit pair nested again in a natural cavity (but failed because of flooding at the chick stage). This pair was one of only two in Monks Wood to suffer a nest failure and then attempt to breed again in the same year (12.5% of failed nests where both adults survived), the other of which was successful. Clutch size in first broods ranged from 4 to 10 eggs (mode = 7; mean = 7.59 ± 1.25 sd, $n = 95$) and the number of young fledged from successful nests was 1–10 (mode = 7; mean = 6.95 ± 1.88 sd, $n = 63$).

## DISCUSSION

The majority of Marsh Tit nest-cavities in our study area were located in knotholes in live, medium-sized, Common Ash trees, at 0–4 m in height. Shrub species were rarely used for nesting, nor were tree stems with a dbh < 10 cm, probably because of an absence of suitable holes. Common Ash was over-utilized as a nest-site and English Oak and Field Maple apparently avoided. However, we assumed that the availability of potential nest-cavities was uniform across stems of different sizes and species, so it is possible that Common Ash was over-represented owing to that species providing more potential nest-sites than other species. There is little comparable data on tree species usage from elsewhere in Europe, but all of the common trees used for nesting in Bialowieza (Poland) and Germany (Wesolowski 1996) were rare or absent in Monks Wood. This indicates that Marsh Tits are flexible in their choice of nest-tree, utilizing a range of species according to their availability in differing contexts (Wesolowski 1996). Further adaptability in nest placement was shown in the frequency of nests located in medium-sized and large trees, which were used relative to their abundance with no sign of selection.

Marsh Tit nests were most frequently positioned within 1 m of the ground, and these lowest nests suffered more predation than those placed higher, as found by Nilsson (1984) in Sweden. Wesolowski (2002) found no relationship between nest height and predation in Bialowieza, however, and nests within the height category of 0–2 m in our study did not suffer greater predation than higher nests, indicating that the risk quickly diminishes with height (Nilsson 1984). The mean height of nest-holes at 3.0 m was above the zone of greatest predation risk, and broadly similar to smaller studies from elsewhere in Europe (reviewed in Wesolowski (1996)), including England (Morley 1953), but differed from the more detailed studies in Sweden (1.1 m; Nilsson 1984) and Bialowieza (5.6 m; Wesolowski 1996). Variation among nest heights was great in our study, however, ranging from ground level to 10 m.

There was no indication that nest-hole availability was limiting for Marsh Tits in Monks Wood, because the rate of hole re-use in the subsequent year was 12.6% compared with 35.5% in Bialowieza, where holes are superabundant (Wesolowski 2006). Although some nest-holes may have become unavailable by the following year, which we did not quantify, we did not record any Marsh Tit pairs that were unable to secure a nest-cavity. This indicated that potential nest-sites for Marsh Tits were also abundant in the secondary woodland of Monks Wood, allowing Marsh Tits to change holes frequently despite a relatively high number of parid nest-competitors (Wesolowski *et al.* 2006, Carpenter 2008). Furthermore, while Blue Tits may successfully compete for nest-holes with the Willow Tit *P. montanus* (Lewis *et al.* 2009) our observations suggest that Marsh Tits are frequently able to defend their nests against this species. Although one pair was usurped by the larger Great Tit, Marsh Tits frequently nest in cavities with a small entrance (Wesolowski 2002) which will generally exclude this species. The variation in nest-sites used by Marsh Tits in our study, and others, suggests that it is unlikely that nest-cavities are limiting for this species across much of Britain, and competition for nest-holes does not appear to be a serious issue (Siriwardena 2006).

Predation was the major cause of nest failure in our study, although the observed rate of failure in natural nests was among the lowest recorded for this species in Europe (Cramp & Perrins 1993, Wesolowski 2002), despite a large assemblage of common predators (Appendix). This failure rate was also much lower than for similar species in Britain, with 30.0% of Willow Tit nests failing (Lewis *et al.* 2009) and 50.5% of Crested Tit *Lophophanes cristatus* nests failing (Denny & Summers 1996). However, these species are primary cavity-nesters, which are limited to excavating nest chambers in soft wood, whereas Marsh Tits nest in secondary cavities, and frequently in live wood, where the harder walls may offer greater protection from predation (Christman & Dhondt 1997, Wesolowski 1996, 2002). Yet, we found little evidence that Marsh Tits strongly avoided nesting in dead wood, and we did not find that dead wood carried a significantly enhanced predation risk. However, as reported from Bialowieza, old woodpecker holes seemed to be avoided (Wesolowski 2002). Great Spotted Woodpeckers and Common Weasels were the most frequent nest predators in our study, as reported from elsewhere (Ludescher 1973, Dunn 1977, Nilsson 1984), although small mammals were the most significant group of predators overall (Wesolowski 2002). There was little evidence that Grey Squirrels were significant nest predators (Newson *et al.* 2009), although this species attacked nests at the egg and chick stages in both dead and live wood.

The failure rate of nests in our wider study area (18.4%) was similar to the 15% derived from Siriwardena (2006) using nest records from across Britain (109 failures out of 730 nests), despite 58% of those records coming from nestboxes (compared with 5% in our study). Nilsson (1984) also found no difference in predation rates among natural Marsh Tit nests and those in nestboxes and this suggests that use of nestbox data may not overly bias studies of nest survival in this species, particularly as the majority of nest predators are small mammals (which can generally enter nestboxes through the entrance hole just as easily as natural nests). The estimated nest failure rate for the outlying woods was higher than the observed rate for Monks Wood, indicating that small woods may suffer higher rates of nest predation. The two sample sizes were uneven, however, and the failure rates were derived using different methods, so comparisons should be treated with caution. A small sample size may have led to an overestimation of the general failure rate in the outlying woods, although further clarification would be required using a larger data set.

In addition to nesting failure, birds in a further 12.4% of Monks Wood territories occupied during the spring period failed to reach the nesting stage. One significant cause was the disappearance of potential breeding adults. These losses were almost certainly because of predation, as these birds did not relocate to the wider area (Broughton *et al.* 2010), and 19.2% of unsuccessful nests also failed owing to disappearance of the female. We have little information on the predators responsible, except the remains of two birds found as Eurasian Sparrowhawk *Accipiter nisus* prey and observation of occasional unsuccessful attacks by this species. Eurasian Sparrowhawks can remove a significant proportion of adult tits during spring (Geer 1978, Dhondt *et al.* 1998) and may have been responsible for many of the 'disappeared' Marsh Tits, although other possibilities include Eurasian Jay *Garrulus glandarius* and Common Kestrel *Falco tinnunculus*, both of which were also observed attacking adult Marsh Tits. The majority of disappeared birds were females, which may be particularly vulnerable to avian predation when developing/laying eggs, incubating and brooding owing to the very frequent calling when soliciting food from the male (Morley 1949, Nilsson & Smith 1988), which may attract attention. Such predation of adult birds away from the nest, resulting in nest failure, may be responsible for some of the 'desertion' reported in other nest studies (Wesolowski 2002).

The most common reason for birds in potential breeding territories birds failing to nest was the lack of recruits at the beginning of spring. Of the few instances where lone females were present in a territory, this was alleviated by engaging in polygyny with the male from a neighbouring pair (Broughton 2006). Polyandry was never observed, however, and the number of females appeared limiting. Although a distinct phase of spring immigration has been observed at this site (Broughton *et al.* 2010), of which the majority of incoming birds were females, numbers were insufficient to form pairs with all lone males or act as replacements for predated birds. Furthermore, there appeared to be no resident floating population of potential replacements by the time that the population began nesting (Cederholm & Ekman 1976). These phenomena may stem from barriers to successful dispersal and immigration (Broughton *et al.* 2010) and/or differing rates of overwinter survival between the sexes. Juvenile Marsh Tits generally become established in a 1:1 sex ratio during the previous summer, with potential recruits out-numbering territory or flock vacancies (Nilsson 1989, Broughton *et al.* 2010). Factors altering this ratio must then act during late summer, autumn and winter. We are currently unable to confirm or explain a lower over-winter survival rate among females, although work is ongoing.

Our results, when viewed in the context of previous work (Siriwardena 2006, Wesolowski 2002), confirm that there is little evidence for nest failure being a primary factor in the decline of the British Marsh Tit. However, insufficient numbers of spring recruits and the predation of potential breeding birds before nesting may act as an extra pressure upon populations. Even for a study area such as Monks Wood, in a stable and relatively large meta-population (Broughton *et al.* 2010), the number of territories that contained potential breeding birds that failed to reach the nesting stage at all, because of a lack of recruits or replacements, was almost as many as the number of territories that were unsuccessful because of nest predation. Barriers to recruitment may be more acute in the wider landscape where habitat is more fragmented, as 74% of English woods are 10 ha or smaller (Forestry Commission 2001) and able to support only 1–2 average-sized territories. Dispersal from marginal territories and among smaller woods is also less successful (Broughton *et al.* 2010, Alderman *et al.* forthcoming). Consequently, an increase in Marsh Tit mortality could interact with dispersal ability in highly fragmented landscapes to reduce overall recruitment and population productivity. Furthermore, if nest failure rates in smaller woods are genuinely higher than for large woods, this would compound the effect of fragmentation on mortality and recruitment. As such, future work focussing on the causes and timing of mortality and the influence of habitat fragmentation on Marsh Tit survival and productivity would be valuable.

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## APPENDIX

Observed (*) or potential predators of breeding adult Marsh Tits, nests or fledglings within Monks Wood and neighbouring woods, with estimated abundance:

Eurasian Badger *Meles meles*: common*
Red Fox *Vulpes vulpes*: common
American Mink *Mustela vison*: rare
European Polecat *Mustela putorius*: rare
Stoat *Mustela erminea*: common*
Common Weasel *Mustela nivalis*: common*
Feral Cat *Felis catus*: rare
Brown Rat *Rattus norvegicus*: common
Wood Mouse *Apodemus sylvaticus*: abundant*
Bank Vole *Myodes glareolus*: abundant
Grey Squirrel *Sciurus carolinensis*: common*
Eurasian Sparrowhawk *Accipiter nisus*: common*
Common Kestrel *Falco tinnunculus*: common*
Tawny Owl *Strix aluco*: common
Great Spotted Woodpecker *Dendrocopos major*: common*
Eurasian Jay *Garrulus glandarius*: common*

# 6 PATTERNS OF DISPERSAL AND RANGING BEHAVIOUR

Chapter 5 indicated that factors limiting recruitment into territories in spring may impact on the breeding productivity of Marsh Tits. The current chapter therefore considers dispersal and ranging behaviour, which are the mechanisms by which birds locate and move between territories. There have been no systematic studies of Marsh Tit dispersal in the highly fragmented habitats of Britain, with the only information on movements coming from the recovery of 108 ringed birds (Sellers 1984), of which only 15% had moved distances greater than 5 km. Studies from elsewhere in Europe reported maximum dispersal distances of only 1.6-7.5 km (Nilsson 1989; Amann 1997), suggesting that Marsh Tits could be susceptible to habitat fragmentation (Fuller et al. 2005; section 1.3).

Paper V in this chapter, Broughton et al. (2010), was designed to address the critical lack of information on Marsh Tit dispersal and ranging behaviour in Britain, utilising a large search area of fragmented habitat, and a large number of birds ringed as adults and nestlings. By conducting searches and censuses at three points in the annual cycle, over six years, it was possible to determine the timing and progression of juvenile dispersal, and the movements of adults between breeding attempts.

Broughton et al. (2010) contains several findings that provide key insights into Marsh Tit ecology and the potential pressures upon populations in Britain. Firstly, the study found that juvenile dispersal distances were very short, typically a kilometre or less and traversing approximately two or three territories, with juveniles born in small woods usually being compelled to leave them in order to move away from their parents' territory. Secondly, juveniles born in these smaller woods were less successful at establishing within the wider population than those born in a larger wood, and there was an indication that gaps between woods had a barrier effect that inhibited dispersal. Immigrants comprised an important part of the breeding population in the study area, and impediments such as gaps between woods may have limited their number (see also Figure 2). Immigration was further constrained by dispersal behaviour largely being restricted to two very short time periods each year. The summer dispersal phase was the main juvenile dispersal period and was extremely rapid, appearing to last only a matter of days. As such, there was only a limited period when vacancies in breeding territories could be filled, as most birds were extremely sedentary once settled. Unfilled vacancies could also precipitate emigration of settled birds from a territory during the second dispersal phase in the following spring, involving widowed or unpaired birds that were seeking a breeding opportunity. This phenomenon was also observed by Amann (2003) in Switzerland, and meant that the death of one bird in a pair could lead to loss of both birds from a territory, and perhaps local extinction in a small wood, if potential recruits found it difficult to reach the territory.

Although some floating, non-territorial individuals were detected in the population during autumn and winter, which could fill vacancies opportunistically, they were uncommon and it was evident that ease of rapid and safe movement through the landscape between woods is a fundamental part of the population ecology of Marsh Tits. The ability of juveniles to disperse and settle in summer and then survive until spring, perhaps to disperse again, is vital to enable the replacement of adult birds lost over autumn and winter or during the breeding season. The immigration of such recruits prevents the abandonment of breeding territories by widowed birds, and repopulates vacant territories. Broughton et al. (2010) therefore identifies key ‘bottlenecks’ in the Marsh Tit’s annual cycle and is a rare example of a detailed study of the timing and spatial limits of dispersal in a woodland bird. The study also points to a negative feedback mechanism in fragmented habitat if connective habitat between woodlands is reduced, thereby inhibiting dispersal, reducing immigration and recruitment, and hence depressing the breeding productivity of a population and the propagation of further potential recruits.

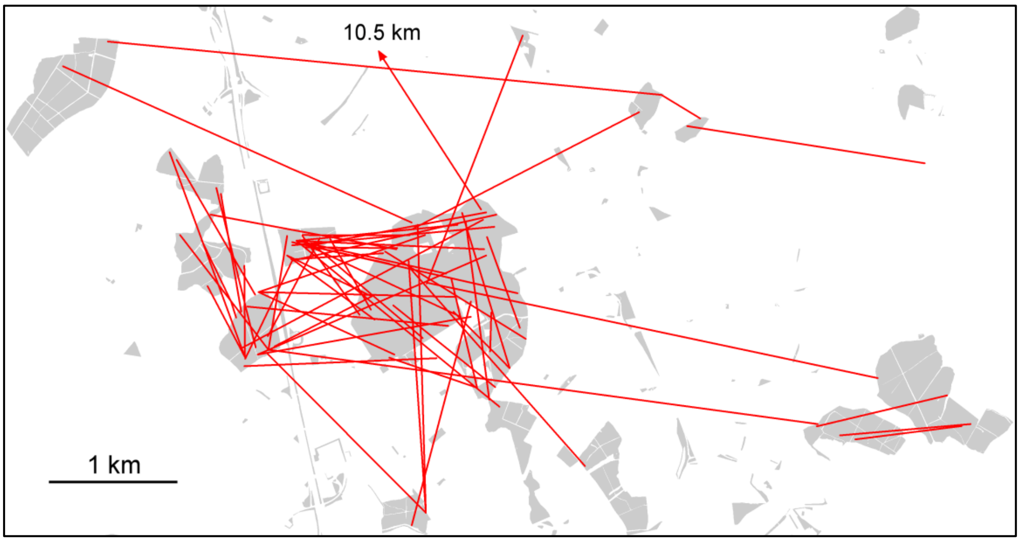

Figure 2. All dispersal movements of ringed Marsh Tits between woodland fragments over the full duration of the Monks Wood study (2003-2012). Red lines indicate 66 movements of 56 individuals, representing only 9% of all birds ringed and subsequently relocated during the study. See Figure 1 (p. 28) and Broughton et al. (2010) for further detail on the study area and methods.

## 6.1 Paper V:

*Bird Study* (2010) **57**, 458-472

# Dispersal, ranging and settling behaviour of Marsh Tits *Poecile palustris* in a fragmented landscape in lowland England

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**Capsule** Natal dispersal was rapid and distances were short. Winter ranging and breeding dispersal were limited. Few birds undertook large movements.

**Aims** To investigate the natal and breeding dispersal of Marsh Tits, including the timing of dispersal movements.

**Methods** Nestlings, juveniles and adults were ringed and searched for over 4500 ha during summer, autumn–winter, and spring over six years. Dispersal distances were measured as metric distances and multiples of territory widths. Ranging distances were compared with dispersal distances.

**Results** Median distances of natal dispersal were 2.6 territory widths for males (704.5 m) and 3.1 territory widths for females (1065.0 m). Median distances of breeding dispersal were 0.2 territory widths for males and females (58.6 and 53.1 m respectively). Most natal dispersal was completed soon after independence, with further movement in spring. Breeding dispersal was also detected during these periods. Median ranging distances were short, and some winter floaters were identified.

**Conclusion** Marsh Tits had short dispersal distances, with most dispersal activity occurring in June. Results suggested that dispersal behaviour was sensitive to habitat fragmentation, resulting in poor settling success outside of the natal wood. Habitat fragmentation may, therefore, be a contributory factor in the decline of the Marsh Tit population in Britain.

The dispersal behaviour of birds is a fundamental process in the regulation of populations, and is an essential consideration in species conservation strategies (Newton 1998, Walters 2000). Although the understanding of dispersal behaviour remains incomplete (Desrochers *et al.* 2007, Sharp 2009), a growing literature has demonstrated its importance as an influence on breeding density and distribution (Greenwood *et al.* 1979, Matthysen & Currie 1996, Hansson *et al.* 2002) and as a means of inbreeding avoidance (Szulkin & Sheldon 2008).

Two major types of dispersal are recognised; natal dispersal describes the movement of an individual between the place of birth and the place of first attempted reproduction, and breeding dispersal describes the movement between two successive reproductive attempts (Clobert *et al.* 2001). How habitat fragmentation interacts with these processes has been the subject of increased attention in recent decades, as landscapes become increasingly modified through human activity (Matthysen *et al.* 1995, Verhulst *et al.* 1997, Van Houtan *et al.* 2007). Habitat fragmentation may influence extinction, colonization and recruitment probabilities by mediating the dispersal of individuals through a landscape (Matthysen & Currie 1996, Dale 2001, Brooker & Brooker 2002, Dolman *et al.* 2007, Fahrig 2007).

Marsh Tits are small (10–12 g) Palaearctic passerines that are largely confined to mature temperate woodland (Cramp & Perrins 1993, Hinsley *et al.* 2007) and are declining across much of their European range (Burfield & van Bommel 2004). The British population fell by 66% between 1969 and 2006 (Eaton *et al.* 2009), although the reasons for this decline are unknown (Fuller *et al.* 2005). One contributory factor may be habitat fragmentation (Fuller *et al.* 2005), with

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Marsh Tits showing a negative response to declining patch size and increasing isolation (Enoksson *et al.* 1995, Hinsley *et al.* 1996). A limited tendency or ability of birds to move between habitat fragments would support the hypothesis of habitat fragmentation being a factor in the species' decline, although information on dispersal capabilities is scarce. A study of post-fledging movements in Switzerland found maximum settling distances of 1250 m for 26 males and 1550 m for 6 females (Amann 1997). Recoveries from the British Trust for Ornithology (BTO) ringing scheme found that only 15% of 108 records were of movements greater than 5 km (Sellers 1984), although the age, sex and timing of movement was unknown for the majority of birds. The only systematic data on natal dispersal distances (NDDs) comes from Sweden (Nilsson 1989), for which maxima of 4600 m for males and 7300 m for females were reported. Translating the NDDs into the number of territories traversed gave medians of 3.9 for males and 6.7 for females. Data on Marsh Tit breeding dispersal are also rare, with two limited studies reporting that adults rarely changed territories between years (Morley 1953, Amann 2003).

There are few dispersal data for other species in the *Poecile* genus, which are characterised by low breeding densities and high territoriality in comparison with other European parids (Smith 1992, Otter 2007). Orell *et al.* (1999) found respective mean NDDs of 1601 m and 1787 m for male and female Willow Tits *P. montana* in northern Finland. The estimation of dispersal distances for this species in Sweden were hampered by low rates of subsequent detection of birds ringed as nestlings; a problem also found with Siberian Tits in Finland *P. cinctus* and Black-capped Chickadees *P. atricapilla* in British Columbia (Smith 1967, Ekman 1979, Virkkala 1990). The only relatively well-studied parids are Great Tits *Parus major*, which are habitat generalists with a different social behaviour to *Poecile* species, breeding at high densities in nestboxes and flocking in non-territorial winter groups (Dhondt & Hublé 1968, Greenwood *et al.* 1979, Dhondt 1979, Enoksson *et al.* 1995, Verhulst *et al.* 1997, Matthysen *et al.* 2005). Great Tit NDDs in England exceeded that of Swedish Marsh Tits by less than half a territory width, although territories of the former were smaller and so metric distances were less (reported maxima of about 3500 m for males and about 4300 m for females) (Greenwood *et al.* 1979, Nilsson 1989).

There is little information on the timing of parid dispersal. Dhondt (1979) found that Great Tits underwent two stages of natal dispersal; one immediately after independence and further movement in autumn. Greenwood *et al.* (1979) considered that the most significant movements in this species were in late winter. Further underlining differences between these genera, however, Weise & Meyer (1979) reported a rapid dispersal phase for newly-independent Black-capped Chickadees and considered that natal dispersal had essentially ended by late summer. Ekman (1979) also found that juvenile Willow Tits become territorial before late summer, although some non-territorial birds remained transient, possibly owing to inadequate opportunities to become established.

In this study we investigated the natal and breeding dispersal of Marsh Tits in fragmented woodland in an English landscape dominated by intensive arable agriculture. We recorded the spatial distribution of movements and settling locations for adults and juveniles. The temporal progression of natal dispersal was assessed at several stages between independence and breeding and compared with the ranging behaviour of adults and juveniles during the non-breeding period. The causes of breeding dispersal were also investigated. Results are interpreted within the context of habitat fragmentation and the decline of the British Marsh Tit population.

## METHODS

### Study area and species

The study was conducted between 2003 and 2010 in 11 patches of mature woodland set in 4500 ha of an arable landscape matrix in Cambridgeshire, UK. Monks Wood National Nature Reserve (52° 24′ N, 0° 14′ W) (Steele & Welch 1973) formed the central and largest patch in the study area, with all other patches located within 3 km of its perimeter. The patches were classified as four 'inner woods' and seven 'outer woods' (Fig. 1). Woodland patch area ranged from 4.1 ha to 160.3 ha, comprising 8.0% of the landscape as 278.7 ha of semi-natural oak–ash–maple *Quercus–Fraxinus–Acer* stands and 83.1 ha of pine–spruce–oak–ash *Pinus–Picea–Quercus–Fraxinus* plantation. The mean distance between a patch and its nearest neighbour was 282.8 m (sd = 280.7, range 5.9–923.5), with the largest gap in interconnecting hedgerows being 256.2 m. Dispersal distances of up to 5 km could be detected within the study area, although woods up to 2 km beyond this were searched during unrelated spring censuses throughout all or part of the study period. This extended search area (Fig. 1) took the maximum detection distance to

**Figure 1.** Study area in northwest Cambridgeshire, UK, showing four inner woods (black; Monks Wood is the largest patch in the centre), seven outer woods (dark grey), five woods in the extended search area (outlined black), and small areas of interspersed trees and shrubs (pale grey). The dotted line is the A1(M) motorway, and the dot-dashed line is the East Coast Main Line railway.

7 km, which approached or exceeded the maximum NDD previously recorded for Marsh Tits (Amann 1997, Nilsson 1989) and encompassed about 90% of ringing recovery distances for British Marsh Tits (Sellers 1984).

A total of 411 Marsh Tit nestlings (370 in Monks Wood, 41 in other inner woods) were marked using uniquely-numbered BTO alloy rings and individual combinations of colour-rings in 2004–09 (91% in 2006–09), from a total of 56 successful nests in natural cavities and 4 in nestboxes. Breeding was highly synchronised and single-brooded in our study population (Broughton *et al.* 2008), and the timing of independence was determined by observation or allowing 14 days post-fledging for family break-up to occur (Nilsson & Smith 1985, Amann 1997). A total of 127 ringed juveniles were sighted or recaptured after independence. Full-grown birds were caught using cage-traps and mist-nets at a network of 37 temporarily baited sites 400–500 m apart within the inner woods. Trapping at each site took place over 2–3 days, primarily during the 'non-breeding period' of July–January in 2003–10, with concentrated effort between August and November. Trapping continued until no new individuals were being seen or caught at a site on a trapping day. A total of 233 unknown juveniles and 32 adults were ringed as per nestlings and all birds were aged and sexed according to Broughton *et al.* (2008), or by breeding behaviour. In all years except 2008, essentially all Marsh Tits present in Monks Wood had been colour-ringed by November, with only recaptures and sightings of known birds being made until the following year. This allowed the timing of subsequent immigration into Monks Wood to be determined. Approximately 80–90% of birds in the remaining inner woods were ringed each year, except 2008 (about 50%).

The mean number of all juveniles caught or identified in Monks Wood during each non-breeding period (excluding 2008) was 60.4 (sd = 10.0, range 48–71, $n = 5$), which was used to calculate a mean density of 0.38 juveniles ha$^{-1}$. Annual spring territory density remained stable throughout the study period, at 0.13–0.15 territories ha$^{-1}$ of wooded habitat. The inner woods supported a higher Marsh Tit population, however, with a maximum of 32 territories compared with 14 in the outer woods.

## Natal dispersal

In order to determine the timing and progression of NDD, ringed juveniles were searched for during three periods between independence and the following breeding season: the initial, non-breeding, and spring periods. The initial period attempted to define dispersal in June, within one to two weeks of independence. All woods were thoroughly searched on at least two visits, using playback of recorded song, in order to locate as many juveniles as possible. Search effort was incomplete in the outer woods prior to 2006, however, although few nestlings (9% of the sample) were ringed during this time. Bird locations were registered on large-scale maps and digitised in ARCGIS version 9.2 geographical information system (GIS) (ESRI Inc., Redlands, CA, USA). Multiple registrations for a single individual were reduced to a single location by generating a location-weighted centroid (geographical centre) depicting the mean geographical position of all coordinates, which was assumed to represent the focal point of activity and, hence, settling.

Further searching was undertaken in the non-breeding period (July–January) during trapping at the baited sites and observations elsewhere within the inner woods. Single intensive searches of the outer woods were undertaken during October–January in an attempt to find settled birds and those which may have relocated from the inner woods since June. This reduced effort, in comparison to the inner woods, reflected the smaller Marsh Tit population of the outer woods and the lower likelihood of a ringed bird settling as distance from the natal site increased. Observation centroids were derived as for the initial period, and distances were generated and compared between centroids in the initial and non-breeding periods, and also between the natal nest-site and the non-breeding period.

Searches during the 'spring period' of February–May took place in order to locate colour-ringed juveniles on their prospective breeding territories. The inner woods were searched on a minimum of four visits in 2004–09, although systematic searching of the outer woods took place only in 2007–09. Casual spring searches of the outer woods took place in 2004–06, however, during detailed bird censuses for other projects, and no dispersed birds were found in any year. This indicated that birds were unlikely to have been missed in the outer woods during an absence of systematic spring searches.

Territorial birds were located with the aid of playback of recorded song, and followed for up to two hours per visit, with particular attention paid to territorial behaviour, and movements were plotted on large-scale maps. Territory maps were generated from the plotted observations as described in Broughton *et al.* (2006). Territory polygons were digitised in ARCGIS and the centroid of the territory was derived.

Step-wise movements for each juvenile between independence and the following spring were measured as the geometric (straight-line) distance between centroids in successive dispersal periods. NDD was determined as the geometric distance between the natal nest-site and the breeding territory centroid.

### Breeding dispersal

Ringed adults were located during the spring period as per first-year birds. Breeding dispersal was measured as the geometric distance between territory centroids of the same individual in two successive years, which included first year birds. A total of 79 breeding dispersal distances were determined for 40 males, with 59 determined for 33 females. Dispersal events for the same individual in different years were considered independent, as mortality of partners and neighbours generated differing opportunities for pairings and territory location in each year. Territory switchers were defined as those birds whose territory centroids did not fall within the territory boundary of the previous year, indicating a significant change in territory location.

### Ranging of adults and juveniles

Systematic trapping at the network of baited sites allowed the ranging distances of adults and juveniles during the non-breeding period to be compared with dispersal distances in order to establish whether natal dispersal was ongoing. If natal dispersal was still underway during this period we predicted that juvenile ranging movements would be greater than those of adults. Ranging distances were calculated for each bird as the maximum distance between the first observation and any subsequent re-sighting at a different location in the same period. Median values of the maximum ranging distance in any non-breeding period for each individual were derived for males and females. Movement values of zero were excluded from analyses in order to limit spatial autocorrelation. Birds were considered to have an equal chance of being detected at all baited sites due to similar effort at each, although each site was only visited on several consecutive days during the non-breeding period. As such, increased ranging by an individual would not be detected once we had left its range, and the number of movements recorded varied between individuals.

We therefore assumed that median movements derived from all individuals of either sex in all non-breeding periods were representative.

In order to investigate movements of juveniles during the non-breeding period in more detail, and more accurately discern the timing of dispersal activity, ranging distances were also calculated for the summer (July–September) and autumn–winter (October–January) stages for males and females of this age group. These ranging distances were compared with those for the full non-breeding period of adults and juveniles.

### Analysis

Measurement of metric dispersal distances (m) may carry little biological meaning in fragmented landscapes, as it takes no account of territory density or areas of inhospitable habitat (Greenwood & Harvey 1982). Thus, dispersal distances were primarily calculated as the number of territory widths, which was defined as 255.2 m by taking the diameter of a circle of the mean territory area during the study period (5.1 ha, se = 0.15, $n$ = 167). Territory widths were only calculated across wooded habitat that was occupied at least once during the study period. Where the straight-line paths between centroids crossed open fields between or within woods, these distances were excluded. Some metric distance results are also presented, however, to enable comparison with other studies.

Owing to non-normal distributions of dispersal distances we used non-parametric methods to compare median values of untransformed data. Kruskal–Wallis tests were used to compare dispersal distances between years, with Mann–Whitney *U*-tests used to compare dispersal distances using sex or search period as groupings. All tests were two-tailed and performed using MINITAB version 15 (Minitab Inc., State College, PA). We assumed that the stability of the breeding population throughout the study period minimised the effect of variation in density on dispersal distances (Nilsson 1989). Annual data were combined in order to improve sample sizes where tests showed no significant differences between years, or where sample sizes were too small to permit tests between three or more years.

Analyses of dispersal distances may be biased by effects of study area and detection probability (Baker *et al.* 1995), and we limited this effect by adopting a large search area. The detection probability for surviving ringed adults appeared to be 100% in consecutive spring periods, with no failures to locate birds during a spring period which were subsequently seen alive. All ringed juveniles located in a spring period had been detected during the preceding non-breeding period. No ringed birds were observed in the extended search area and only one was recorded beyond it. This apparently high detection rate suggested that the methodology was sufficient in determining natal and breeding dispersal distances for extant ringed birds uniformly across the study area, with the search area exceeding effective settling distances. In order to test whether limited search effort in the outer woods prior to 2007 may have biased some results, however, we performed a comparison between 2004–06 and 2007–09 using the largest sample available, this being distances moved between the natal nest-site and the non-breeding period. No significant differences were found (see Endnote a), suggesting that variation in search effort did not influence results.

While the vast majority of ringed birds present during the non-breeding and spring periods were considered to have been detected, the shorter sampling time of the initial period in June resulted in a known degree of incomplete detection. Only 45% of those juveniles that were ringed as nestlings and were present during the non-breeding period were initially detected in June. However, comparison of dispersal distances between the natal nest-site and the non-wintering period for males and females of both groups (those detected in June and those not detected until the non-breeding period) revealed no difference for either sex (see Endnote b). This suggested that the dispersal behaviour of the June sample of birds did not deviate from that of birds first detected in the non-breeding period, with both groups having dispersed similar distances between the natal and wintering site. As such, we did not consider that weighting of dispersal distances was required in order to account for the comparatively low detection in the June initial period. In addition, owing to the demonstrably high detection probability during other periods, we made no attempt to model the probability of detection or survival (which is the focus of ongoing study), being confident that the estimates of median dispersal distances were not biased towards shorter values.

## RESULTS

### NDD

Median values of NDD indicated that females dispersed further than males (Table 1), although this was not statistically significant and sample sizes were insufficient

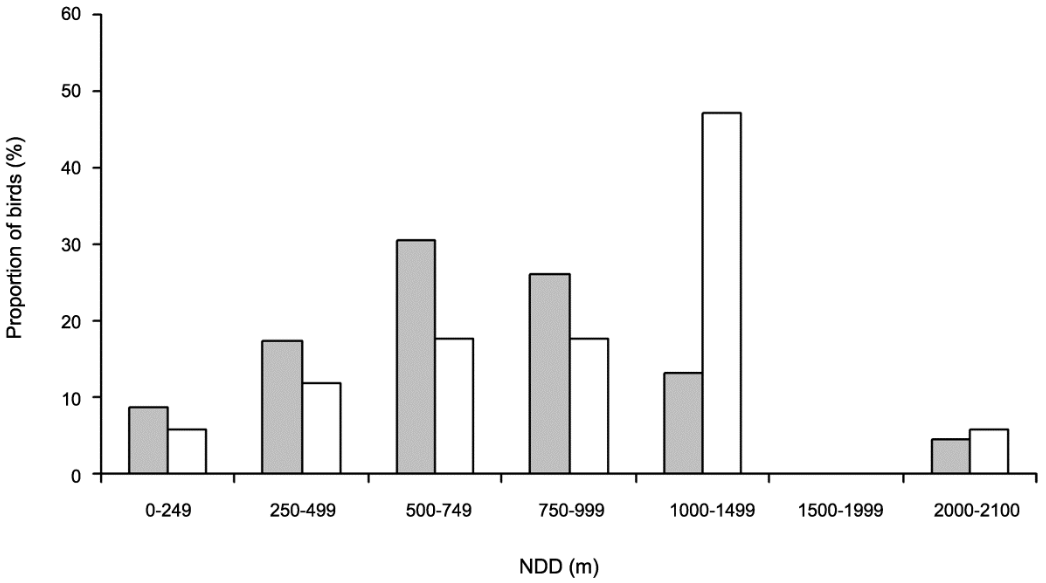

**Figure 2.** Metric natal dispersal distances (NDDs) of juvenile Marsh Tits; $n$ = 23 males (shaded bars) and 18 females (open bars). Median values, males = 704.47 m; females = 1065.00 m.

to test for differences between years. More than half (67.6%) of males and 47.1% of females settled less than three territory widths from their natal site, with 8.7% of males and 5.9% of females moving less than one territory width. The longest metric NDD was 2071.7 m for females and 2007.6 m for males, with substantially more females than males dispersing further than 1 km (Fig. 2).

Of the 411 nestlings that fledged, 30.3% were later re-sighted in the study area, but only 9.8% settled to enter the local breeding population (56.1% being male). Of these, 24.4% settled in a different habitat patch from their natal wood (33.3% of females, 17.4% of males), although only two birds (4.9%) dispersed to the more distant outer woods. As more females than males settled outside of their natal woods, travelling greater geometric distances in order to reach a neighbouring habitat patch, this would have contributed to female NDD peaking at 1000–1499 m (Fig. 2).

### Initial period

The median distance achieved by females during the initial period of dispersal (natal nest-site to initial period) was greater than that of males (Table 1), although the difference was only half a territory width and was not statistically significant. There was no difference in median dispersal distances between those years with sufficient sample sizes (Appendix 1). In terms of metric distances, males dispersed up to 1228.2

**Table 1.** Comparison of median dispersal distances between male and female Marsh Tits, expressed as the number of territory widths traversed during each dispersal period.

| Dispersal period | Male ($n$) | Range | Female ($n$) | Range | $U$ | $P$ |
|---|---|---|---|---|---|---|
| Breeding dispersal | 0.23 (79) | 0.00–4.76 | 0.21 (59) | 0.00–1.45 | 5574.5 | 0.719 |
| Natal dispersal | 2.63 (23) | 0.75–5.15 | 3.06 (18) | 0.95–4.88 | 447.5 | 0.358 |
| Natal nest-site to initial period | 2.28 (35) | 0.55–4.40 | 2.61 (25) | 0.84–4.99 | 981.5 | 0.200 |
| Initial period to non-breeding period | 0.75 (30) | 0.06–3.91 | 0.47 (22) | 0.00–1.27 | 923.5 | 0.018 |
| Non-breeding period to spring period | 0.55 (43) | 0.11–4.36 | 0.56 (38) | 0.03–4.25 | 1723.5 | 0.712 |
| Natal nest-site to non-breeding period | 2.06 (65) | 0.63–7.23 | 2.74 (46) | 0.43–7.09 | 3244.0 | 0.018 |

Initial period, June; non-breeding period, July–January; spring period, February–May; comparisons made using Mann–Whitney $U$-tests.

m and females 1534.7 m (median = 585.2 m for males, 746.2 m for females).

### Non-breeding period

Median distances moved between the initial and non-breeding period were less than one territory width for males and females (Table 1), suggesting little further dispersal since the initial period. There was insufficient data to test for an effect of year for either sex. Distances were significantly greater for males than for females (Table 1), however, and analysis of ranging within the non-breeding period indicated that this was related to greater movements of males during the autumn–winter stage (Table 2). While the maximum movements during summer were similar for both sexes, and differed little from those of adults of the same sex throughout the non-breeding period, juvenile males made larger maximum movements than other birds during autumn–winter. This difference approached statistical significance when compared with juvenile females (Table 2), and was statistically significant when compared with adults of either sex (Appendix 2). One male undertook a movement of 10.5 km during this time, being reported by a member of the public, and was the only bird recorded outside of the study area. Of the 7.7% of juveniles that ranged across distances greater than 750 m (approximately three territory widths) during a non-breeding period, the majority (69.2%) were male.

Females moved further than males between the natal nest-site and the non-breeding period (Table 1) but, while significant, the difference was less than one territory width. There was no effect of year on this measure for either sex (Appendix 1).

### Spring period

There was no significant difference in the median number of territory widths moved between the non-breeding and spring periods for juveniles ringed as nestlings (22 males, 14 females) when compared with those first caught during the non-breeding period (21 males, 24 females) (males: $U$ = 479.0, $P$ = 0.497; females: $U$ = 474.0, $P$ = 0.874). Combining the samples showed the median number of territory widths moved between the non-breeding and spring periods to be just over one half for each sex (Table 1). This was less than winter ranging distances (Table 2), indicating limited movement by the population prior to spring. There was no significant effect of year for either sex (Appendix 1).

Some individuals undertook significant movements between the non-breeding and spring periods, however, with 7.0% of males and 5.3% of females traversing at least three territory widths during this time, but only 3.7% of birds moving further than 1 km. These birds included unpaired individuals and apparent winter floaters, all of which moved to a vacant territory (most containing an unpaired bird).

### Timing of juvenile dispersal

Comparison of median movement distances of juveniles between the three consecutive dispersal periods (initial, non-breeding and spring; Table 1) revealed significant differences for both sexes (males: $H$ = 32.66, df = 2, $P$ < 0.001; females: $H$ = 39.63, df = 2, $P$ < 0.001). Post-hoc analysis using pair-wise comparisons indicated that movement between the natal nest-site and the initial period was significantly greater than that between other periods, for both sexes (Appendix 3). In addition, comparison of median NDD with movements between the natal nest-site and initial period showed no significant difference for either sex (Appendix 3), indicating that the initial period of dispersal was similar to NDD.

Median dispersal distances (territory widths) between the natal nest-site and the initial and non-breeding periods were expressed as proportions of median NDD

**Table 2.** Comparison between median distances of maximum ranging, expressed as territory widths, for male and female Marsh Tits using Mann–Whitney *U*-tests.

| | Male (*n*) | Range | Female (*n*) | Range | *U* | *P* |
|---|---|---|---|---|---|---|
| Juveniles | | | | | | |
| Summer | 0.94 (62) | 0.04–3.77 | 0.94 (41) | 0.04–2.92 | 3308.5 | 0.571 |
| Autumn–winter | 1.39 (67) | 0.32–3.60 | 1.10 (54) | 0.04–5.51 | 4445.5 | 0.062 |
| Non-breeding | 1.27 (113) | 0.04–4.82 | 1.06 (86) | 0.04–6.00 | 12193.5 | 0.304 |
| Adults | | | | | | |
| Non-breeding | 1.03 (31) | 0.04–3.15 | 0.93 (24) | 0.06–3.04 | 889.5 | 0.722 |

Comparisons are made for the non-breeding period (July–January) and, for juveniles, the comprising stages of summer (July–September) and autumn–winter (October–January).

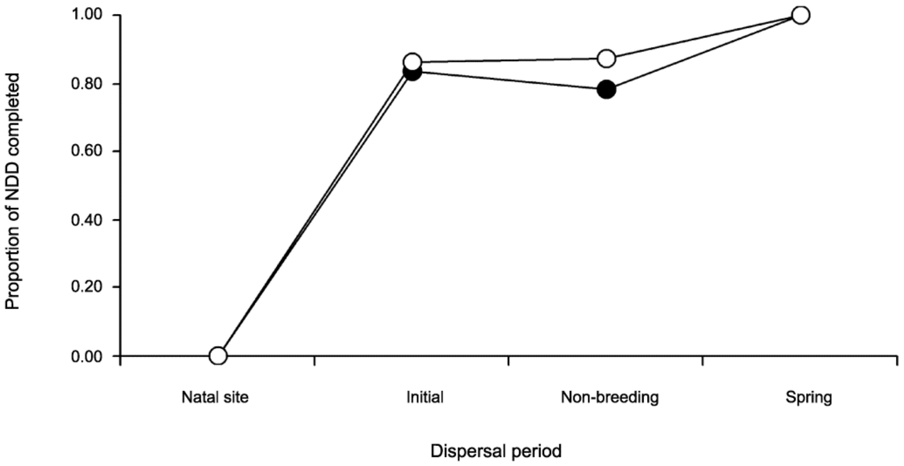

**Figure 3.** Completion of natal dispersal distance (NDD) between each dispersal period, as a proportion of total NDD, for male (closed circles) and female (open circles) Marsh Tits. Dispersal distances calculated as the number of mean territory widths (255.2 m) traversed through occupied habitat.

(Fig. 3). This allowed the relative contribution of each dispersal period to NDD to be identified for each sex, indicating that females completed 86.3% and males 83.6% of NDD during the initial period of dispersal. Little or no progress was made between the initial and non-breeding periods, with the remaining small fraction of NDD being completed between the non-breeding and spring periods.

The observed immigration of new birds into Monks Wood during the late winter and spring in 2004–08 revealed only one arrival prior to February (Fig. 4). The majority of birds arrived during March and April, comprising 2.3–22.2% of the breeding population in the wood each year. Immigrants were composed of juveniles (61.5%) and adults (15.4%), with 23.1% being un-aged, and the majority (69%) being female.

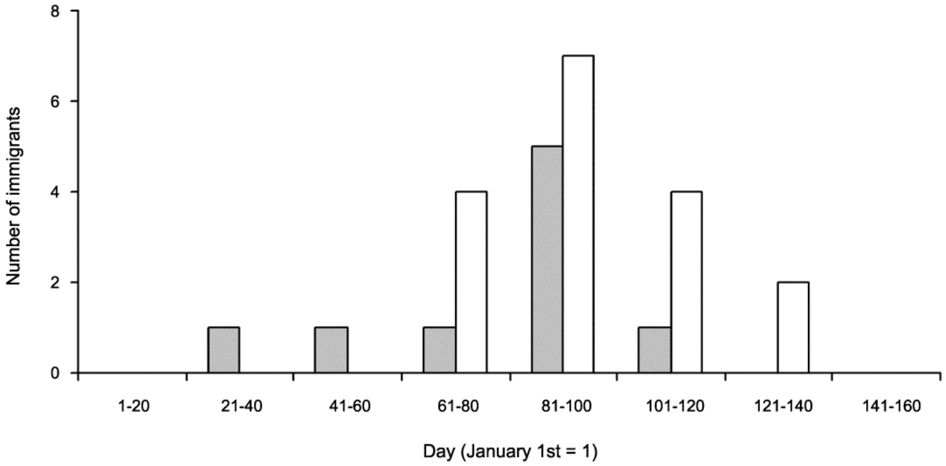

**Figure 4.** Timing of arrival of male (shaded bars) and female (open bars) immigrant Marsh Tits dispersing into Monks Wood during and late winter and spring in 2004–08. Data for adults and juveniles are combined.

Males arrived in a more concentrated period than females. The origin of six immigrants (23.1%) was known as ringed birds from the neighbouring inner woods, being composed of previously unpaired birds or those whose putative or known mate had disappeared.

## Breeding dispersal

Breeding dispersal distance, measured as the median number of territory widths, was short for both males and females (Table 1), with no effect of year (Appendix 1). Only 5.1% of female and 6.3% of male breeding dispersal events involved distances of more than one mean territory width, indicating that the majority of birds occupied a similar breeding territory in consecutive springs.

The incidence of territory switching was similar for females (17.0% of 59 dispersal events) and males (13.9% of 79 dispersal events), averaging 2.8% and 2.3% of annual movements respectively. More than half of male (54.7%) and female (70.0%) territory switchers relocated to an adjacent territory less than one mean territory-width away. The most commonly detected circumstances of territory switching in both sexes were the disappearance of a neighbour and/or being widowed, and the availability of a mate in the new territory (Table 3). Male territory switchers dispersed up to 1818.9 m between breeding territories, and females 728.1 m (Fig. 5), but only two female switchers (20.0%) and one male (9.1%) successfully switched between different woods. Not all attempts at switching were successful, and two ringed males were observed singing alone across multiple territories over several days in spring after immigrating from a different wood, apparently prospecting for mates. One eventually located a female and bred, while the other returned alone to its original territory. Four female territory

**Table 3.** Circumstances of territory switching between consecutive spring periods for adult Marsh Tits.

| Circumstances of territory switching | Proportion of switching events (%)<br>Male (*n* = 11) | <br>Female (*n* = 10) |
|---|---|---|
| Disappearance of neighbour | 90.91 | 80.00 |
| Disappearance of mate | 45.45 | 70.00 |
| Divorcing mate | 18.18 | 30.00 |
| Availability of mate in new territory | 72.73 | 90.00 |

Categories are not exclusive for each individual.

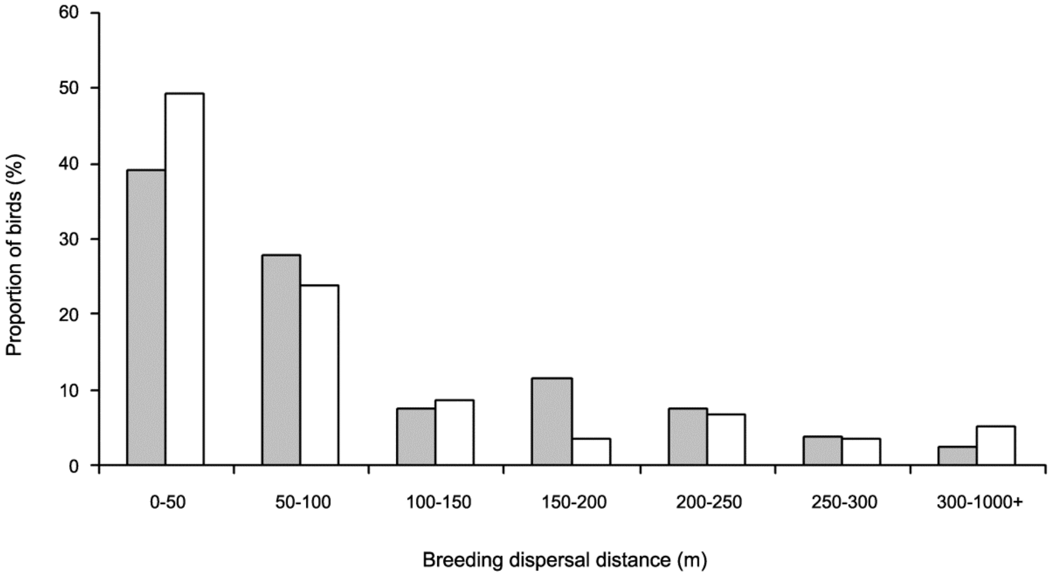

**Figure 5.** Metric breeding dispersal distances of Marsh Tits, between two consecutive spring periods; *n* = 79 movements of 40 males (shaded bars) and 59 movements of 33 females (open bars). Median values, males = 58.56 m; females = 53.11 m.

switchers appeared to divorce their mates and return alone to their original territory in June, immediately after breeding, although the timing of most dispersal events could not be determined with precision.

## DISCUSSION

A high degree of territory fidelity was apparent among adult Marsh Tits, with distances between consecutive territory centroids being shorter than breeding dispersal distances reported for other parids (Harvey *et al.* 1979, Virkkala 1990, Orell *et al.* 1999, Andreu & Barba 2006, Valcu & Kempenaers 2008). Amann (2003) obtained similar results for Marsh Tits in Switzerland, with a comparable mean proportion of adults switching territories between years (2–3%). All territory switches recorded by Amann (2003) occurred during spring, and spring immigration into Monks Wood involved some adults undertaking breeding dispersal. Spring territory switchers appeared to be seeking breeding opportunities, most being unpaired or widowed birds that joined another unpaired or recently widowed bird. Some adults relocated up to 1.8 km between different woods in order to achieve this, although unsuccessful attempts at switching suggested that some breeding dispersal was exploratory as well as opportunistic. There was evidence that some breeding dispersal was of an 'out and back' nature, comprising post-breeding movements of divorcing birds returning to previous territories. Such movements have been recorded for Marsh Tits by Morley (1953), and also Eurasian Nuthatches (Matthysen 1998), and suggest complex temporal interactions between the priorities of habitat quality, site fidelity and mate availability (Greenwood & Harvey 1982, Valcu & Kempenaers 2008).

Median values of Marsh Tit NDD were substantially greater than those of breeding dispersal, as is typical of many bird species (Greenwood & Harvey 1982). NDD was similar to or shorter than comparable measures for other parids (Greenwood *et al.* 1979, Weise & Meyer 1979, Robbins *et al.* 1986, van Tienderen & van Noordwijk 1988, Orell *et al.* 1999, Matthysen *et al.* 2005, Van de Casteele & Matthysen 2006) and Eurasian Nuthatch (Matthysen 1998). The only previous work on Marsh Tit NDD found a positive correlation with population density (Nilsson 1989), although dispersal distances were greater and population density was lower than in our study. This implies that other factors, such as landscape composition, may mediate the effect of population density on NDD for this species, as in the Eurasian Nuthatch (Matthysen 1998), although an absence of patch size and connectivity information from other studies made comparisons difficult.

While Marsh Tits in our study achieved less territory-width dispersal during NDD than Great Tits in southern England (Wytham Wood), they moved greater metric distances (Greenwood *et al.* 1979). Marsh Tit territories were 6.4 times larger than those of Great Tits in Wytham Wood, however; the latter offering a greater area of continuous habitat (231 ha) than any patch in our study. This enabled Great Tits to move through a larger area of habitat and encounter many more territories than were available to Marsh Tits. In order to achieve the median territory-width NDD of Wytham Wood Great Tits, therefore, many more Marsh Tits in our study would have had to leave their natal wood and settle in a neighbouring patch. Few birds achieved this, however, as less than a quarter of ringed recruits from all woods became established outside of their natal patch. Furthermore, only 4.9% of recruits settled in the peripheral outer woods, even when territories remained vacant (pers. obs.). A similar steep decline in settling rate between woods has been observed in Great Tits (Verhulst *et al.* 1997). Barrier effects may explain these truncated dispersal distances and low rates of inter-patch settling if birds are unwilling to cross areas of non-habitat (Desrochers & Hannon 1997, Groom & Grubb 2006). One juvenile Marsh Tit was observed, during initial dispersal in June, attempting to cross 416 m of open fields between woodland patches. On three occasions the bird was seen to fly about 100 m over the field before aborting the attempt and returning. It was still in the original patch when observation ended, but was not present several days later.

Nonetheless, evidence suggests that some Marsh Tits do emigrate from natal woods. Using a modelling approach, Alderman *et al.* (in press) found that juveniles dispersing from edge territories in Monks Wood were less likely to settle in the natal wood than those from interior territories. Excluding Monks Wood, which is significantly larger than the other habitat fragments in our study area, only one bird from the inner woods settled in its natal patch in the current study. Thus, low rates of inter-patch settling could also be explained by a higher mortality among birds attempting to disperse out of the natal wood, owing to a lack of resource knowledge in unfamiliar areas, vulnerability to predation or failure to find habitat patches in the landscape (Dale 2001). Barrier effects that delay dispersal (Lens & Dhondt 1994) may accentuate mortality, as arrival on a home-range before congeners is critical for successful establishment in Marsh Tits (Nilsson & Smith 1985, Nilsson 1989, Alderman *et al.* in press). Higher settling success among those birds demonstrating greater philopatry may, therefore, have skewed successful dispersal towards short distances.

Hinsley *et al.* (1996) demonstrated that the probability of Marsh Tit occupation was only about 70% for woods of 10 ha, yet 74% of English woods are smaller than this (Forestry Commission 2001). Consequently, the majority of woodland fragments in England may only support one to two average-sized territories. Our results and those of Nilsson (1989) indicate that few juveniles settle within a territory width of their natal site, requiring emigration from small natal woods and recruits having to come from elsewhere. Even in a relatively large habitat patch such as Monks Wood, a proportion of the breeding population was composed of immigrants, as in Wytham Wood Great Tits (Verhulst *et al.* 1997). Our results suggest that there are spatial constraints on successful inter-patch dispersal, however, and increased habitat fragmentation may result in reduced recruitment of immigrants (Matthysen & Currie 1996, Dale 2001, Fahrig 2007). Woods could then be vulnerable to local extinctions through stochastic events, such as predation. Evidence that widowed adults will leave territories in order to seek breeding opportunities suggests that loss of one bird in a pair may lead to both birds disappearing from a wood, which will accelerate extinction within small fragments as isolation increases. Marsh Tits in highly modified landscapes such as England may, therefore, be particularly vulnerable to local extinctions as a result of the interaction between behavioural ecology and increasing habitat fragmentation (Hinsley *et al.* 2009).

The majority of Marsh Tit natal dispersal was completed within two weeks of independence in June, with little further movement by most birds over the non-breeding period. This was similar to the rapid dispersal of the closely-related Black-capped Chickadee (Weise & Meyer 1979), but contrasted with movements of juvenile Great Tits (Dhondt 1979), which underwent staggered dispersal into the autumn. Unlike Great Tits, juvenile Marsh Tits are highly territorial immediately after dispersal (Amann 1997, Nilsson & Smith 1988) and, in common with other *Poecile* species, cache food during late summer and autumn (Sherry & Hoshooley 2007). This early settling and territoriality may serve as a spacing mechanism that secures abundant food resources in summer, limits intraspecific competition and facilitates caching for long-term exploitation. Further dispersal during winter would result in the loss of this stored resource, although a rapid dispersal phase may limit the ability to find suitable habitat in fragmented landscapes.

Almost 8% of juvenile Marsh Tits ranged over wide distances after initial settling in our study, however, particularly males in winter. Some birds were repeatedly observed using several neighbouring woods, and one commuted over 1 km per day. These individuals appeared to be winter floaters that were unattached to a typical home-range or to conspecifics. Nilsson & Smith (1988) found a similar proportion of floaters among their Marsh Tit population, although Ekman (1979) concluded that almost half of juvenile Willow Tits appeared to be floaters in late summer.

Excluding winter floaters, Nilsson & Smith (1988) found that Swedish Marsh Tits formed stable winter flocks consisting of an adult pair and unrelated juveniles that defended a group home-range, as in the Willow Tit and Black-capped Chickadee (Hogstad 1987, Smith 1992). In contrast, our population appeared to be structured in the manner of Amann's (1997) Swiss Marsh Tits in which most juveniles initially established territories overlapping those of adults, with borders becoming relaxed in late summer and the number of birds in winter flocks being small, yet changeable. Similarly, juveniles in our study showed a high degree of territoriality during the initial period, frequently occurring in pairs and showing heightened aggression to playback of recorded song (pers. obs.). The restricted ranging of most birds indicated that settled home-ranges had been adopted during the non-breeding period, but these appeared to overlap to some extent and not be exclusively defended, as the individuals occurring at given trap sites or observed foraging together was not constant.

The reason for these differences in winter social structure is unknown, but may be sub-specific and related to climate and latitude, with similar differences being noted between Scandinavian and British Willow Tits (Lewis *et al.* 2009). Marsh Tits in all social systems establish exclusive breeding territories from late winter, however (Morley 1953, Nilsson 1989, Amann 2003, Broughton *et al.* 2006). During this period (February in Cambridgeshire) dominant pairs evict juveniles from breeding territories (Morley 1953, Amann 2003), which may exclude them from their winter home-range. This behaviour coincided with the beginning of the spring dispersal period that primarily took place between February and April in our study. Greenwood *et al.* (1979) considered that the most significant movements of natal dispersal in the Great Tit took place during territory establishment in late winter and early spring. While a well-defined period of spring dispersal was detected for Marsh Tits in our study, this was much less important than post-independence dispersal, representing only 13–22% of the population's NDD. Large spring movements by adults and juveniles were observed between territories within the same wood as well as between woods, apparently driven by the seeking of breeding or territorial opportunities by widowed, unpaired or evicted birds (for those of known origin). The origin of many immigrants was unknown, however, and may have been from outside of the study area. Ringed juveniles that disappeared from the area after eviction in February did not return as replacements, suggesting a high mortality or extensive movements among these birds, rather than a cryptic floating population. Immigration may, therefore, be a highly ephemeral phenomenon, with transient birds rapidly moving through an area before settling or dying.

### Conclusions

The results of the present study suggest that the dispersal behaviour of Marsh Tits could contribute to the species' sensitivity to habitat fragmentation. Large territories and a low breeding density may combine with short dispersal periods to limit dispersal distances, reducing settling success as habitat patch size decreases and isolation increases. While the condition of standing woodland in Britain may have improved for Marsh Tits since the 1970s, due to increasing understorey and woodland maturity (Kirby *et al.* 2005, Amar *et al.* 2006, Hinsley *et al.* 2007), the area of mature deciduous woodland fell significantly between 1947 and 1965 (Mason 2007). This period of widespread loss of habitat led, chronologically, into an era of consistent loss of interconnecting hedgerows (Hunting Surveys & Consultants Ltd. 1986) and a steep decline in the Marsh Tit population (Baillie *et al.* 2009). Habitat fragmentation may, therefore, facilitate the decline of Marsh Tit populations on a landscape scale.

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## ENDNOTES

a. Males: $U = 568.0$, $P = 0.193$, $n = 20$ in 2004–06 and 46 in 2007–09; females: $U = 387.0$, $P = 0.424$, $n = 18$ in 2004–06 and 28 in 2007–09.

b. Males: $U = 1312.0$, $P = 0.174$, $n = 30$ detected in June and 35 not detected in June; females: $U = 641.0$, $P = 0.513$, $n = 20$ detected in June and 26 not detected in June

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## APPENDIX 1. EFFECT OF YEAR ON DISPERSAL DISTANCES (MEASURED AS TERRITORY WIDTHS) FOR MALE AND FEMALE MARSH TITS WHERE SUFFICIENT ANNUAL DATA WERE AVAILABLE, USING THE KRUSKALL-WALLIS *H*-TEST STATISTIC

| | *H* | df | *P* |
|---|---|---|---|
| Breeding dispersal | | | |
| Male | 1.34 | 5 | 0.931 |
| Female | 0.57 | 4 | 0.967 |
| Natal nest-site to initial period | | | |
| Male | 0.46 | 2 | 0.796 |
| Female | 0.61 | 2 | 0.739 |
| Non-breeding period to spring period | | | |
| Male | 3.99 | 3 | 0.262 |
| Female | 0.42 | 2 | 0.809 |
| Natal nest-site to non-breeding period | | | |
| Male | 4.79 | 2 | 0.091 |
| Female | 2.83 | 3 | 0.419 |

## APPENDIX 2. COMPARISON OF MEDIAN DISTANCES OF MARSH TIT RANGING MOVEMENTS IN THE NON-BREEDING PERIOD (JULY–JANUARY) AND THE COMPRISING SUMMER (JULY–SEPTEMBER) AND AUTUMN–WINTER (OCTOBER–JANUARY) PERIODS FOR MALES AND FEMALES

| | Juvenile male | | | Juvenile female | | |
|---|---|---|---|---|---|---|
| | Non-breeding | Summer | Autumn–winter | Non-breeding | Summer | Autumn–winter |
| Adult male | 8455.0 | 2849.0 | **3600.5** | 6015.0 | 1405.5 | 2374.0 |
| Adult female | 8089 | 2708 | **3354.0** | 5741.0 | 1320.5 | 2206.0 |

Figures are values of the Mann–Whitney *U*-test statistic; statistical significance of $P < 0.05$ is indicated by bold type.

## APPENDIX 3. COMPARISON OF MEDIAN DISTANCES OF MARSH TIT MOVEMENTS BETWEEN DIFFERENT DISPERSAL PERIODS: INITIAL (JUNE), NON-BREEDING (JULY–JANUARY), SPRING (FEBRUARY–MAY) AND NATAL DISPERSAL DISTANCE (NDD; NATAL NEST-SITE TO SPRING) FOR MALES AND FEMALES

| | Male | | Female | |
|---|---|---|---|---|
| Dispersal period | Natal nest-site to initial | Initial to non-breeding | Natal nest-site to initial | Initial to non-breeding |
| Initial to non-breeding | **1519.0** | NA | **916.0** | NA |
| Non-breeding to spring | **1947.0** | 1226.0 | **1185.0** | 662.0 |
| NDD | 731.0 | – | 414.0 | – |

Figures are values of the Mann–Whitney *U*-test statistic; statistical significance of $P < 0.05$ is indicated by bold type.

# 7 PATTERNS OF DISTRIBUTION CHANGE AND HABITAT COVERAGE

Understanding the processes operating during the Marsh Tit's decline is critical for identifying remedial measures that may enable population recovery. The current chapter attempts to broaden the perspective of study by investigating large-scale patterns of habitat fragmentation and changes in the distribution of the Marsh Tit across England and Wales, using knowledge gained from earlier chapters to inform analyses and interpretation.

The majority of the Marsh Tit population decline occurred between the two national bird atlas surveys of 1968-72 (Sharrock 1976) and 1988-91 (Gibbons et al. 1993) (Baillie et al. 2010), and this period also saw a range contraction of 17% (Gibbons et al. 1993). The two atlas surveys achieved near-complete coverage in Britain at a matching resolution of 10 km, and so can be considered reliable and highly-suited to identifying those areas where Marsh Tits were lost between atlas periods and those where they persisted. The spatial datasets of bird distribution could then be combined with high-resolution habitat data from satellite imagery and field surveys (e.g. Fuller et al. 1994; Forestry Commission 2001) to allow spatial analyses of habitat in areas where Marsh Tit occupation status differed. However, despite indications from Britain and elsewhere that Marsh Tits may be particularly sensitive to habitat fragmentation (Opdam et al. 1985; Nilsson 1989; Hinsley et al. 1996), no studies have yet investigated the relationship between the patterns of Marsh Tit range contraction and the distribution of habitat.

The results from chapters 5 and 6 provided further impetus for such a study, by indicating that the Marsh Tit's short dispersal distances can be further constrained by habitat fragmentation and poor connectivity between woodland, which may inhibit recruitment and reduce breeding opportunities. Fortunately, as a specialist of broadleaved woodland (chapter 3), the Marsh Tit's habitat is easily mapped using remote sensing (Fuller et al. 1994) or classified in the field (Forestry Commission 2001). However, although high-resolution satellite data of woodland distribution was available from the CEH Land Cover Map 1990 (Fuller et al. 1994) that coincided with the second bird atlas, there were no comparable habitat data for the period of the first bird atlas. As such, a full spatio-temporal analysis of the relationship between contemporary changes in both Marsh Tit and woodland distribution was impossible. Instead, regional summary data from woodland inventories (Forestry Commission 2001, 2002) could be used to test for broad relationships between regional changes in Marsh Tit distribution and woodland cover, although this contained a temporal mismatch that could not be fully corrected.

A large variety of metrics have been used to quantify habitat fragmentation (Fahrig 2003), although Cunningham & Johnson (2011) found that for woodland habitat the percentage cover of the landscape was the most simple and parsimonious. Consequently, Paper VI in this chapter (Broughton et al. in review) adopted this method for a spatial analysis of the relationship between the distribution of woodland habitat and that of the Marsh Tit. Analyses were repeated for a further two declining woodland birds for comparison: the Willow Tit and the Lesser Spotted Woodpecker.

This approach was generally successful, with Broughton et al. (in review) finding a strong relationship between woodland cover and changes in the patterns of bird distributions. The percentage of woodland cover was greatest in those areas where each of the three species had persisted between bird atlas periods, was significantly lower in those areas where each species had been lost, and was lowest of all in those areas where each species had never been recorded. This indicated that the ability of less wooded landscapes to support Marsh Tits, Willow Tits or Lesser Spotted Woodpeckers had decreased over time, strongly implying that habitat fragmentation was an increasingly important factor in the persistence of these species. However, analyses of habitat change showed that woodland cover had actually increased in all regions over time (see section 1.3), and this may have had a buffering effect for Marsh Tits, which were less likely to be lost from areas where habitat had increased the most. Broughton et al. (in review) speculates that the mechanism of Marsh Tit decline that was buffered against was reduced connectivity between individual woods, perhaps exacerbated by increased mortality driving a need for more frequent replacement by immigrating recruits. By drawing together several areas of Marsh Tit ecology and novel spatial analyses of national bird atlas and habitat data, Broughton et al. (in review) is potentially a significant development in the understanding of the Marsh Tit’s decline and indicates where further research should be directed. Similarly, the study also provides new insights in the declines of the Willow Tit and Lesser Spotted Woodpecker, species for which information on spatial ecology is currently lacking.

# 7.1 Paper VI: RELATIONSHIPS BETWEEN PATTERNS OF HABITAT COVER AND THE HISTORICAL DISTRIBUTION OF THE MARSH TIT, WILLOW TIT AND LESSER SPOTTED WOODPECKER IN BRITAIN

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This paper is currently in review, having being submitted for a special issue (conference proceedings) of the journal *Ecological Informatics*.

## ABSTRACT

Spatial analysis of remotely-sensed land cover data in conjunction with species distribution atlases can reveal large-scale relationships between animal taxa and their habitats. We investigated the historical distribution patterns of three declining woodland birds, the Marsh Tit (*Poecile palustris*), Willow Tit (*Poecile montana*) and Lesser Spotted Woodpecker (*Dendrocopos minor*), in relation to a parsimonious landscape metric for describing habitat availability in Britain. Bird distributions were derived from two field-based atlas surveys, conducted in 1968-1972 and 1988-1991, and used to classify areas of the landscape for each species as retained, lost or gained between atlas periods, or unoccupied in both. We used remotely-sensed land cover data from 1990 to compare percentage habitat cover between landscape areas classified by bird occupation, and regional summary data from national woodland inventories to investigate changes in habitat cover and bird distributions. Percentage habitat cover was a sufficient landscape metric with which to explain the distribution pattern of all three bird species; habitat cover was greatest in areas where each species was retained between atlas surveys, significantly less in areas from which species were lost, and least in areas that remained unoccupied. Losses in the distribution of the Marsh Tit were less in regions that experienced the greatest increase in habitat cover, but there was no evidence of a relationship for the other two species. Similarity in habitat cover values suggested that information on the spatial ecology of the comparatively well-studied Marsh Tit could be used as a proxy for the data-poor Willow Tit. Significantly greater habitat cover values for the Lesser Spotted Woodpecker supported the assumption that this species occupies large territories in Britain. The results suggested that the habitat cover required to retain each species in the landscape had increased during the 1970s and 1980s, and possible causes are discussed. Further bird atlas and land cover datasets will enable repeat studies of greater detail over a longer timeframe.

## INTRODUCTION

Landscape and habitat information from remote sensing has become a common tool in studies of biodiversity (Nagendra, 2001), with the ability to provide comprehensive coverage of landscape composition and habitat structure at a high spatial resolution (e.g. Hill and Broughton, 2009; Morton et al., 2011). However, comparable information on the range, richness and abundance of target species are rarely available at a similar scale. Birds are an exception in some regions, due to their popularity as study subjects and the relative ease of detecting most species, and Britain is one of the most data-rich regions of the World with regard to spatial information of bird distribution and land cover. Comprehensive ornithological atlases have been produced at intervals of approximately 20 years for the whole of Britain since 1968 at a spatial resolution as fine as 2 km tetrads (Gibbons et al., 1993). In addition, national land cover maps have been generated from remote sensing and ground-truth information approximately every decade since 1990 at a spatial resolution of 25 m or less, employing a minimum mappable unit of as little as 0.5 ha (Morton et al., 2011). Regional or tetrad-based summary data at varying spatial scales are also available from historical agricultural censuses (Siriwardena et al., 2000) and woodland inventories (Forestry Commission, 2003).

Such data have been employed in exploratory studies aimed at defining associations of bird species and habitat types using cluster analysis (Fuller et al., 2005a, 2007), the identification of important areas for conservation based on species richness (Brown et al., 1995), and to identify the broad spatial patterns of change in species distribution (Donald and Greenwood, 2001; Gaston and Blackburn, 2002). Other studies have focussed on individual or small groups of species to test a specific habitat-driven hypothesis (Gibbons et al., 1994; Donald and Evans, 1995). Most targeted studies that have used land cover classifications to test relationships with bird distribution or abundance have focussed on farmland birds (Donald and Evans, 1995; Gates and Donald, 2000, Siriwardena et al. 2000), which have long been a cause of conservation concern in Britain (Newton, 2004). The decline of some woodland bird species has also generated significant interest (Fuller et al., 2005b) and site-based studies have been undertaken for some species of conservation priority (Hinsley et al., 2007; Lewis et al., 2009; Holt et al., 2010). While some of these studies incorporated a spatial element (Charman et al., 2010), targeted large-scale investigations of the relationships between landscape composition and the distribution of declining woodland species remain uncommon (Wilson et al., 2005).

In this study, we aimed to investigate the relationships between the historical distribution patterns of habitat and the Marsh Tit (*Poecile palustris*), Willow Tit (*Poecile montana*) and Lesser Spotted Woodpecker (*Dendrocopos minor*), three woodland bird species that underwent substantial population declines (> 60%) and contractions in range from the 1970s in Britain (Gibbons et al., 1993; Baillie et al., 2010), the causes of which remain unknown (Fuller et al., 2005b). The bird species were chosen for study on the basis of their broadly similar ecologies within the wider group of declining woodland birds, specifically their non-migratory and sedentary behaviour (Cramp, 1985; Cramp and Perrins, 1993). Only the Marsh Tit is well-studied in terms of its habitat preferences and spatial requirements in the highly-fragmented woodlands of Britain, occupying relatively large territories of 4-5 ha and having short dispersal distances (Broughton et al., 2006, 2010, in press; Hinsley et al., 2007; Alderman et al., 2011). In Sweden, the Lesser Spotted Woodpecker occupied breeding territories of 43 ha (Wiktander et al., 2001) and has previously been linked to locally high woodland cover in England (Charman et al., 2010), but there is no detailed information on the landscape ecology of this species in Britain. Similarly, data describing the spatial habitat requirements of the Willow Tit are also lacking.

Habitat configuration can be an important factor in moderating the effect of habitat coverage on woodland birds (Dolman et al., 2007), and a wide variety of metrics have been used to assess its effects (Fahrig, 2003). In a comparative analysis using remote sensing data, however, Cunningham and Johnson (2011) found that percentage cover of woodland habitat was the most parsimonious metric for explaining the occurrence of bird species in the landscape. We followed the findings of Cunningham and Johnson (2011) and used percentage habitat cover to attempt to explain the pattern of historical distribution of the selected bird species, testing the response of each to changes in habitat cover using a combination of spatially explicit and regional summary data. By providing an understanding of the role of habitat cover in earlier patterns of bird distributions, the results may provide insights into the causes of local extinctions (Radford et al., 2005). Furthermore, by comparing responses to habitat cover of the relatively well-studied Marsh Tit and the two lesser-known species, inferences might be made regarding the spatial ecology of the latter. Finally, the ability to describe habitat using a single landscape metric, and generate ecologically meaningful results, would support the use of percentage habitat cover as an efficient and accessible metric for investigating spatial habitat and bird distribution data (Cunningham and Johnson, 2011).

## MATERIAL AND METHODS

### Bird distribution data

Spatial data describing the historical distributions of Marsh Tit, Willow Tit and Lesser Spotted Woodpecker in Britain were available at 10 km cell resolution from two national bird atlas surveys, conducted in 1968-1972 (Sharrock, 1976) and 1988-1991 (Gibbons et al., 1993). The bird atlases were derived from field surveys during the breeding seasons (April-July) within each 10 km grid square of the British National Grid (BNG), a scale that was sufficient to encompass multiple bird territories if appropriate habitat was present. We used the minimum level of breeding evidence available from each atlas to describe bird distribution (detection of presence in a 10 km square) to generate a binary variable of presence or absence for each atlas period. Confirmation of breeding for these three species can be difficult to obtain yet they are all territorial and highly sedentary (Cramp, 1985; Cramp and Perrins, 1993), so presence during the breeding season is strongly indicative of residence. Comparison between the two bird atlases therefore allowed the mapping of distribution change and persistence for each species by allocating each 10 km square to one of four occupation classifications for each species, these categories containing squares that were retained, lost or gained between the two atlas periods, or remained unoccupied in both. Although the two atlases employed differing methodologies, they are considered to be sufficiently comparable in this way (Greenwood et al., 1997).

### Woodland habitat data

National-scale habitat data that were approximately contemporaneous with the second bird atlas (1988-1991) were available from the Land Cover Map of Great Britain 1990 (LCMGB), a raster dataset containing 25 land cover-type classifications at a 25 m cell resolution, produced using supervised maximum likelihood classifications of Landsat Thematic Mapper data (Fuller et al., 1994). The LCMGB combined summer and winter data to achieve an overall accuracy of 80-85% when referenced to ground-truth data, and had a minimum mappable unit of < 1 ha (Fuller et al., 1994). The Marsh Tit is predominantly associated with deciduous woodland (Hinsley et al., 2007), and this habitat was represented in the LCMGB by the single classification of ‘deciduous broadleaved and mixed woodlands’ (class 15). The Willow Tit and Lesser Spotted Woodpecker also occur in this habitat, but are further associated with more open wooded environments such as scrub, carr or orchards (Cramp, 1985; Cramp and Perrins, 1993). This additional habitat was represented in LCMGB by the classification of ‘deciduous scrub and orchards’ (class 14), which was combined with class 15 to characterise habitat for these two bird species. LCMGB class 14 was relatively insignificant at a national scale, however, representing just 5% of the combined habitat area with class 15.

Spatial data for woodland habitat coverage that was contemporaneous with the first bird atlas period (1968-1972) were unavailable, preventing a parallel comparison of changes in bird and habitat distributions over a similar time period. However, summary data for changes in woodland habitat cover that partially overlapped the timeframe between bird atlases were available from two national woodland inventories, from 1979-1982 and 1994-2000 (Forestry Commission, 2003) (hereafter ‘the woodland surveys’). Although the woodland surveys used different methodologies, comparative figures were available that quantified the change in coverage of broadleaved woodland and scrub habitat between them, including all patches greater than 0.25 ha in extent (Forestry Commission, 2003). It was further possible to exclude woodland from the 1994-2000 survey that was planted after 1990 where this was classified as ‘High Forest Category 1’ (stands that were or had the potential to attain a size and quality suitable for sawlog production). This enabled a partial correction in the temporal mismatch between the period of the second woodland survey and second bird atlas, providing approximate data for assessing relative change in habitat coverage over a coincidental period of 1979-1990. Although further changes in woodland coverage are likely to have occurred in the non-coincidental time periods, more accurate data were unavailable. The single habitat classification (broadleaved woodland and scrub) was therefore used for all three bird species.

### Regionalisation of data

In order to generate a sample for statistical analyses, we divided Britain into the composite geopolitical regions of Wales, Scotland (excluding the Western Isles and Northern Isles) and eight administrative English Regions (with Greater London subsumed within the Southeast Region) (Fig. 1). The classified 10 km squares of bird distributions that fell wholly, predominantly (in the case of squares on regional boundaries) or partially (in the case of coastal squares) within each geographical region were extracted in an ArcGIS 9.3.1 environment (ESRI 2009, Redlands, CA, USA) for each of the three bird species. The total landscape area within 10 km squares of the same classification in each region was derived, with areas of sea in coastal squares being excluded. The sampling unit for analyses was therefore the aggregated landscape area of each bird occupation classification within each region, and not individual 10 km squares. Summary data of habitat coverage as classified in the woodland surveys were available for the same regions as the bird atlas data.

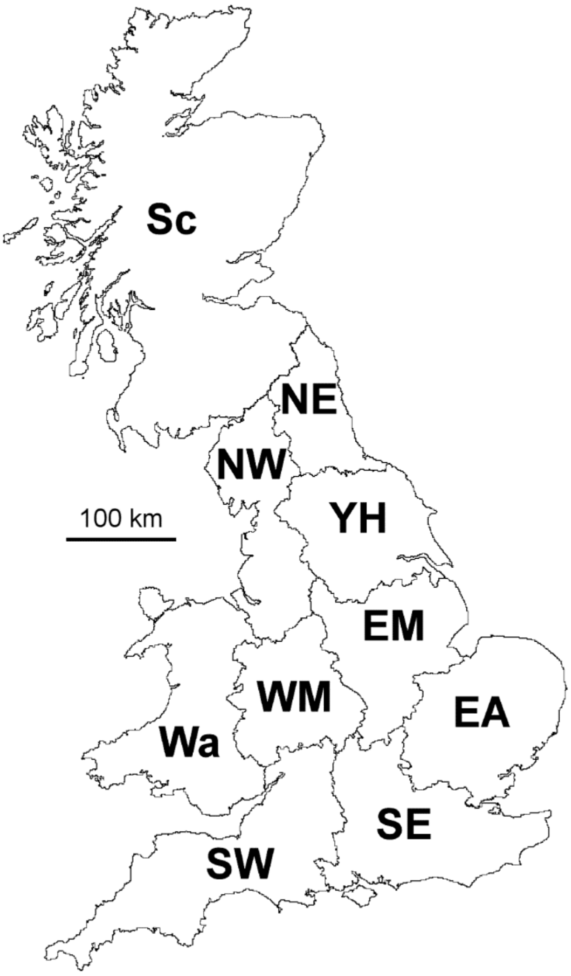

Figure 1. Regions of Britain used in the summary and analyses of habitat and bird atlas data:
Sc = Scotland (excluding the Western Isles and Northern Isles);
NE = Northeast England;
NW = Northwest England;
YH = Yorkshire and the Humber;
EM = East Midlands;
WM = West Midlands;
Wa = Wales;
EA = Eastern England;
SE = Southeast England (incorporating Greater London);
SW = Southwest England.

**Analyses**

For each regional landscape area classified by occupation type for each bird species, we determined the percentage cover of habitat derived from the LCMGB. To limit bias from small sample areas, regions were excluded from analyses if the landscape classified by bird occupation was composed of less than an arbitrary five 10 km squares and if these were less than 5% of the total number of squares present in a region, as relatively minor variation could be related to stochastic effects (Hinsley et al., 2006). Percentage habitat cover for each pair of the four occupation classifications (retained, lost, gained, unoccupied) were compared within each bird species by testing for pair-wise differences in the median values for the regions, where a minimum of six regions in each occupation classification were available for analysis using a two-tailed Wilcoxon signed-rank test. Habitat cover values for the Lesser Spotted Woodpecker and Willow Tit were compared with the Marsh Tit by performing similar tests between the corresponding occupation classifications for each species.

While spatial autocorrelation was presumed to be inherent within the data, we attempted to minimise negative effects by the aggregation of dispersed and coarse resolution 10 km squares within the regional samples, and by using the simplified analytical approach that made minimum assumptions regarding the structure of the data. Although repeated testing was used in analyses of habitat coverage between occupation classifications and also temporal change, we followed Moran's (2003) recommendations in rejecting use of a Bonferroni-type correction.

We tested for relationships between the change in a species' distribution and the change in percentage habitat cover in a region using a multiple linear regression approach in R version 2.9.1 (The R Foundation for Statistical Computing, 2009). The response variable of change in species distribution was generated by taking the natural logarithm of the product of the number of the 10 km squares in a region that were occupied in the second bird atlas divided by the number of squares that were occupied in the first atlas, i.e. the proportional change in distribution between atlases. The two predictor variables used in the models were percentage change in habitat cover between the two woodland surveys (as a percentage of a region's total area), and the percentage habitat cover for each region from the second woodland survey (partially corrected to 1990). We included both habitat predictor variables (coverage and change), plus an interaction term, in a saturated model and used backward elimination to determine the effect of each term to reach a minimum adequate model containing only statistically significant parameters. In particular, we wished to examine whether any relationship between change in bird distribution and change in habitat cover was influenced by the existing habitat cover of the region.

## RESULTS

### Comparisons of bird distribution and habitat coverage

For the Marsh Tit, the median percentage cover of woodland habitat in the areas of regions that were retained between atlases (Table 1) was significantly greater than habitat cover in those areas that were lost or remained unoccupied (Table 2).

| Region | Retained | Lost | Gained | Unoccupied | Region total | Change in MT distribution (%) |
|---|---|---|---|---|---|---|
| EA | $3.6^{160}$ | $1.8^{32}$ | $3.9^{3}$ | $0.7^{19}$ | $1.6^{214}$ | -15.1 |
| EM | $5.8^{74}$ | $3.8^{43}$ | $2.6^{6}$ | $2.7^{35}$ | $2.5^{158}$ | -31.6 |
| NE | $2.9^{41}$ | $2.0^{26}$ | $2.4^{4}$ | $0.9^{25}$ | $1.2^{96}$ | -32.8 |
| NW | $5.8^{45}$ | $3.5^{30}$ | $3.7^{14}$ | $3.1^{73}$ | $2.5^{162}$ | -21.3 |
| SE | $11.7^{180}$ | $5.5^{30}$ | $7.9^{3}$ | $2.6^{12}$ | $5.3^{225}$ | -12.9 |
| SW | $8.1^{236}$ | $6.2^{31}$ | $4.2^{2}$ | $2.1^{16}$ | $3.9^{285}$ | -10.9 |
| Wa | $12.7^{130}$ | $11.8^{43}$ | $15.4^{20}$ | $9.4^{61}$ | $6.4^{254}$ | -13.3 |
| WM | $5.7^{116}$ | $4.3^{11}$ | $5.6^{3}$ | $\underline{1.0^{2}}$ | $2.8^{132}$ | -6.3 |
| YH | $4.5^{67}$ | $4.8^{55}$ | $4.2^{12}$ | $3.8^{34}$ | $2.4^{168}$ | -35.3 |
| Sc | $\underline{2.3^{7}}$ | $\underline{2.4^{9}}$ | $\underline{2.4^{10}}$ | $\underline{2.4^{871}}$ | $2.6^{897}$ | 6.3 |
| Median[a] | 5.8 | 4.3 | 4.2 | 2.7 | 2.6 | -14.2 |

[a] Median values exclude regions with small sample areas (underlined).

Table 1. Percentage change in Marsh Tit (MT) distribution by region between the 1968-1972 and 1988-1991 bird atlases, and median values of percentage habitat cover in areas classified by Marsh Tit occupation as retained, lost or gained between atlases, or remaining unoccupied in both. Superscript values refer to the number of 10 km bird atlas squares in each classification. Regions: Sc = Scotland (excluding the Western Isles and Northern Isles); NE = Northeast England; NW = Northwest England; YH = Yorkshire and the Humber; EM = East Midlands; WM = West Midlands; Wa = Wales; EA = Eastern England; SE = Southeast England (incorporating Greater London); SW = Southwest England.

Samples were too small to test areas that were gained between atlases. A similar pattern was observed for the Willow Tit (Table 3) and Lesser Spotted Woodpecker (Table 4), with the median value of percentage habitat cover being greatest for areas of the regions where occupation was retained between atlases (Table 2). Habitat cover was significantly less in areas where the species were lost, but least cover was present in areas which remained unoccupied. Areas where Willow Tits were gained between atlases had a habitat cover that was significantly greater than areas that were lost or unoccupied, but not significantly different from areas that were retained. For the Lesser Spotted Woodpecker, areas which were gained were not distinct from any other categorisation (Table 2). There was no difference between the Marsh Tit and Willow Tit in the percentage habitat cover of corresponding occupation categories (Table 5), but those of the Lesser Spotted Woodpecker were significantly greater than those of the Marsh Tit (Tables 1, 4 and 5).

| | Retained | Lost | Gained |
|---|---|---|---|
| | *W* (*P*) | *W* (*P*) | *W* (*P*) |
| Marsh Tit | | | |
| Lost (*n* = 9) | 44.0 (0.01) | - | - |
| Gained | - | - | - |
| Unoccupied (*n* = 8) | 36.0 (0.01) | 36.0 (0.01) | - |
| Willow Tit | | | |
| Lost (*n* = 10) | 51.0 (0.02) | - | - |
| Gained (*n* = 10) | 24.0 (0.76) | 3.0 (0.01) | - |
| Unoccupied (*n* = 9) | 45.0 (0.01) | 45.0 (0.01) | 45.0 (0.01) |
| Lesser Spotted Woodpecker | | | |
| Lost (*n* = 8) | 38.0 (0.04) | - | - |
| Gained (*n* = 8) | 24.0 (0.44) | 15.0 (0.73) | - |
| Unoccupied (*n* = 8) | 33.0 (0.04) | 33.0 (0.04) | 32.0 (0.06) |

Table 2. Results of pair-wise Wilcoxon signed rank (*W*) tests of median percentage habitat cover between areas of each region classified by bird occupation as retained, lost or gained between two bird atlases surveys, or remaining unoccupied in both. Sample size was insufficient to perform the test with gained occupation for the Marsh Tit.

### Changes in bird distribution and habitat coverage

In examination of the effect of habitat cover change on the proportional change in Marsh Tit distribution within regions, all regions showed an increase in percentage habitat cover of between 0.4% and 2.4%. Backward elimination of terms in the multiple regression analyses indicated that there was no significant interaction between the change in habitat cover and the remaining cover in a region ($F_{5,6}$ = 2.56, $P$ = 0.17). The minimum adequate model depicted a significant effect on Marsh Tit distribution change of habitat cover change only: log(proportion distribution change) = 0.17 percentage change in habitat cover + -0.45; this explained 57% of the variance ($F_{1,7}$ = 10.37, $P$ = 0.02). Although all regions experienced a proportional decline in Marsh Tit distribution between the two atlases (Table 1), the model indicated that a greater increase of habitat during this period was associated with a lower loss of Marsh Tit distribution. No significant relationships or habitat effects were found in models examining the distribution changes of Lesser Spotted Woodpecker or Willow Tit (results not shown).

| Region | Retained | Lost | Gained | Unoccupied | Region total | Change in WT distribution (%) |
|---|---|---|---|---|---|---|
| EA | $4.5^{126}$ | $2.6^{51}$ | $3.4^{13}$ | $1.2^{24}$ | $1.6^{214}$ | -21.5 |
| EM | $5.6^{114}$ | $2.8^{22}$ | $3.5^{11}$ | $0.1^{11}$ | $2.5^{158}$ | -8.1 |
| NE | $3.1^{33}$ | $2.8^{18}$ | $2.0^{15}$ | $1.2^{30}$ | $1.2^{96}$ | -5.9 |
| NW | $5.0^{46}$ | $4.7^{29}$ | $5.7^{8}$ | $3.7^{79}$ | $2.5^{162}$ | -28.0 |
| SE | $12.6^{164}$ | $10.1^{24}$ | $13.2^{13}$ | $4.3^{24}$ | $5.3^{225}$ | -5.9 |
| SW | $10.2^{85}$ | $9.1^{50}$ | $11.1^{46}$ | $6.7^{104}$ | $3.9^{285}$ | -3.0 |
| Wa | $13.7^{119}$ | $12.6^{33}$ | $13.9^{40}$ | $10.7^{62}$ | $6.4^{254}$ | 4.6 |
| WM | $6.1^{110}$ | $6.8^{7}$ | $7.2^{13}$ | $\underline{9.5^{2}}$ | $2.8^{132}$ | 5.1 |
| YH | $5.0^{85}$ | $4.5^{31}$ | $6.5^{15}$ | $4.0^{37}$ | $2.4^{168}$ | -13.8 |
| Sc | $3.8^{29}$ | $2.8^{40}$ | $3.7^{16}$ | $2.6^{812}$ | $2.6^{897}$ | -34.8 |
| Median[a] | 5.3 | 4.6 | 6.1 | 3.7 | 2.6 | -21.5 |

[a] Median values exclude regions with small sample areas (underlined).

Table 3. Percentage change in Willow Tit (WT) distribution by region between the 1968-1972 and 1988-1991 bird atlases, and median values of percentage habitat cover in areas classified by Willow Tit occupation as retained, lost or gained between atlases, or remaining unoccupied in both. Superscript values refer to the number of 10 km bird atlas squares in each classification. Regions as for Table 1.

## DISCUSSION

The methodology was successful in identifying significant relationships between percentage habitat cover and the pattern of bird distribution for all three species. Those areas of the regions that retained each species between atlas periods had significantly greater habitat cover than those areas from which the species were lost or which were never occupied. There was little evidence of a relationship between the change in bird distribution and the measured change in woodland habitat cover, except for the Marsh Tit where losses in distribution were less in regions that showed the greatest increase in habitat coverage. This suggested a partial buffering effect of increasing habitat on the factors generating the decline in distribution.

| Region | Retained | Lost | Gained | Unoccupied | Region total | Change in LSW distribution (%) |
|---|---|---|---|---|---|---|
| EA | $4.2^{135}$ | $3.5^{36}$ | $2.6^{19}$ | $1.6^{24}$ | $1.6^{214}$ | -9.9 |
| EM | $6.9^{36}$ | $5.6^{25}$ | $5.4^{27}$ | $3.6^{70}$ | $2.5^{158}$ | 3.3 |
| NE | $\underline{0.0^{0}}$ | $\underline{6.2^{2}}$ | $\underline{3.2^{8}}$ | $\underline{2.0^{86}}$ | $1.2^{96}$ | 300.0 |
| NW | $5.4^{38}$ | $6.1^{21}$ | $5.8^{8}$ | $3.3^{95}$ | $2.5^{162}$ | -22.0 |
| SE | $13.0^{150}$ | $8.8^{28}$ | $9.1^{22}$ | $6.8^{25}$ | $5.3^{225}$ | -3.4 |
| SW | $10.4^{83}$ | $8.7^{97}$ | $13.7^{16}$ | $7.8^{89}$ | $3.9^{285}$ | -45.0 |
| Wa | $15.0^{57}$ | $13.6^{43}$ | $14.9^{37}$ | $11.4^{117}$ | $6.4^{254}$ | -6.0 |
| WM | $6.1^{76}$ | $6.6^{20}$ | $6.3^{25}$ | $8.4^{11}$ | $2.8^{132}$ | 5.2 |
| YH | $6.2^{24}$ | $5.2^{16}$ | $5.3^{28}$ | $4.3^{100}$ | $2.4^{168}$ | 30.0 |
| Sc | $\underline{0.0^{0}}$ | $\underline{0.0^{0}}$ | $\underline{0.0^{0}}$ | $\underline{0.0^{0}}$ | $2.6^{897}$ | 0.0 |
| Median[a] | 6.6 | 6.4 | 6.1 | 5.5 | 2.6 | -1.7 |

[a] Median values exclude regions with small sample areas (underlined).

Table 4. Percentage change in Lesser Spotted Woodpecker (LSW) distribution by region between the 1968-1972 and 1988-1991 bird atlases, and median values of percentage habitat cover in areas classified by Lesser Spotted Woodpecker occupation as retained, lost or gained between atlases, or remaining unoccupied in both. Superscript values refer to the number of 10 km bird atlas squares in each classification. Regions as for Table 1.

| | Retained | Lost | Unoccupied |
|---|---|---|---|
| | $W$ ($P$)$^{n}$ | $W$ ($P$)$^{n}$ | $W$ ($P$)$^{n}$ |
| Willow Tit | 7.0 (0.08)$^{9}$ | 6.0 (0.06)$^{9}$ | 7.0 (0.14)$^{8}$ |
| Lesser Spotted Woodpecker | 35.0 (0.02)$^{8}$ | 36.0 (0.01)$^{8}$ | 36.0 (0.01)$^{8}$ |

Table 5. Comparisons of Willow Tit and Lesser Spotted Woodpecker with Marsh Tit, using pair-wise Wilcoxon signed rank (*W*) tests of median percentage habitat cover in areas of regions classified by bird occupation as retained or lost between two bird atlases surveys, or remaining unoccupied in both.

While significant relationships were detected in our analyses, interpretation required consideration of the data limitations. The temporal mismatch between the bird atlas and woodland survey data may partly explain the lack of significant results for Willow Tit and Lesser Spotted Woodpecker in the habitat change analyses. Differing methodologies used to produce the two bird atlases also led to variation in the intensity of survey coverage (Greenwood et al., 1997), an effect that could be more acute for species that can be difficult to detect (such as the Lesser Spotted

Woodpecker). Placing the greatest emphasis on comparisons between areas that had recorded the same occupation status in both bird atlases (i.e. present in both, or absent in both) could minimise potential effects, as these categories may be assumed to be the most reliable observations due to the repeated result.

There is, however, strong support for apparent shifts in bird distribution being treated as genuine, as the net reduction of distribution in most regions for each species is corroborated by substantial and widespread declines in populations recorded from other surveys (Baillie et al., 2010). The significant relationship between bird abundance and spatial distribution (Lawton, 1993) reinforces the conclusion that observed losses in distribution were not an artefact of the survey methods. Furthermore, while some differences in median habitat cover between occupation classifications may have been within the uncertainty terms of the data, the differences between the retained, lost and unoccupied classes were statistically significant for all species. In addition, the pattern of habitat cover and occupation was the same for all species, with median cover in those areas from which a species was lost being intermediate between those from which the species was retained and which remained unoccupied. This indicated a genuine ecological signal in the observed patterns, and not artefacts resulting from inaccurate categorisation or poor data precision.

The results also supported previous work on these bird species, and provided some novel insights. The large territories and short dispersal distances of the Marsh Tit (Broughton et al., 2006, 2010) are consistent with a requirement for well-wooded landscapes, and a strong connection between habitat cover and landscape occupation was apparent in the results. Charman et al. (2010) reported a significant relationship between continued persistence of Lesser Spotted Woodpecker in woods in southern England and a higher proportion of woodland within a 3 km radius of each site. Our results reinforced this finding in a wider landscape context, but provided additional information by quantifying the median value of habitat cover associated with occupation within and across regional landscapes. Median habitat cover was greater in all Lesser Spotted Woodpecker occupation categories when compared to corresponding categories of the Marsh Tit, indicating that the former required a greater spatial extent of habitat to maintain occupation. This suggested that the breeding territories of Lesser Spotted Woodpecker were significantly larger than the 4-5 ha recorded for Marsh Tits (Broughton et al., 2006), and perhaps more similar to the mean 43 ha described for the Lesser Spotted Woodpecker in Sweden

(Wiktander et al., 2001). This appears to be the first evidence of the spatial habitat requirements of the Lesser Spotted Woodpecker on a landscape scale in Britain, and provides some support for the assumption that the large territories recorded in Sweden can be used to contextualise British studies of the species (Charman et al., 2010).

Data on the spatial ecology of the Willow Tit in Britain is also lacking, and there is limited information on habitat preferences (Lewis et al., 2007, 2009). Our study is the first national-scale spatial analysis of the relationship between the distribution pattern of the Willow Tit and cover of its perceived habitat. Willow Tits, like Lesser Spotted Woodpeckers, were retained in areas with a relatively high cover of woodland and scrub habitat, but the median values of habitat cover in the occupation categories did not differ significantly from those of the Marsh Tit. This indicated that the spatial requirements and territory extent of Willow Tits, and potentially their dispersal capabilities, were similar to those of the Marsh Tit. In the absence of specific data for the Willow Tit, therefore, this result implies that information on the territory size and dispersal behaviour of the closely-related Marsh Tit may be used as a valid interim proxy. Such information is crucial for the formulation of effective management and conservation of remaining populations of the Willow Tit, which is one of the most rapidly declining species in Britain (Baillie et al., 2010).

The observed relationship between bird distribution and habitat cover in all three species described a contraction in range to areas of greatest habitat cover; all were lost from areas with habitat cover that was intermediate between those where they were retained and those which were never occupied. This suggests an increase in the habitat threshold required to maintain these species in the landscape during the 1970s and 1980s, leading to local extinctions as areas with an intermediate cover became unable to support them. One possible mechanism for this effect is the widespread loss of hedgerows throughout Britain during the period between the two bird atlases (Hunting Surveys and Consultants, 1986). This is consistent with a metapopulation hypothesis of increasing landscape resistance to dispersal and recruitment, resulting in local extinctions of all three species in areas of declining connectivity between relatively sparse habitat cover (Opdam, 1991). Field studies from Britain and The Netherlands support this theory, with Marsh Tit dispersal being less successful between smaller woods and from woodland-edge territories (Broughton et al., 2010; Alderman et al., 2011), and occupation by this species and

Lesser Spotted Woodpecker becoming less likely as isolation of habitat patches increased (Opdam et al., 1985). In order to confirm this effect, a more detailed spatial analysis of habitat configuration and connectivity would be required, using a greater range of landscape metrics than percentage habitat cover alone (Cunningham and Johnson, 2011). The datasets employed in this study were unable to characterise connective linear features for the period concerned, such as riparian tree corridors or hedgerows, which may also form important breeding habitat for the Willow Tit and Lesser Spotted Woodpecker (Cramp, 1985; Cramp and Perrins, 1993). In particular, detailed and spatially explicit data for hedgerow distribution are not available on a national scale.

There is no indication of a decline in productivity of the Marsh Tit and Willow Tit in Britain (Baillie et al., 2010), which undermines an alternative hypothesis of fewer recruits being produced in source areas of high habitat cover to disperse and populate sink areas of lower cover. In addition, a general increase in woodland area (Section 3.2), maturation and understorey in British woods (Amar et al., 2010) would appear to favour Marsh Tits (Hinsley et al., 2007) and perhaps Lesser Spotted Woodpeckers (Charman et al., 2010), although habitat quality is likely to have degraded for Willow Tits (Lewis et al., 2009). There have been no investigations of survival trends for these species, however, despite a substantial increase in the Sparrowhawk, potentially a major predator (Baillie et al., 2010; Broughton et al., 2011). Further information is required on the demographic processes and spatial dynamics of populations, and also the size and composition of Willow Tit and Lesser Spotted Woodpecker territories.

## CONCLUSIONS

The use of percentage habitat cover as a single metric to describe habitat availability in the landscape (Cunningham and Johnson, 2011) was successful in explaining broad patterns of Marsh Tit, Willow Tit and Lesser Spotted Woodpecker distribution. The results identified a unifying trend of all three species being sensitive to differences in percentage habitat cover, with this being most acute for the Lesser Spotted Woodpecker, but only the Marsh Tit showed a relationship with the regional change in habitat cover. This suggested an effect of confounding variables on the decline of these species, such as decreased survival or connectivity between habitat, but the current analyses were insensitive to these factors. In addition to the need for demographic studies in order to fully understand the declines of these species, further detailed analyses of habitat configuration and isolation would be valuable.

The availability of British land cover maps for 2000 (Fuller et al., 2005c) and 2007 (Morton et al., 2011), and a bird atlas in production for 2007-2011 (BTO, 2012), offers comprehensive repeat surveys with which to investigate the relationships between bird species and their habitat. Future studies may also test theories of biogeography or predict responses to climate change (Donald and Fuller, 1998) using the increasingly robust time-series data. These opportunities, however, would be enhanced by detailed information on the spatial ecology and habitat associations of target species in order to populate models with realistic variables, determine the parameters of spatial analyses, and provide an appropriate ecological context in which to interpret the results.

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# 8 DISCUSSION

Carpenter (2008) contained a comprehensive literature review that identified seven potential factors that may have contributed to the substantial decrease in range and abundance of the Marsh Tit in Britain since the 1960s. Of these, Carpenter (2008) considered that a reduction of invertebrate prey and a deleterious impact of climate change were improbable, and also discounted an effect of increased nest predation by citing Siriwardena's (2006) results. Habitat fragmentation and reduced annual survival were considered as possible contributory factors, but Carpenter (2008) did not test these hypotheses. Instead, Carpenter (2008) focussed investigations on woodland habitat and inter-specific competition by studying the habitat associations of Marsh Tits and relationships with potential competitor species. Carpenter (2008) concluded that woodland understorey structure was important for Marsh Tits, and a probable degradation of this feature was likely a major driver of the species' decline. It was speculated that loss of understorey would have led to a direct reduction in habitat quality and also intensification of inter-specific competition, both of which may have reduced annual survival.

The present work contains a large amount of new information on the ecology and behaviour of the Marsh Tit in Britain, which was sufficient to revisit several of the key theories highlighted by Carpenter (2008). Using some novel analytical techniques and detailed datasets, the papers presented within the chapters of this thesis represent a substantial progression of the identification of the likely causes of the decline of the Marsh Tit, and also a development of the methods of investigating habitat selection by woodland birds.

## 8.1 Marsh Tit territories and habitat selection

Chapters 3 and 4 show that Marsh Tits occupy large territories in British woods, ranging in area from 1.5 to 14.1 ha with a mean of 5.6 ha. This is more than double the mean area reported by Southern & Morley (1950) in Oxfordshire, which could be explained by their small sample and/or methodological differences. The purpose of these large territories is unclear, but sedentary pairs may be isolating sufficient resources for exclusive use throughout the year and securing access to cached food items (Dhondt 2007). The effect of this behaviour, however, is to limit Marsh Tits to a naturally low population density in woodlands and to create a requirement for large areas of habitat.

These spatial constraints on Marsh Tit occupation are exacerbated by the specific habitat requirements identified in chapters 3 and 4. Marsh Tits show a clear preference for a mature woodland structure, with a tall canopy of broadleaved trees over a substantial understorey of shrubs and young trees (Broughton et al. 2006, 2012b, 2012b). There is a particular affinity for a near-closed tree canopy in excess of 15 m tall and understorey within the 1-4 m height band (Hinsley et al. 2007; Carpenter et al. 2010; Broughton et al. 2012a). There appears to be no preference for any of several common tree species in territory selection (Broughton et al. 2006, 2012a), while a predominance of Common Ash around nest sites was probably related to tree height (Broughton et al. 2012b). Carpenter et al. (2010) reported a positive relationship between Marsh Tit occupation and shrub species richness, but Hinsley et al. (2007) found no such relationship and Broughton et al. (2006) found no selection for individual shrub species (see also Carpenter 2008). Overall, therefore, the structure of deciduous woodland appears to be the overwhelming factor determining Marsh Tit occupation, although further work to determine the minimum requirements of species richness would be valuable.

Due to a less favourable habitat structure near the woodland edge, a wood of 4.5 ha is required to accommodate a minimum territory of 1.5 ha of high quality habitat for a single pair of Marsh Tits (Broughton et al. 2012a). However, 74% of woods in England and Wales are smaller than 10 ha, and so potentially able to support only two high-quality territories (Forestry Commission 2001, 2002). Nevertheless, the area of broadleaved woodland in England and Wales increased by 16% between 1965 and 2000, and most is now approaching maturity in the absence of active management (Kirby et al. 2005; Hopkins & Kirby 2007). As such, the area of the Marsh Tit’s broad habitat type has increased since the 1960s, which would be expected to create a more benign environment, yet the species declined in abundance by 71% between 1967 and 2009 (Baillie et al. 2010).

## 8.2 The impact of deer and management on Marsh Tit habitat

A reduction in habitat quality within woodlands due to loss or deterioration of the understorey, as speculated by Fuller et al. (2005), Siriwardena (2006) and Carpenter (2008), could explain the paradox of increasing woodland area coinciding with a declining Marsh Tit population. However, the evidence from Amar et al. (2010) and Kirby et al. (2005) now points to the conclusion of habitat deterioration as a significant factor in the Marsh Tit’s decline as being improbable. Regardless of increasing deer populations or reduced woodland management, there is no evidence of a widespread decline in understorey coverage, density, or species richness across the English and Welsh range of the Marsh Tit (section 1.3). Overall, understorey cover has increased in all height bands since the 1980s (Amar et al. 2010) and open areas within woods have become increasingly overgrown (Kirby et al. 2005). On a regional basis, Amar et al. (2010) showed that understorey vegetation in the 2-4 m height band (which is most preferred by Marsh Tits) had increased in most areas and declined in none (Table 1, section 1.3.2). Shrub species richness has also remained stable overall (Amar et al. 2010). While there is strong evidence that deer can have significant local impacts on low-growing vegetation, which may be detrimental to some bird species that feed or nest near or on the ground (Perrins & Overall 2001; Holt et al. 2010), there is no evidence that this has negatively affected Marsh Tits on a landscape scale: Newson et al. (2012) found no relationship between the abundance of Marsh Tits and deer across England, and Carpenter et al. (2010) found a positive association between signs of deer activity and the presence of Marsh Tits in southern England and Wales (though see Amar et al. 2006 for caveats). As such, there is compelling evidence against the hypothesis of a widespread deterioration in habitat quality for Marsh Tits resulting from the impact of deer or reduced woodland management.

The majority of evidence for deer damage in British woodlands comes from studies of coppice (Dolman et al. 2010), where established shrubs and trees are removed by felling and the regrowth is then browsed by deer. Therefore, while deer may prevent the re-establishment of the understorey layer that is essential to Marsh Tits, it is coppice management that periodically destroys existing understorey and prevents woodland developing into the mature state that Marsh Tits prefer (Rackham 2006). Broughton et al. (2012a) show that the existence of extensive understorey does not necessarily require ongoing management, and it is notable that the only area of Monks Wood that was permanently avoided by Marsh Tits was the area of active coppice. This is despite a recent history of very high populations of Muntjac deer in the unmanaged areas of the wood (Cooke 2006). Consequently, the reintroduction of extensive coppicing in British woodlands, which is being promoted as a management and conservation priority (Forestry Commission England 2007; Plantlife 2011), may be a more significant threat to Marsh Tit habitat than deer activity, although in combination the two may lead to a permanent loss of understorey shrubs. As only 21% of British broadleaved woodland was classified as coppice in 1947, falling to just 4% in 1967 (Hopkins & Kirby 2007), the widespread adoption of coppicing would be a substantial intervention and the potential negative impacts upon ‘high forest’ species should be considered. Besides the Marsh Tit, birds affected may include declining species such as the Lesser Spotted Woodpecker and Hawfinch (*Coccothraustes coccothraustes*), but also species that have experienced population increases such as the Eurasian Nuthatch, Great Spotted Woodpecker and Coal Tit (*Periparus ater*).

## 8.3 Characterising woodland habitat for Marsh Tits and other species

Airborne remote sensing techniques such as lidar have several clear advantages over visual recording of ground-based sample plots for describing woodland bird habitat, particularly for species with large territories such as the Marsh Tit. These advantages include the comprehensive characterisation of woodland structure over the entire territory or woodland, and the quantification of vegetation height and coverage at much greater spatial resolution and sampling density than can be achieved by ground-based observation (Bradbury et al. 2005; Hinsley et al. 2006; Vierling et al. 2008). In the first analysis of Marsh Tit habitat using lidar data, Broughton et al. (2006) identified a key relationship between occupation and woodland canopy height that was previously unknown, and which was not detected by ground-based proxy measurements of tree stem diameter (dbh). Broughton et al. (2012a) and Broughton et al. (2012b) further developed the methods of combining remote sensing and bird distribution data to quantify habitat preferences, using lidar data of the overstorey and understorey layers, optical imagery of overstorey tree species distribution, and a time series of territory data and nest-sites. This revealed further novel information regarding the determinants of Marsh Tit occupation and nest placement that was not available from previous studies, and also confirmed some results from earlier work (summarised in Broughton et al. 2012a). The major limitation of remote sensing compared with ground-based observation at present is the inability to map understorey vegetation by species, but visual recording is also constrained in this respect by the limited spatial scale and resolution of sample plots. As such, further developments of remote sensing techniques may offer the best hope of overcoming such obstacles, perhaps using the principles of airborne mapping of tree species (Hill et al. 2010).

The integration of data from bird territory mapping, lidar and optical imagery has substantial potential for widespread application in woodland bird research. Habitat selection studies of the declining Willow Tit and Lesser Spotted Woodpecker, for example, have relied on vegetation sample plots based on the general location of unmarked birds or nest-sites to represent the woodland structure of territories (Charman et al. 2010, 2012a; Lewis et al. 2007, 2009a; Stewart 2010). Yet, these species occupy territories of a similar or greater extent as the Marsh Tit's, and so the application of territory mapping and remote sensing may reveal important detail in the relationships between occupation, territory composition and habitat structure which are currently unapparent. Remote sensing could also be used in the monitoring of vegetation structure over time to quantify the effects of management and deer activity at the woodland scale. Ground-based full-waveform lidar may offer an alternative to airborne data acquisition, and provide efficient measurement of vegetation at extremely high sampling densities, perhaps revealing novel structural indices that enable detailed comparison between sites and time-periods (Vierling et al. 2008).

## 8.4 Marsh Tit breeding success

Chapters 4 and 5 demonstrate that a reduction in nesting success or the availability of nest-sites have not driven the decline of the British Marsh Tit (cf. Fuller et al. 2005). Marsh Tits show flexibility in their choice of nest-site, and the breeding habitat of mature woodland has increased over time (Broughton et al. 2011). Results from the Monks Wood study population also support the important national perspective of Siriwardena (2006) in showing that Marsh Tit nesting success remains high, at more than 80%, and there has been no reduction in nest productivity. Nest-site competition from Blue Tits and Great Tits, and nest predation by Great Spotted Woodpeckers or other species, is negligible at the national and local population scales (Fuller et al. 2005; Siriwardena 2006; Broughton et al. 2011).

While active nests have a high chance of success, Broughton et al. (2011) identified that one in eight potential breeding territories in the study population failed to reach the nesting stage. This was due to territories being occupied by lone birds (typically males) entering spring, and also the probable predation of paired birds just prior to nesting, with insufficient recruits arriving in time to form new breeding pairs. These findings showed that dispersal, immigration and settling success, possibly interacting with over-winter survival and spring mortality, can have a significant effect on Marsh Tit productivity by moderating the number of territories that produce young.

## 8.5 Dispersal and settling success

Chapter 6 showed that dispersal is a critical factor in the population ecology of Marsh Tits, and a potential bottleneck. Dispersal distances are short, the dispersal phases in summer and spring are of limited duration, and once birds are settled they are highly sedentary (Broughton et al. 2010). Consequently, habitat fragmentation may inhibit successful dispersal, and gaps between woodlands are likely to represent significant barriers to the movement of birds through the landscape. This is supported by direct observation and patterns of dispersal (Broughton et al. 2010), and the declining probability of Marsh Tit occupation as woodland isolation increases (Opdam et al. 1985). In the predominantly small woods of England and Wales (section 8.1), dispersing juveniles will often be required to move between woodland patches to escape the parental territory, and Broughton et al. (2010) indicated that such birds are less successful at becoming established than those which are able to disperse within a large woodland area.

Those juveniles which become established after summer dispersal may be required to disperse again in the following spring if a potential breeding partner has not arrived or survived (Broughton et al. 2010). Widowed adults may also undergo spring dispersal and abandon their territory in an attempt to find a breeding opportunity if a suitable breeding partner does not arrive in time. This suggests that increased mortality could interact with dispersal by increasing the need for birds to move between woodland patches in order to form breeding pairs, but that increased barriers to dispersal would lead to the poor recruitment and reduced productivity described in section 8.4. As the success of dispersal and settlement appears related to the degree of woodland fragmentation, such as the size and proximity of woodland patches and the ease of moving between them (Opdam et al. 1985; Hinsley et al. 1995; Broughton et al. 2010), then reduced connectivity between woodlands would reduce the ability of Marsh Tits to achieve this.

Marsh Tits probably move between woods using hedgerows, trees and bushes on field margins and along roads. Although there is no published direct evidence that Marsh Tits rely on such features, Bellamy & Hinsley (2005) showed that Blue Tits and Great Tits behave in this way and Alderman et al. (2011) showed that dispersing Marsh Tits were more likely to leave a woodland territory if it was adjacent to a hedgerow ‘exit’. Radiotracking of 12 Marsh Tits at Monks Wood during the winter of 2007/8 also revealed birds using hedgerows and tree lines, but never crossing open fields (R.K. Broughton and P.E. Bellamy, unpublished data).

Therefore, the loss of approximately one fifth of the hedgerow length in England and Wales between 1969 and 1993 (section 1.3.4) is likely to have reduced the dispersal ability of Marsh Tits by degrading the connectivity between woodlands. While this hypothesis appears highly plausible, there is little detailed historical data of hedgerow distribution with which to test such a theory using time series of Marsh Tit distribution data, and it remains largely speculative.

## 8.6 Landscape ecology of the Marsh Tit

The landscape ecology of the Marsh Tit indicates that the species is adapted for heavily-wooded landscapes. Populations are characterised by a low-density of sedentary pairs that require extensive areas of mature woodland and low habitat fragmentation in order to accommodate their large territories and limited dispersal ability. If woodland connectivity were reduced through a broadly uniform removal of hedgerows across the landscape, then dispersal and settling success would be expected to have been reduced most in areas where woodland fragmentation was greatest. This is because smaller woodland patches could support fewer birds than large woods and so produce relatively fewer potential recruits, and barriers to dispersal success would be comparatively greater for heavily-fragmented habitat due to the larger distances between territories.

Broughton et al. (in review) looked for this effect in the national distribution data for Marsh Tits and woodland, and identified a pattern of significantly greater loss of Marsh Tit populations during the 1970s and 1980s where the percentage cover of deciduous woodland in the landscape was relatively low in 1990. As habitat coverage is strongly correlated with other indices of habitat fragmentation (Cunningham & Johnson 2011), this is good evidence that the decline of the Marsh Tit in England and Wales was concentrated in areas where habitat fragmentation remained relatively high. Because the area of woodland increased in every region over time (Broughton et al. in review), and there is no indication of a regional decline in habitat quality (sections 1.3, 8.1 and 8.2), a reduction in woodland connectivity through loss of hedgerows or non-woodland trees seems the most likely habitat factor to explain this effect (chapter 7).

## 8.7 Mortality

While the previous sections indicate that a reduction in woodland connectivity is likely to have reduced the dispersal success of Marsh Tits in fragmented landscapes, results from chapter 5 suggest that this effect could be exacerbated by an increase in the mortality of full-grown birds. This would increase the requirement for immigration and dispersal at the same time as the likelihood of success was declining. Supporting this hypothesis of increased mortality, Siriwardena (2006) postulated that a decrease in annual survival may be the mechanism by which Marsh Tit populations have declined, and Carpenter (2008) also considered this to be fully consistent with her results. An interaction of increased mortality and reduced dispersal capability could generate a negative feedback loop, whereby a reduction in dispersal success as habitat connectivity decreased meant that Marsh Tits lost through higher mortality were increasingly unlikely to be replaced, thereby resulting in lower productivity and so fewer potential recruits to disperse and replace the greater losses. In parids, causes of mortality are dominated by predation and starvation (Perrins 1979; Smith 1991), and these factors are discussed below in the context of Marsh Tits.

### 8.7.1 Predation

The most frequent predator of full-grown Marsh Tits is probably the Eurasian Sparrowhawk, which is the major predator of tits in Britain (Perrins et al. 1979). This species has experienced a 152% increase in abundance between 1975 and 2008 after recolonising lowland England during a recovery from organochlorine poisoning (Newton 1986; Baillie et al. 2010). It is possible that the recovery of the Eurasian Sparrowhawk resulted in increased predation of Marsh Tits, although this has not been tested. However, the disappearance of Marsh Tits during the pre-breeding and nesting period reported in Broughton et al. (2011) has strong parallels with reported depression of Blue Tit numbers in spring due to Eurasian Sparrowhawk predation (Geer 1978; Dhondt et al. 1998). While McCleery & Perrins (1991) reported that Eurasian Sparrowhawks did not reduce the overall breeding population of Great Tits on re-colonisation of Wytham Woods, Krebs (1971) found that Great Tit pairs which were experimentally removed in spring were quickly replaced by birds from sub-optimal habitat outside the wood. This is in contrast to the Marsh Tits studied at Monks Wood (Broughton et al. 2011), where many birds that disappeared during spring were not replaced until after the nesting period. Therefore, predation of

Marsh Tits would often result in the permanent loss of a breeding opportunity in that territory for that year.

Eurasian Sparrowhawk predation of Marsh Tits could also be significant during the non-breeding period, by removing birds which had already dispersed, settled and established pairs in territories. Such losses would be unlikely to be replaced until the following spring dispersal period, if at all (Broughton et al. 2010, 2011). Marsh Tits typically occur at a substantially lower population density than Blue Tits or Great Tits (Carpenter 2008), and so may be expected to suffer lower levels of absolute predation than the commoner tits. However, it is perhaps plausible that the substantial population increases of the two commoner tits that coincided with the recovery of the Eurasian Sparrowhawk (Baillie et al. 2010) have created a 'predator pit' for Marsh Tits in some areas. Such an effect was suggested by Millon et al. (2009) for thrushes (*Turdidae*) in Denmark, where a comparatively high abundance of Common Blackbirds (*Turdus merula*) may have maintained Eurasian Sparrowhawks at a relatively high level and led to disproportionate predation of the low-density Song Thrush (*Turdus philomelos*). Further work is required to determine whether predation by Eurasian Sparrowhawks has contributed to the Marsh Tit's decline, possibly as an additive effect in an interaction between woodland isolation and dispersal ability. Field studies and spatio-temporal analyses of distribution and population data (cf. Millon et al. 2009; Newson et al. 2010) would be valuable in this respect.

### 8.7.2 Inter-specific competition

The increased abundance of Blue Tits and Great Tits since the 1960s may have also led to elevated mortality of Marsh Tits through an intensification of inter-specific competition for food resources or foraging space. Evidence points to a positive relationship between numbers of Marsh Tits and these potential competitors during the breeding season (Siriwardena 2006; Carpenter 2010), although Carpenter (2008) found apparent effects of inter-specific competition between dominant Blue Tits and subordinate Marsh Tits in winter. These included comparatively less time spent foraging by Marsh Tits and a pattern of competitive exclusion from oak trees where the density of Blue Tits was relatively high. It is, therefore, possible that competition may have its greatest impact during the non-breeding period when food is most limiting (for a review of this effect on other species see Alatalo 1982). There is an overlap between Marsh Tits and both Blue Tits and Great Tits in foraging niche and winter diet (Betts 1955; Carpenter 2008), and so increased numbers of these species could result in greater and more rapid denudation of the food resources within a Marsh Tit's territory during autumn and winter, when food is limiting for tits (Gibb 1954a; Alatalo 1982). Furthermore, Blue Tits and Great Tits may readily leave woodlands in order to escape food shortages and exploit e.g. the large number of garden bird-feeders (Gibb 1954b; Gosler 1993; Chamberlain et al. 2005), whereas the sedentary Marsh Tits tend to remain within the vicinity of their territories throughout the winter (Gibb 1954b; Broughton et al. 2010). As such, a high density of competitors may exclude Marsh Tits from preferred foraging areas and reduce the food resources within their home-range, while the competitors themselves are not restricted by these spatial and resource limitations.

As with the recovery of the Eurasian Sparrowhawk, the broadly coincidental increase in populations of the Blue Tit and Great Tit during the Marsh Tit's decline is superficially suggestive of a link. As increased mortality during the non-breeding period has previously been implicated in the decline of the Marsh Tit (Siriwardena 2006; Carpenter 2008), and is further supported by this thesis, the relative impact of avian predation and inter-specific competition on Marsh Tit demography requires detailed investigation at a variety of spatial scales and throughout the annual cycle.

# 9 CONCLUSIONS

## 9.1 Causes of the decline of the British Marsh Tit

The work contained within this thesis has made a substantial contribution to the understanding of the causes of the reduction in range and abundance of the British Marsh Tit. While further evidence is required to identify with certainty the specific drivers of the decline, this work and that of Carpenter (2008) have been able to discount several leading hypotheses, generate plausible new interpretations, and prescribe a focussed selection of remaining priorities for future research.

Carpenter (2008) dismissed climate change and a reduction of invertebrates as contributing to the decline of the Marsh Tit, and these topics were not considered in the current work. New evidence presented in chapter 5 confirms that a reduction in nest success due to predation or competition can also be discounted as a contributory factor. Notably, however, the previously-favoured hypothesis of deteriorating habitat quality as a consequence of damage by deer or a lack of woodland management now also appears unconvincing, as chapters 3-4 and sections 1.3 and 8.1-8.2 outline how the habitat features most preferred by Marsh Tits have increased or remained stable on a regional and national scale. Instead, the evidence suggests that a reduction in woodland connectivity may be a more pertinent factor by reducing dispersal success, particularly in heavily-fragmented landscapes (chapter 6 and 7). The most likely cause of reduced connectivity is the loss or deterioration of hedgerows or other non-woodland trees and shrubs in the landscape, which may have ultimately resulted in Marsh Tits becoming extinct in small, isolated woods and areas of heavily-fragmented habitat.

It is possible that increased mortality has acted to exacerbate a reduction in dispersal success and play a contributory role in the Marsh Tit's decline. This may have operated by increasing the demand for dispersal and immigration while the capacity for such was declining, thereby compounding the effect of reduced connectivity. The likely result of such an influence would be a decrease in the frequency of arrival of dispersing Marsh Tits into territories where they are required to form breeding pairs, and the reduced persistence of birds in these territories if they remained alone or widowed for prolonged periods. Increased predation by Eurasian Sparrowhawks and inter-specific competition from Blue Tits and/or Great Tits during the non-breeding period are possible causes of elevated mortality rates for Marsh Tits, but further work is required to test this.

## 9.2 Management recommendations for Marsh Tit conservation

Carpenter (2008) offered habitat management recommendations for the conservation of Marsh Tits, based upon the available evidence at the time, but these can now be updated and addressed at those public, private and charitable organisations that inform and implement national policy, particularly where there may be conflict with other conservation or economic objectives (see Amar et al. 2006; Forestry Commission 2007; Plantlife 2011). The key factors determining Marsh Tit occupation in woodland appear to be the area and maturity of the wood, and its proximity and connectivity to neighbouring woodland patches that hold existing populations. Maximising these elements would, therefore, aid conservation of Marsh Tits or the recolonisation of the former range. Specific criteria include providing a minimum of 4.5 ha of mixed deciduous woodland to accommodate a single pair, a mature tree canopy exceeding 15 m in height and 80% canopy closure, and a minimum of 40% ground coverage by understorey vegetation that largely exceeds 4 m in height. Maintaining or increasing the area of woodland in the landscape, and also the connectivity between woods via hedgerows or tree lines, would have clear benefits. Populations in woods more than *c*.2.5 km apart are unlikely to exchange recruits on a regular basis, and this distance and frequency will be reduced if connective trees or hedgerows are intermittent or scarce. Connectivity between woods could be improved by the planting of hedges or fast-growing ‘stepping stones’ of shrubs or trees, such as willows or sallows (*Salix* spp.), Silver Birch or European Elder (*Sambucus nigra*).

Extensive coppice management would appear to be detrimental to Marsh Tits by destroying existing habitat and arresting woodland maturation. Marsh Tits in the Monks Wood study area were demonstrably able to tolerate small areas of infrequent coppicing, such as ‘scallop’ cuts along rides or glades, but rotational coppicing on a compartmental basis has the potential to seriously degrade Marsh Tit habitat by limiting the height and maturity of trees and shrubs and preventing tree canopy closure. Nest-sites do not appear limiting for Marsh Tits in British woods, and provision of nest-boxes may instead lead to increases in the density of potential competitor species, such as the Blue Tit and Great Tit. While the evidence for a widespread negative impact of inter-specific competition or a ‘predator pit’ (Millon et al. 2009) is currently lacking or inconclusive, the precautionary principle suggests that routine provision of nestboxes for tits should be avoided in woods where Marsh Tits are to be retained or encouraged.

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ABBREVIATIONS

| | |
|---|---|
| ASNW | ancient semi-natural woodland |
| BAP | Biodiversity Action Plan |
| BTO | British Trust for Ornithology |
| BU | Bournemouth University |
| CEH | Centre for Ecology & Hydrology |
| dbh | diameter at breast height [of a tree stem] |
| DCHM | digital canopy height model |
| Defra | Department for Environment, Food and Rural Affairs |
| GIS | geographical information system |
| IUCN | International Union for the Conservation of Nature |
| JNCC | Joint Nature Conservation Committee |
| Lidar | light detection and ranging |
| NNR | National Nature Reserve |
| PAWS | planted ancient woodland site |
| PECBMS | Pan-European Common Bird Monitoring Scheme |
| RSPB | Royal Society for the Protection of Birds |
| RWBS | Repeat Woodland Bird Survey |

APPENDIX 1A

# Separation of Willow Tit and Marsh Tit in Britain: a review

Richard K. Broughton

*ABSTRACT* Separation of the British races of Willow Tit *Poecile montana* and Marsh Tit *P. palustris* is notoriously difficult. Numerous identification criteria have been proposed during the past 50 years, based primarily on information gained from examination of birds in the hand, although none are judged to be wholly reliable. The best separation feature for birds in the field is considered to be voice, yet the vocal repertoires of both species have not been fully documented. Despite some work to assess the reliability of distinguishing characteristics, some current texts continue to place emphasis on discredited criteria for field identification, or on those of use only for in-hand examination. This paper reviews the separation criteria in the current literature in order to clarify the most important and reliable characters for the separation of this species pair. New information is provided from examination of skins and live birds, and on diagnostic vocalisations. A clarification of the races occurring in Britain is also provided. Recommendations are made for the key criteria to be used for field, photographic and in-hand identification, with a primary focus on voice, bill marks, cheek pattern, plus wing and tail measurements and the presence or absence of a clear wing panel.

## Introduction

In Britain at least, separation of the Willow Tit *Poecile montana kleinschmidti* and the Marsh Tit *P. palustris dresseri* has been problematic ever since 1897, when it was first discovered that the Willow Tit was present here. The question of separating the two in the field remains one of the biggest challenges offered by resident species and is difficult even in the hand; this species pair is the only one to be given a dedicated appendix in the *Ringers' Manual* (Redfern & Clark 2001). In addition, the BTO Garden BirdWatch survey combines records of Marsh and Willow Tits owing to persistent confusion (Chamberlain *et al.* 2005), while one popular photographic field guide even contains a misidentified image.

The continuing problems of identification have conservation implications. Both species have undergone significant changes in population and/or range in recent decades (Baillie *et al.* 2009) and both are Red-listed (Eaton *et al.* 2009). The Willow Tit, in particular, has become so scarce that in many areas county recorders now require a description to accompany records, and many birders lack sufficient experience with one or both species owing to their progressive scarcity in recent times (Vinicombe 2005). While the current BTO/BWI/SOC Atlas project offers an opportunity to assess the status of both species, accurate identification is vital for this to be successful.

Perrins (1964) tackled the problem by summarising a suite of differences between the two species, but concluded that voice was the only certain means of identification. These criteria were included in later texts (e.g. Perrins 1979, *BWP*) and form the basis of the distinguishing characteristics contained in modern field guides, although some of these lack emphasis when conveying the degree of subjectivity and variability involved. Meanwhile, work during the past decade has sought to quantify the reliability of the differences quoted in the current literature (Scott 1999; Broughton *et al.* 2008a), but this may be too recent or too specialised to have influenced the texts on many bookshelves.

The aim of this paper is to review and update the criteria for the separation of Willow Tits and Marsh Tits that are published in current reference material and leading field guides. It is hoped that clarification of the most important features for identification will help county recorders, birders and Atlas workers to separate the two species accurately. Identification of birds in the field, in photographs, and in the hand is considered.

The identification criteria in each source reference were compared against each other, with the more systematic approaches taking precedence. Further evaluation was based on field experience of both species during long-term research (e.g. Broughton *et al.* 2006, 2008a) and from systematic examination of selected features on 46 specimens of each species after the post-juvenile moult (six live birds and 40 skins in the Natural History Museum, Tring).

### Distribution

The Willow Tit appears to be undergoing severe range contraction in Britain. Comparison between the New Breeding Atlas (Gibbons *et al.* 1993) and (unvalidated) sightings in 2008 (www.birdtrack.net) indicates that the species has been lost from much of southern England, and this is reflected in county reports (e.g. Bacon & Jordan 2004). There were an estimated 8,500 territories in Britain in 2000 (Robinson 2005), but the continued decline over subsequent years (Baillie *et al.* 2009) implies that there may now be far fewer than this. The Marsh Tit, by contrast, is still widely yet thinly distributed across southern Britain and the British population was 52,800 territories in 2000 (Robinson 2005). Both species are declining and extremely localised in Scotland (Forrester *et al.* 2007). The relative abundance of the two species is not equal across Britain; for example, Marsh Tits do not occur on the Humberhead Levels but are locally common in the woods of Cambridgeshire, a situation that is reversed for Willow Tits. However, while geography may be suggestive of identification, particularly where breeding birds are concerned, individuals may also occur as 'accidentals' many tens of kilometres from breeding populations despite the species' typically poor dispersal capabilities (Wernham *et al.* 2002; Forrester *et al.* 2007).

### Behaviour and habitat

Both species are generally regarded as woodland birds (Fuller *et al.* 2005) and in some areas both species may breed in the same wood. The Willow Tit is considered to prefer early successional and scrubby habitats, however, such as Alder *Alnus* carr, old hedgerows and overgrown gravel workings or brownfield sites (Lewis *et al.* 2009; *BWP*), although there are no detailed studies published on the territory requirements of this species in Britain (an area that requires urgent attention). There is good evidence that the Willow Tit's decline has been concentrated in woodland and farmland habitats, however, and that populations in wetter environments (such as carr or wet scrub) have been less affected (Siriwardena 2004).

The Marsh Tit appears to show a greater preference for more extensive woodlands, such as old-growth deciduous woods with a tall, mature canopy and well-developed understorey, and territory size in such habitats averages 4–5 ha (Broughton *et al.* 2006). Both species can occur in a variety of habitats, however, from downland scrub to wooded streams and conifer plantations, and habitat is ultimately an unreliable guide to identification. This is particularly so for lone birds or during the non-breeding season, when both species may also frequent gardens near to breeding territories. Svensson *et al.* (1999) stated that Willow Tits do not visit bird tables in winter, while Marsh Tits will, but this is incorrect; both species are frequent visitors to feeders close to breeding sites when given the opportunity (e.g. Willow Tits at Potteric Carr NR in Yorkshire, and Marsh Tits at Paxton Pits NR in Cambridgeshire).

The only helpful behavioural difference between the two species involves nesting activity, with Willow Tits excavating their own nest hole in rotten wood while Marsh Tits are secondary hole-users that never initiate a hole from scratch (Wesołowski 1999). Marsh Tits will nevertheless commonly enlarge existing

Marcus Conway

**394.** Adult or first-winter Willow Tit *Poecile montana*, South Yorkshire, January 2008. Note the plain whitish cheek patch, being of a similar colour both on and behind the ear-coverts, which extends to the dark cap on the nape. A subtle warm buff 'collar' is present on the neck sides, contrasting sharply with the grey-brown mantle and wing. The bill appears to be uniformly dark, with no pale marks on the upper mandible, although reflected light makes interpretation of this feature difficult. The presence of a wing panel is also difficult to determine, as light reflecting off the edges of the tertials and secondaries is obscuring the degree of any contrast between the feather margins and the mantle. Note the small bib, which has previously been regarded as characteristic of a Marsh Tit *P. palustris*.

Mark Hancox

**395.** Adult or first-winter Marsh Tit *Poecile palustris*, Worcestershire, December 2008. Typical of many sightings at mid range, there are few identification features clearly visible on this bird. The presence or absence of pale bill marks or pale wing panel cannot be determined conclusively, but note the cheek pattern: whitish ear-coverts contrasting with a cold grey-brown wash on the neck sides and rear of the cheek patch is strongly indicative of a Marsh Tit.

holes, carrying away the chippings in the manner of Willow Tits, and may also evict Willow Tits from their own nests or occupy similar holes excavated by Lesser Spotted Woodpeckers *Dendrocopos minor*.

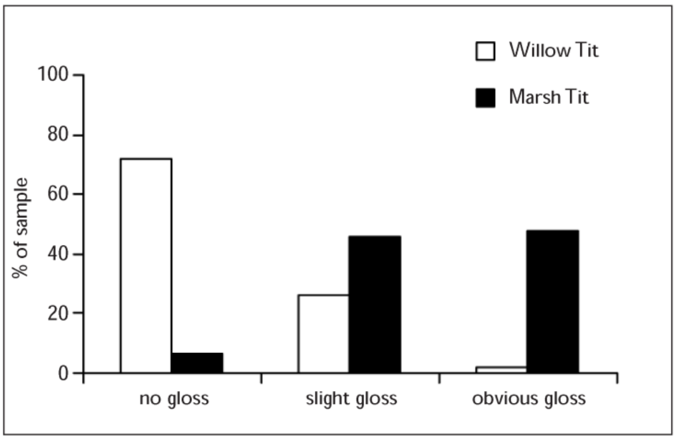


**Fig. 1a.** Assessment of cap gloss on a sample of Willow *Poecile montana* and Marsh Tits *P. palustris* (40 skins and 6 live birds per species).

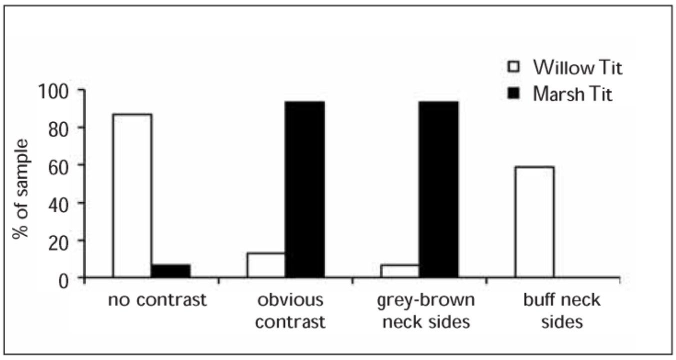


**Fig. 1b.** Assessment of cheek pattern on a sample of Willow *Poecile montana* and Marsh Tits *P. palustris* (40 skins and 6 live birds per species). Comparison of contrast between colour of ear-coverts and neck sides, and presence of warm buff or cold grey-brown tones on the neck sides.

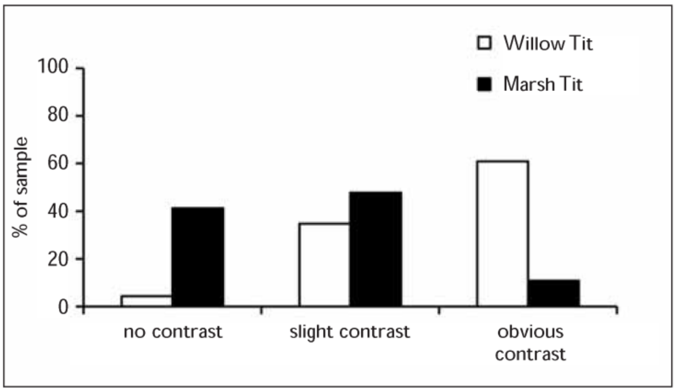


**Fig. 1c.** Assessment of 'wing panel' on a sample of Willow *Poecile montana* and Marsh Tits *P. palustris* (40 skins, 6 live birds per species), comparing contrast between colour of the fringes of tertials and secondaries with that of the mantle.

## *Cap colour and gloss*

A frequent separation criterion appearing in the literature is cap gloss, with the cap of Marsh Tits being described as glossy black and that of Willow Tits as matt, dull or sooty-black or very deep brown (e.g. Perrins 1979, Svensson *et al.* 1999, *BWP*). Scott (1999) found that Willow Tits could also show a glossy black cap, however, while female Marsh Tits may also have dull caps with deep brown tones (Harrap & Quinn 1995). Examination of specimens showed considerable overlap of cap gloss, with 28% of Willow Tits showing slight or obvious gloss and 7% of Marsh Tits showing no gloss (fig. 1a).

Plumage gloss may vary considerably with viewing conditions and is of little use at distance. Lighting will have a significant bearing in photographs, as even a matt surface may reflect in strong light and a glossy surface will appear dull in deep shade (figs. 2a–b & 3a–d).

A further complication, mentioned in all sources, is that juvenile Marsh Tits have consistently dull black or deep brown caps (as do juvenile Willow Tits) and retain these until the end of the post-juvenile moult, in late September (figs. 2c–d). Cap gloss is therefore a highly unreliable characteristic, being difficult to assess in the field, open to misinterpretation in photographs, and variable in the hand.

## *Cap shape*

Many sources state that the cap of the Willow Tit extends farther down the nape than that of the Marsh Tit, or onto the mantle. This was primarily advocated as a feature to use on birds in the hand, but Scott (1999) found no practical difference in the cap shape of the two species and regarded the feature as too subjective to be of any value. My examination of specimens also

**Fig. 2.** Adult and juvenile plumages of Marsh *Poecile palustris* and Willow Tits *P. montana* : 2a adult Marsh Tit (February, © *Garth Peacock*); 2b adult Willow Tit (December, © *John Spink*); 2c juvenile Marsh Tit (July); 2d juvenile Willow Tit (August, © www.grayimages.co.uk)

suggested little value in this feature, with 46% of Marsh Tits adjudged to have the cap extending onto the mantle and 20% of Willow Tits having the cap extending only to the nape. Posture of the bird will clearly influence the appearance of the cap shape on specimens and in photographs, and it may be difficult to assess on individuals under most viewing conditions in the field. Furthermore, even where side-by-side comparisons have been attempted, the feature appears to be of little use (Scott 1999; pers. obs.).

### Bib

Differences in the shape and size of the bib area on the throat are mentioned in all sources, with Willow Tits reportedly showing a relatively large, diffuse bib and Marsh Tits showing a smaller, neater bib. Again, this difference was highlighted primarily for birds in the hand, although Scott (1999) showed bib features to be unreliable due to significant overlap (figs. 2 & 3). Bib size is variable within both species, and is related to sex (King & Muddeman 1995), social rank (Hogstad & Kroglund 1987) and also age (Harrap & Quinn 1995). Added to this variability and overlap apparent in the hand is the difficulty in assessing subtle differences in the size or shape of the bib in the field, and the problematic effect of posture and angle of the bird in photographs (fig. 3). Consequently, the bib is not a particularly useful identification feature.

### Cheek area

The majority of sources specify differences in the appearance of the pale cheek area of both species. Scott (1999) did not examine this character, although several authors agree on the principal differences (Harris *et al.* 1989; Harrap & Quinn 1995; Svensson *et al.* 1999; Gosler & Clement 2007; *BWP*). The key distinction lies with the pattern of colouring on the ear-coverts and the sides of the neck, which together make up the pale cheek patch. On Marsh Tits, the ear-coverts are a clean whitish colour that frequently contrasts with a pale, cold grey-brown wash on the side of the neck (fig. 1b). The transition between the white ear-coverts and grey-brown neck is often quite distinct, following the curve of the ear-coverts themselves (figs. 2a & 3c). This results in many Marsh Tits appearing to have a much smaller white 'face' than Willow Tits.

The Willow Tit's cheek is whitish or with a faint buff wash, but there is usually no abrupt colour transition behind the ear-coverts (figs. 1b & 3d). Instead, Willow Tits frequently show a subtle colour gradient from the ear-coverts to the sides of the neck, with an increasing warm buff suffusion. Where the cheek meets the mantle, the warm buff suffusion can contrast sharply with the grey-brown of the mantle (fig. 2b). In the field, the Willow Tit appears to have a larger, more uniform whitish cheek area in comparison with the 'two-toned' whitish and grey-brown cheek area of the Marsh Tit.

Examination of specimens revealed a moderately high degree of reliability for these differences, with 87% of Willow Tits assessed showing no distinct contrast in the cheek area and 94% of Marsh Tits showing a clear contrast between whitish ear-coverts and pale grey-brown neck sides (fig. 1b). No Marsh Tits displayed warm buff tones to the neck sides, while warm buff was present to some degree on 59% of Willow Tits.

Juveniles are more problematic, as both have wholly whitish cheeks and lack any grey-brown or buff on the neck (figs. 2c–d). Cheek pattern may nevertheless represent one of the better field characters for identification after the post-juvenile moult (i.e. from October onwards), with less overlap than for other plumage features. Particular caution must be exercised on worn adults or potential juveniles, and exposure of photographic images may also create difficulties by misrepresenting contrast or colour.

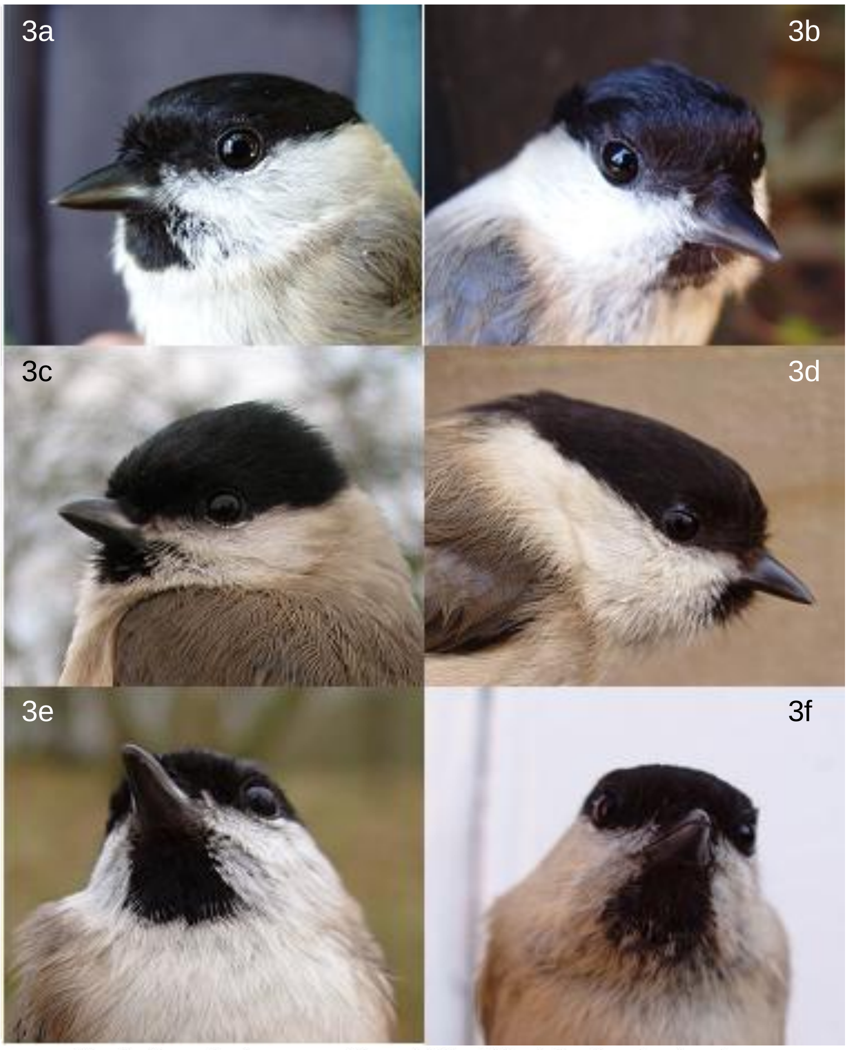


**Fig. 3.** Caps, cheek patterns, bibs and bills of Marsh *Poecile palustris* and Willow Tits *P. montana* : 3a adult male Marsh Tit; 3b adult male Willow Tit; 3c first-winter female Marsh Tit (© *Katie Fuller*); 3d first-winter female Willow Tit; 3e adult male Marsh Tit; 3f adult male Willow Tit.

### *Bill*

Bill morphology is of no practical use (see *BWP* for overlapping measurements). Dewolf (1987) suggested that Belgian Marsh Tits showed pale cutting edges to the mandibles that Willow Tits lacked, and this was reported in Svensson (1992). Redfern & Clark (2001) described British Marsh Tits as displaying a white cutting edge to the lower mandible that was lacking in Willow Tits. Broughton *et al.* (2008a) found a significant difference in markings on the bill, but not as previously described: both species displayed pale cutting edges to the lower mandible, but 97% of Marsh Tits showed a pale mark on the upper mandible, on the bill sides below the nostril, which was lacking on 96% of

**Fig. 4.** Variation in 'wing panel' of Willow *Poecile montana* and Marsh Tits *P. palustris*: 4a first-winter Marsh Tit (February); 4b first-winter Marsh Tit (December); 4c adult Willow Tit (February); 4d adult Willow Tit (February); 4e first-winter Willow Tit (February).

Willow Tits (fig. 3). This characteristic mark appears to be the single most reliable and objective physical feature for separating Marsh Tits and Willow Tits, although it may be very difficult to see in the field. It is often readily apparent in photographs, however, although note that reflected light may obscure or mimic the feature.

### *Colour of flanks/underparts*

The flanks or underparts of the Willow Tit are commonly described as being a warm buff colour and those of the Marsh Tit as being paler or colder grey-brown (Perrins 1979; Harris *et al.* 1989; Harrap & Quinn 1995). Scott (1999) found some overlap with birds in the hand and, although buff flanks were an unambiguous characteristic for all the Willow Tits studied, almost half of the Marsh Tits showed buff flanks too (figs. 2a–b). In addition, 78% of Marsh Tit specimens that I examined showed 'warm buff' flanks, although only 6% of Willow Tits displayed atypical greyish-brown flanks. Furthermore, juveniles of both species tend to have rather pale underparts (fig. 2c–d) until the post-juvenile moult. Individual variation, observer subjectivity (in both perceiving and describing colour), field conditions and colour saturation or lighting in photographs could strongly influence the recording of flank colour and, consequently, little weight should be attached to this feature.

### *Wing panel*

Many sources consider the pale creamy or buff fringes on the tertials and inner secondaries of the Willow Tit as one of the best distinguishing features; these fringes form a distinct pale 'panel' on the closed wing that contrasts with the mantle (figs. 4c–d). In comparison, the wing of the Marsh Tit is more uniform in appearance (fig. 4a). Some authors urge caution, however, stressing that worn Willow Tits may show no pale panel, while fresh Marsh Tits may show a subtle pale panel (Harrap & Quinn 1995; Gosler & Clement 2007; *BWP*). Scott (1999) found that half of the Marsh Tits he studied showed pale fringes on the secondaries, but Harrap & Quinn (1995) stated that Marsh Tits are never as well marked as Willow Tits. This is not so, however, as some Marsh Tits can display a very prominent wing panel (fig. 4b). As with Scott (1999), examination of specimens also revealed a high degree of overlap in the presence of a wing panel, with 59% of Marsh Tits showing some degree of contrast in the wing (fig. 1c). In addition, 'standard' Marsh Tits may also appear to show wing panels in photographs owing to glare or reflectance on the edge of the secondaries, and this may be misinterpreted. While broad creamy margins to the tertials and secondaries are strongly supportive of Willow Tit (fig. 4c), many individuals are less well marked (e.g. figs. 2d & 4e) and the presence or absence of a wing panel is of more limited value than is widely believed, and should be used with caution.

### *Tail*

There is no practical difference in tail length (Harrap & Quinn 1995, *BWP*), or in the extent of white on the outer tail feathers (Harrap & Quinn 1995); both species have a whitish margin to the outer web of the outermost tail feather and no difference between them was apparent when assessing skins or birds in the hand. There is, however, a statistically significant difference in the relative lengths of the tail feathers (du Feu & du Feu 1996; Scott 1999). The difference in length between the outermost tail feather and the longest (innermost) tail feathers is at least 4 mm in the Willow Tit, compared with less than 5 mm in the Marsh Tit, although this has an error rate of up to 23%

(Scott 1999; Redfern & Clark 2001). Viewed from below, the Willow Tit shows a 'stepped' appearance of four successively longer tail feathers from the outermost inwards, compared with two or three in the Marsh Tit (du Feu & du Feu 1996). This contributes to a subtly different tail shape: while the tail of both species has rounded corners, those of the Willow Tit are the more rounded, although this is not obvious in the field (Vinicombe 2005). Although examination of the tail may be of some value for ringers, it is of no practical use for field or photographic identification owing to overlap and the very small measurements involved.

### Size, structure and plumage

The Willow Tit is marginally smaller than the Marsh Tit on average, but there is considerable overlap (*BWP*) and this feature is of limited practical value (Willow Tit range 55–63 mm, Marsh Tit range 58–67 mm). Many sources suggest that the Willow Tit has a different shape from the Marsh Tit, the former being described as 'big-headed', 'bull-necked' or 'short-necked' (Harris *et al.* 1989; Jonsson 1992; Svensson *et al.* 1999; Redfern & Clark 2001), while the Marsh Tit is 'smaller-headed' (Jonsson 1992; Gosler & Clement 2007; *BWP*), although any difference is 'not striking' (Svensson *et al.* 1999). The larger pale cheek area and longer contour feathers of the Willow Tit (Harrap & Quinn 1995) may generate this effect, which is nevertheless highly subjective and heavily reliant on posture and 'fluffing up' of the plumage (figs. 2a–d). The plumage texture of the Willow Tit is often described as 'loose' compared with the 'sleek' appearance of the Marsh Tit, and this effect may also be due to the longer feathers of the former, which have fewer interlocking barbs (Perrins 1979; Harrap & Quinn 1995; my unpublished data).

Juvenile feathers also have fewer barbs than those of adults (Svennson 1992), which results in a loose-textured plumage, and this applies to juvenile Marsh Tits as well as Willow Tits. Moulting Marsh Tits also have scruffy plumage during the summer, and the degree of subjectivity involved in assessing such qualities as 'looseness' and 'sleekness', or 'big-headed' and 'small-headed', is an obvious barrier to their reliability.

### Voice

Voice is generally regarded as being the most certain means of identification, although the full range of vocalisations has not been described previously. Willow and Marsh Tits have extensive vocal repertoires based on the 'chick-a-dee' call structure, as with the congeneric New World chickadees (Haftorn 1993; Harrap & Quinn 1995; *BWP*). In these species the major call type is composed of broadly analogous initial 'chick-a' notes and a variable number of wide-band 'dee' notes at the end, hence *chick-a-dee*. While many calls in the vocal repertoires of Willow and Marsh Tits are very similar, such as simple contact calls, components of the 'chick-a-dee' call are diagnostic, along with two other call types.

#### 'Chick-a-dee' calls

The Marsh Tit's 'explosive' or 'sneezing' *pitchou* call (also written *pichay* or *pitchuu*) is the 'chick-a' note equivalent and is highly distinctive; the Willow Tit produces nothing similar. The call is used in a variety of contexts and is frequently followed by a varying number of *dee* notes to form the full 'chick-a-dee' call, for example *pitchou dee* or *pitchou dee-dee-dee* (fig. 5b). Not all elements of the call may be given, however, and some may be repeated or given in isolation. A complex variety of calls are therefore possible, such as *pit dee-dee*, a simple *chou*, or *pit-it-it*.

The 'chick-a-dee' call of the Willow Tit differs in always lacking the explosive *pitchou* of the Marsh Tit, with the 'chick-a' elements instead being composed of rather thin, high *si*, *zi* or *tsit* notes. The 'dee' notes are also diagnostic, being longer and more buzzing or 'nasal' than those of the Marsh Tit, the full call being transcribed as *si-si dzee dzee*, *si-zur-zur* or *zi-zi taah taah taah* (Harris *et al.* 1989; Harrap & Quinn 1995; Svensson *et al.* 1999). Again, repetition or omission of call elements is common but the key difference is the length of the 'dee' notes, the Willow Tit's generally being 0.25–0.50 seconds long and the Marsh Tit's being 0.2 seconds or less (Harrap & Quinn 1995; *BWP*; figs. 5a & 5b).

Constantine *et al.* (2006) asserted that Willow Tits may emit 'dee' notes on their own (e.g. a *dzee dzee* call) whereas Marsh Tits always include an introductory note such as *pitchou* (e.g. *pitchou dee-dee* rather than just *dee-dee*). This is not always the case for Marsh Tits, however, and a string of stand-alone 'dee' notes is possible (Harrap & Quinn 1995; pers. obs.).

### *Juvenile begging calls*

The begging calls of fledged juveniles are also diagnostic and can be heard in late May and June for a week or two after fledging. Those of the Willow Tit are a series of 2–5 notes that descend the scale and have been described as a 'loud… musical' *dee-doo-derr*, *jzee jzee jzee* or *d'dze'dze'dzah* (fig. 6a) (Lewis 1985; Harrap & Quinn 1995; Vinicombe 2005). The juvenile begging calls of the Marsh Tit have not previously been described, but fledglings are said to be much less vocal than Willow Tit fledglings (Vinicombe 2005; *BWP*). Recent work contradicts this; Marsh Tit fledglings are in fact highly vocal (pers. obs.) and the main begging calls consist of a thin, squeaking *eehs-it* and a trisyllabic, sometimes descending *eehs-is-it* (fig. 6b). The latter is possibly analogous to the descending *dee-doo-derr* of fledgling Willow Tits but, at just c. 0.3 seconds long, is much shorter.

### *Song*

The common songs of Marsh Tit and Willow Tit are also distinctive. The British Willow Tit has one true song, which is a 'melancholy', 'slow' series of descending notes that are reminiscent of the introductory notes of Wood Warbler *Phylloscopus sibilatrix* song, for example *tsui tsui*

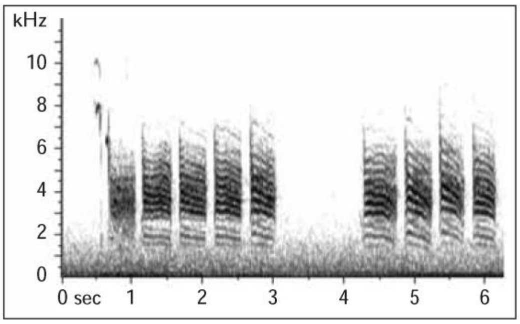


**Fig. 5a.** Willow Tit *Poecile montana* 'chick-a-dee' calls, the first call containing initial *zi-zi* ('chick-a') notes followed by five wide-band *taah* ('dee') notes. The second call lacks introductory notes.

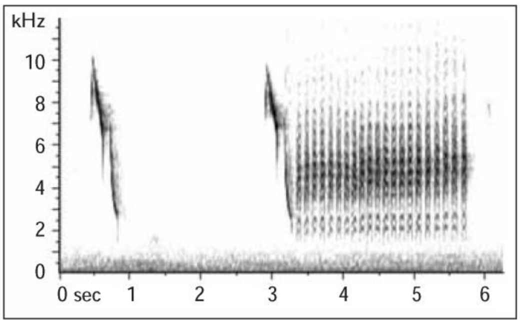


**Fig. 5b.** Marsh Tit *Poecile palustris* 'pitchou' call and full 'chick-a-dee' call, the latter containing a *pitchou* element and 21 'dee' notes.

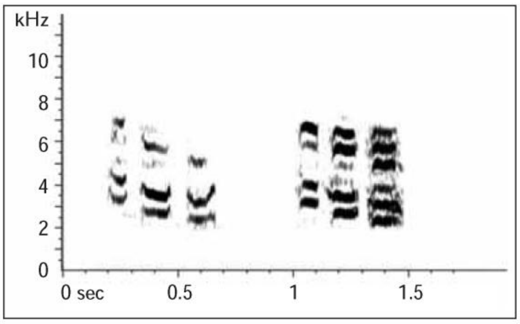


**Fig. 6a.** Two Willow Tit *Poecile montana* fledgling begging calls: *dee-doo-derr*.

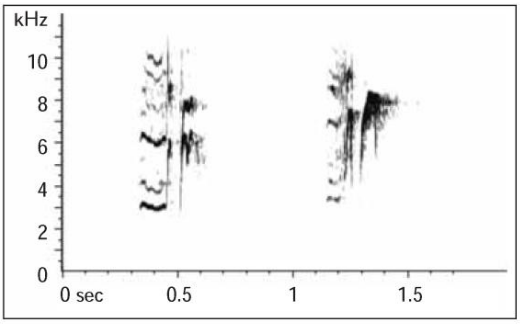


**Fig. 6b.** Two Marsh Tit *Poecile palustris* fledgling begging calls: *eehs-it*.

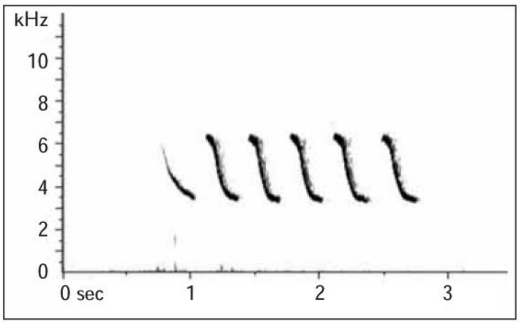


**Fig. 7a.** Willow Tit *Poecile montana* song: *tiu-tiu-tiu…*

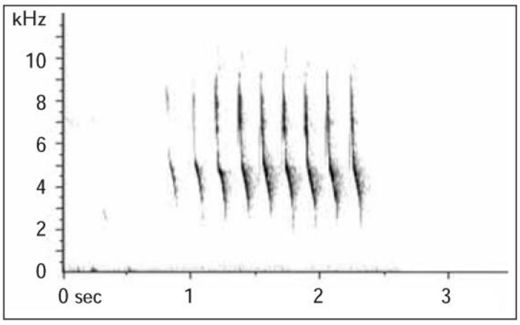


**Fig. 7b.** Marsh Tit *Poecile palustris* common song variant: *schip-schip-schip…*

*tsui…*, *pew pew pew…* or *tiu tiu tiu…* (Harris *et al.* 1989; Svensson *et al.* 1999; Vinicombe 2005; fig. 7a). Other song types attributed to British Willow Tits appear to refer to 'gargle' calls, brief jumbles of wheezing and musical notes given by *Poecile* species during aggressive interactions (Harrap & Quinn 1995; *BWP*). Marsh Tit 'gargles' are not dissimilar, and their variability and infrequency means that they have little value for identification.

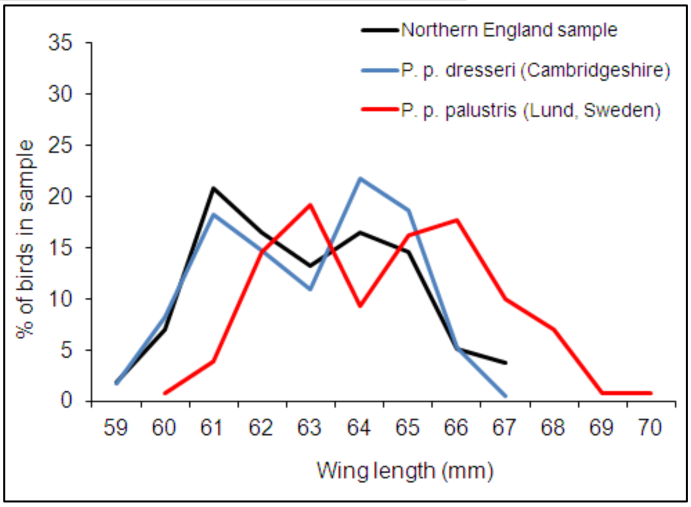


**Fig. 8.** Distribution curves of Marsh Tit wing lengths by percentage of birds in the sample. Bird samples derived from northern England (subspecies to be defined, n = 165), Cambridgeshire (*Poecile palustris dresseri*, n = 230) and Sweden (*P. p. palustris*, n = 130).

In contrast to the Willow Tit, the Marsh Tit has a large variety of true song types. Males may switch between several 'rapid ringing', 'bell-like rattles' such as a monotonous *schip-schip-schip…* (fig. 7b), a rapid Greenfinch *Carduelis chloris*-like *chipchipchip…* or a Coal Tit *Periparus ater*-like *wita-wita-wita* (Harris *et al.* 1989; Svensson *et al.* 1999; *BWP*). The Marsh Tit song is delivered at c. 6–10 notes per second, commonly in bouts of 8–19 notes, compared with the Willow Tit's 2–7 notes delivered at a slower rate of c. 3 per second. One Marsh Tit song variant is very similar to that of the Willow Tit, however, consisting of a much slower series of descending notes: *tiu tiu tiu…* (Harrap & Quinn 1995; pers. obs.), but this appears to be uncommon (0.5 % of 660 song bouts, pers. obs.). Song is generally given from February to May, both sexes may sing, and newly independent juveniles may also sing briefly in June/July (Broughton 2008; *BWP*; pers. obs.).

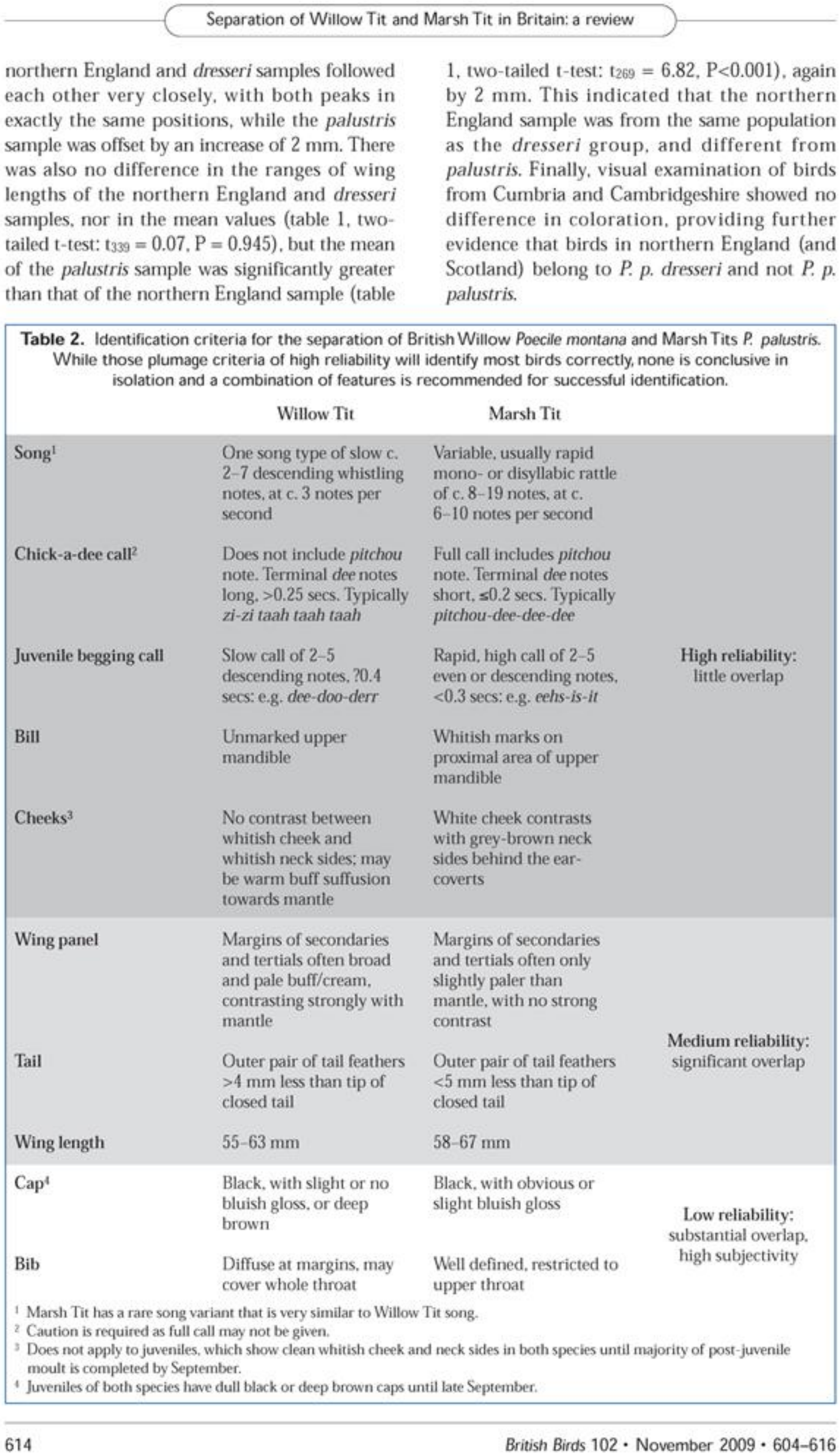
## Other races occurring in Britain

There are just three British records of the Fennoscandian race of Willow Tit *P. m. borealis* (Dudley *et al.* 2006), which is paler and greyer than the British race and less of an identification problem.

Harrap & Quinn (1995) and *BWP* stated that Marsh Tits in northern England and Scotland are of the larger, greyer, nominate race, which also occurs in northern and central Europe. The source evidence for this claim appears erroneous, however, with the measurements provided being well within the range of British *P. p. dresseri* rather than *P. p. palustris* (Clancey 1947; *BWP*). In order to test the claim, I made a comparison of wing lengths of birds from northern England (Cumbria and Northumberland; BTO ringing data) with those of *dresseri* from Cambridgeshire (Broughton *et al.* 2008b) and *palustris* from Sweden (Nilsson 1992). Wing length in Marsh Tits varies with age and sex, creating a bimodal distribution (Nilsson 1992; Broughton 2008b), so samples were checked to ensure that there were similar proportions of males, females, adults and first-years in each (table 1). Sex was not determined for the northern England sample, however, although the shape of the wing-length distribution curve matched that of the other samples (fig. 8), suggesting a similar proportion of the sexes. The curves for the

**Table 1.** Wing-length measurements and proportions of adults, first-years, male and female birds in samples of Marsh Tits from northern England (subspecies to be defined), Cambridgeshire (*Poecile palustris dresseri*) and Sweden (*P. p. palustris*).

| Subspecies and/or origin of sample | Mean wing length (mm) | SE | Range (mm) | n | % adults | % first-years | % male | % female |
|---|---|---|---|---|---|---|---|---|
| Northern England | 62.9 | 0.2 | 59–67 | 165 | 49.7 | 50.3 | ? | ? |
| *P. p. dresseri* (Cambridgeshire) | 62.9 | 0.1 | 59–67 | 230 | 55.2 | 44.8 | 56.5 | 43.5 |
| *P. p. palustris* (Lund, Sweden) | 64.6 | 0.2 | 60–70 | 130 | 51.5 | 48.5 | 51.5 | 48.5 |



northern England and *dresseri* samples followed each other very closely, with both peaks in exactly the same positions, while the *palustris* sample was offset by an increase of 2 mm. There was also no difference in the ranges of wing lengths of the northern England and *dresseri* samples, nor in the mean values (table 1, two-tailed t-test: $t_{339} = 0.07$, $P = 0.945$), but the mean of the *palustris* sample was significantly greater than that of the northern England sample (table 1, two-tailed t-test: $t_{269} = 6.82$, $P<0.001$), again by 2 mm. This indicated that the northern England sample was from the same population as the *dresseri* group, and different from *palustris*. Finally, visual examination of birds from Cumbria and Cambridgeshire showed no difference in coloration, providing further evidence that birds in northern England (and Scotland) belong to *P. p. dresseri* and not *P. p. palustris*.

**Table 2.** Identification criteria for the separation of British Willow *Poecile montana* and Marsh Tits *P. palustris*. While those plumage criteria of high reliability will identify most birds correctly, none is conclusive in isolation and a combination of features is recommended for successful identification.

| | Willow Tit | Marsh Tit | |
|---|---|---|---|
| **Song**[1] | One song type of slow c. 2–7 descending whistling notes, at c. 3 notes per second | Variable, usually rapid mono- or disyllabic rattle of c. 8–19 notes, at c. 6–10 notes per second | **High reliability:** little overlap |
| **Chick-a-dee call**[2] | Does not include *pitchou* note. Terminal *dee* notes long, >0.25 secs. Typically *zi-zi taah taah taah* | Full call includes *pitchou* note. Terminal *dee* notes short, ≤0.2 secs. Typically *pitchou-dee-dee-dee* | |
| **Juvenile begging call** | Slow call of 2–5 descending notes, ?0.4 secs: e.g. *dee-doo-derr* | Rapid, high call of 2–5 even or descending notes, <0.3 secs: e.g. *eehs-is-it* | |
| **Bill** | Unmarked upper mandible | Whitish marks on proximal area of upper mandible | |
| **Cheeks**[3] | No contrast between whitish cheek and whitish neck sides; may be warm buff suffusion towards mantle | White cheek contrasts with grey-brown neck sides behind the ear-coverts | |
| **Wing panel** | Margins of secondaries and tertials often broad and pale buff/cream, contrasting strongly with mantle | Margins of secondaries and tertials often only slightly paler than mantle, with no strong contrast | **Medium reliability:** significant overlap |
| **Tail** | Outer pair of tail feathers >4 mm less than tip of closed tail | Outer pair of tail feathers <5 mm less than tip of closed tail | |
| **Wing length** | 55–63 mm | 58–67 mm | |
| **Cap**[4] | Black, with slight or no bluish gloss, or deep brown | Black, with obvious or slight bluish gloss | **Low reliability:** substantial overlap, high subjectivity |
| **Bib** | Diffuse at margins, may cover whole throat | Well defined, restricted to upper throat | |

[1] Marsh Tit has a rare song variant that is very similar to Willow Tit song.
[2] Caution is required as full call may not be given.
[3] Does not apply to juveniles, which show clean whitish cheek and neck sides in both species until majority of post-juvenile moult is completed by September.
[4] Juveniles of both species have dull black or deep brown caps until late September.

## Conclusions

Separating British Willow Tits and Marsh Tits remains difficult and many of the published identification criteria have been shown to be unreliable or highly subjective. With experience, separation of these two species can be straightforward, but it may not be possible to assign all individuals to species (particularly juveniles and those not seen or heard well) and it is best to leave these birds unidentified.

Features such as cap, bib, structure, colour of underparts, habitat and behaviour (except that of extensive nest excavation) appear to have limited or negligible value for identification, owing to the degree of overlap. Tail shape is of use only in the hand. Wing panel is more useful and less subjective, but is also undermined by a large degree of variation, overlap and misinterpretation, and should be used with caution, as a supporting characteristic only. Cheek pattern has less overlap than wing panel and appears to be a more reliable plumage feature (discounting juveniles), particularly the subtle warm buff neck sides on Willow Tits (where present) and a clear transition from white to cold grey-brown on Marsh Tits. Cheek pattern may also be easier to see than wing panel in the field. Bill marks offer the most objective and reliable visual means of separation but may be very difficult to see in the field or obscured on photographs and are therefore primarily of use for birds in the hand. Where visible, however, presence or absence of bill marks has a very high degree of reliability on its own.

Voice remains the most reliable distinguishing feature in the field, notably the diagnostic *pitchou* call of the Marsh Tit, which is unequivocal for identification. The longer, more buzzing 'dee' note of the Willow Tit's 'chick-a-dee' call is also diagnostic once learnt, although confusion may be caused by unfamiliarity or where county recorders receive only an ambiguous written description. Furthermore, lone birds or those visiting feeders may not call at all. Song is very useful, although the slow Marsh Tit variant is a potential pitfall. Juvenile begging calls are also diagnostic but are of limited value due to their brief availability.

While some identification criteria have been refined and improved, some discarded and the reliability of others quantified, the technique for the separation of Marsh and Willow Tits remains much as that stated by Perrins (1964) – in that no single physical feature is conclusively diagnostic, and a combination of several features must be used (table 2). Assessment of the following characteristics, in descending order of reliability and importance, is recommended for accurate separation: voice, presence/absence of bill marks (primarily in the hand or on photographs), cheek pattern, tail feather lengths (only in the hand), and presence/absence of broad pale margins to the tertials and secondaries that contrast strongly with the mantle. Bib shape and cap gloss may occasionally be useful but should be used only with extreme caution as minor supporting features.

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Mark Hancox

**396.** Adult or first-winter Marsh Tit *Poecile palustris,* Worcestershire, February 2009. The cheek pattern shows a clear demarcation between the whitish ear-coverts and the cold grey-brown wash on the neck sides, giving little contrast between the rear of the cheek patch and the mantle when compared to Willow Tit. Small pale marks are discernible at the proximal end of the upper mandible. Combined presence of both of these features will identify almost all non-calling Marsh Tits correctly, after the post-juvenile moult. Note the thick-necked appearance, due to posture, which may have been wrongly considered as suggestive of Willow Tit *P. montana.*

APPENDIX 1B

*Ringing & Migration* (2008) **24**, 88–94

# Ageing and sexing Marsh Tits *Poecile palustris* using wing length and moult

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Ageing and sexing Marsh Tits *Poecile palustris* presents some difficulties for ringers. Wing length has previously been found to be useful for sexing English Marsh Tits, although the replacement of all juvenile rectrices and greater coverts by first-year birds made ageing difficult. We examined Marsh Tits of known age and sex and found that 93.5% of birds could be sexed correctly using wing lengths of ≤ 62 mm for females and ≥ 63 mm for males. Wing length was also an indicator of age: many first-years had shorter wings, but most also retained some juvenile rectrices and greater coverts after the post-juvenile moult, and could be readily aged using these features. We found a primary moult period of 67 days for adult Marsh Tits, with a mean onset of 27 May.

The Marsh Tit *Poecile palustris* is a problematic species for ringers; males and females are similar in plumage (Svensson 1992) and current ageing techniques are subtle and unreliable (King & Muddeman 1995).

Nilsson (1992) found wing length to be a reliable method of sexing nominate-race Marsh Tits in Sweden, with males having longer wings. Gosler & King (1989) found a strongly bimodal distribution for wing length, due to sexual dimorphism, in a small sample of birds in south-central England. Using a larger sample, King & Muddeman (1995) were later able to validate the use of wing length for sexing birds from this same population, but they were unable to confirm the reliability of sexually dimorphic plumage characters, such as bib size, suggested by Gosler & King (1989). Svensson (1992) listed two criteria for distinguishing adult Marsh Tits from first-year birds after the post-juvenile moult (referred to as 'first-years' hereafter), these being shape of the rectrices (rounded and fresher in adults, pointed and worn in first-years) and retention of juvenile greater coverts (JGCs) in some first-years, creating a subtle moult limit. Nilsson (1992) found that first-years had shorter wing lengths than adults, although there was substantial overlap. Rectrix shape is used to age several tits (Svensson 1992), including the closely related Willow Tit *P. montana* (Laaksonen & Lehikoinen 1976) and Black-capped Chickadee *P. atricapilla* (Smith 1991), although King & Muddeman (1995) found it to be unreliable for their Marsh Tit population due to differences in wear and the tendency of some juveniles to replace the whole tail during the post-juvenile moult. King & Muddeman (1995) also found JGCs in only 2% of their sample (one bird), suggesting that this criterion may be of limited value. Current knowledge therefore suggests that, in England, only adult Marsh Tits undergoing wing moult during the summer (Ginn & Melville 1983) may be separated reliably from the majority of first-years.

The aims of this study were, firstly, to test King & Muddeman's (1995) main findings on the use of wing length, JGCs and rectrix shape to age and sex Marsh Tits, using a large sample of birds of known age and sex. Secondly, the relationship of wing length to age and sex, and the period of adult primary moult and post-juvenile moult, were investigated.

## METHODS

### Study sites and data collection

Research in the Monks Wood area (Cambridgeshire, eastern England, 52°24'N 0°14'W) between 1993 and 2008, and Wytham Woods (Oxfordshire, central England, 51°46'N, 1°19'W) between 2004 and 2007, generated morphometric data for 182 Marsh Tits of known age and sex over 663 handlings. Birds were caught using baited traps or mist nets, including 70 birds first ringed as pulli, and fitted with a unique combination of colour rings and a BTO aluminium ring. A total of 154 individuals were examined at Monks Wood and 28 at Wytham Woods. Breeding data, including laying and hatching dates, were collected from the Monks Wood population for 11 nests in 2005, 15 in 2006, 20 in 2007 and 17 in 2008. A weather station at Monks Wood provided data for the calculation of warmth sum values (the

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sum of daily maximum temperatures) from 1 March to 25 April (McCleery & Perrins 1998) each year until 2007.

### Ageing and sexing

Birds ringed as pulli were of known age on subsequent capture. Other birds were attributed to age groups based on the following criteria. Juveniles (EURING code 3J) could be aged due to the loose texture of the feathers and sparseness of underwing coverts (Jenni & Winkler 1994), first-year birds (EURING codes 3 and 5) were aged on first capture using rectrix shape where possible, and adults (EURING codes 4 and 6) could be aged on first capture during summer using the presence of wing moult. In the absence of wing moult, birds with no juvenile rectrices were not aged due to the possibility of first-years having replaced the tail and thus being indistinguishable from adults. Measurements of individuals examined as both first-years and adults were included in both age classes and, along with repeat measurements from adults in subsequent years, were analysed for evidence of an increase in wing length with age. Birds were sexed using the presence of a brood patch (breeding females) and breeding behaviour, including 'courtship-feeding', incubation and singing, with song being exceptional among female Marsh Tits (Broughton 2008).

In 2007, 53 known first-year birds from Monks Wood were assessed for the extent of post-juvenile moult, including the greater coverts (GCs). The number of retained JGCs was recorded for the right wing and tails were examined for the number and position of any feathers that had been replaced (numbered from innermost feather R1), these being identified by differential wear and shape. A small number of birds examined in 2003–06 provided additional data on tail moult (15 birds) and JGCs (four birds). Fourteen birds examined in 1993–95 and 2008 provided additional data for timing of post-juvenile moult.

### Wing length

Wing length (maximum chord, measured to 1 mm) was collected for 130 males and 100 females between July and March across all years, including 48 birds examined in both first-year and adult plumage and incorporated into both categories. Adults and first-years were examined in all months of the sampling period, with trapping effort deployed progressively throughout the study area until all birds of both age classes had been captured at each trap site. Bias towards trapping date and age or sex was thus avoided. Moult scores were recorded for adults undergoing primary moult (110 scores from 86 birds). Where the same adults were examined in consecutive years, only the first wing-length measurement was included in analyses. This may, however, have potentially excluded longer wing lengths from individuals as they age. To test this, the data were analysed for any change in wing length among 18 individual adults trapped in two different years. To test the effect of wear on an individual's wing length over the annual sampling period, which may have influenced the measurement recorded due to the date of sampling, two measurements of wing length for 24 individuals were compared after a period of at least three months during the same sampling period (pooled for age and sex due to small sample sizes: nine males, 15 females; 18 first-years, six adults). Measurement error was considered negligible due to 90% of birds being examined by one of the authors (RKB) and measurements being highly consistent among and between ringers involved.

### Statistical and moult analysis

Simple probability analysis and t-tests were used for the analyses of wing length. Primary moult of adults was investigated using an Underhill–Zucchini model (Underhill & Zucchini 1988) to determine moult duration and onset. We applied a Type 3 model to moult scores from birds undergoing active primary moult during the period 1993–2008 (excluding 1997 and 2002–03), converting the moult scores for each feather to mass of new feather material grown (primary moult mass score, or 'PMS'). PMS was derived by weighing each primary feather of a single Marsh Tit and expressing these values as a proportion of the total mass (Dawson 2005). The mass values for primaries 1–10 (inner–outer), as a proportion of the total, were as follows: 0.082, 0.084, 0.093, 0.110, 0.125, 0.133, 0.132, 0.122, 0.095 and 0.024. PMS was then calculated for each bird as the sum of each mass value multiplied by the moult score for the corresponding primary, and the sum divided by the number of moult score categories (5). This procedure gave a measure of moult stage that was less influenced than the standard numerical score by the variable lengths and weights of the different primary feathers (Dawson & Newton 2004), thus improving linearity.

The moult data were examined for annual differences that may have biased the overall estimates of moult onset and duration, and small sample sizes led to the exclusion of data from 1995 and 1998–99 from subsequent analyses. Excluding these years and fitting a regression on date to the PMS data for each year showed no statistically-significant difference between slopes (two-tailed F-test: $F_{9, 57} = 1.61$, $P = 0.13$), but clear differences in intercepts (two-tailed F-test: $F_{9, 57} = 4.03$, $P < 0.001$), consistent with a common duration of moult but with annual variation in the mean date of onset. We therefore modified the Type 3 analysis to allow for annual differences in mean onset of moult, and applied this to 77 mass-based moult scores from the 74 birds that were in active moult. The relationship between timing of moult and the breeding cycle was examined by correlating (Pearson product–moment correlation) the model output with mean annual laying dates. As data for the timing of egg-laying were available for only a small number of years, and date of egg-laying has been found to be strongly linked to spring temperatures in the Marsh Tit (Dolenec 2006), timing of moult was also correlated with warmth sum values, which were used as a proxy for laying date and were available for a greater number of years.

## RESULTS

### Ageing and moult

Only 29.4% (20/68) of first-year Marsh Tits had replaced one or more rectrices. Only six birds displayed symmetrical moult of at least one pair of rectrices (Fig 1), two of which had replaced most of the tail, except R6 on one bird and R4–R6 on the other. One bird had replaced the whole tail. Fifteen birds showed asymmetrical replacement of rectrices, with at least one rectrix replaced but not the corresponding feather on the other side of the tail. Of these, nine birds had replaced just one rectrix, most commonly R1 or R6, with asymmetrical replacement most often involving the outer tail feathers (Fig 1). Replaced feathers were not fully grown on birds examined between 11 July and 11 August across all years, except for one bird with a full-grown replacement on 14 July 2005 and one with shed feathers on 23 October 2005.

Retained JGCs were found in 93.0% of first-years (53/57). Only four birds (7.0%) were judged to have moulted all JGCs. Retained JGCs were distinctive due to an obvious moult limit in the feather tract, and were characterised by pale buffish tips and a slightly greater length than the new inner GC. Up to five JGCs were detected on some birds, although four was the most frequent (Fig 2). Juveniles were already undergoing post-juvenile body moult in 2007 by the time of first capture on 19 July, and the last birds had not completed until 10 October. The period of active growth observed in the rectrices was therefore consistent with true moult for most birds, although the extent of replacements due to accidental feather loss could not be determined. The timing of the onset of post-juvenile moult was difficult to determine due to lack of data, although juveniles examined up to 3 July in other years had not yet begun (14 birds). One of these birds had dropped or lost two outer tail feathers between 1 and 3 July, but this was attributed to accidental loss as juvenile rectrices are generally only moulted after body moult has begun (Jenni & Winkler 1994). Post-juvenile moult was therefore estimated to have generally begun in early to mid July and ended in early October, this period being somewhat later than the June–Sept window given by Ginn & Melville (1983).

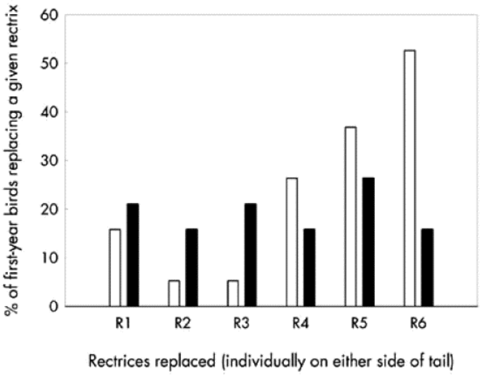

**Figure 1.** Percentage of those first-year Marsh Tits that replaced at least one given rectrix (R) on either side of the tail (n = 20 birds), showing whether each rectrix was replaced symmetrically in pairs (black, n = 6 birds) or asymmetrically and not in pairs (white, n = 15 birds). Only one bird (5%) replaced the whole tail.

For adult primary moult, Fig 3 shows PMS against date, fitted with the Type 3 Underhill & Zucchini (1988) model that shows the mean progression of adult primary moult in the Monks Wood Marsh Tit population. The mean (± se) date of onset of primary moult was 27 May ± 1.6 days, with a mean duration of 67.4 ± 3.8 days (n = 10 years). The entire population had completed primary moult by the end of August each year, marking the end of the period where wing moult could easily be used to separate adults and first-years. The mean date for completion of primary moult was 2 August, however, indicating that many adults could not be aged using moult after the end of July, and some from as early as mid July.

Although the mean date of onset of primary moult varied between years, there was no consistent trend for a progressively earlier or later onset across years (r = 0.05, *P* = 0.90, n = 10). Mean onset of primary moult was, however, highly associated with mean onset of egg-laying for the same population in those years with breeding data (2005–08)

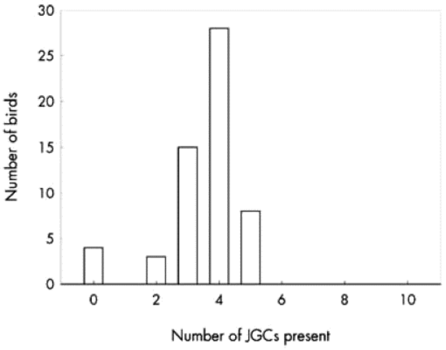

**Figure 2.** Frequency of the number of unmoulted juvenile greater coverts (JGCs) retained by first-year Marsh Tits (n = 58 birds).

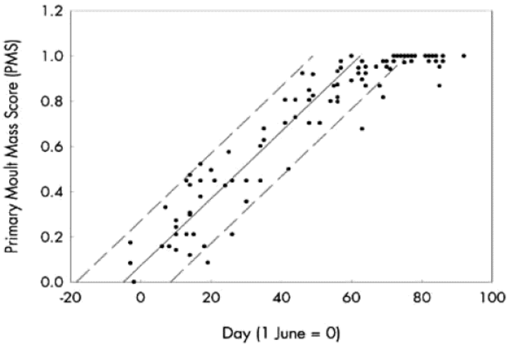

**Figure 3.** Marsh Tit primary feather moult across all years in the Monks Wood area (110 scores from 86 birds), expressed as primary moult mass score (PMS) against day, with a fitted model showing mean progression of moult (solid line) and the 2.5 and 97.5 percentiles (dashed lines). The model used was a Type 3 Underhill & Zucchini (1988) model, allowing for annual differences in mean onset of moult, and was derived from a subset of 77 scores from 74 birds in active moult.

(r = 0.97, *P* = 0.03, n = 4), although the sample size was small. There was a moderate negative relationship between earlier mean onset of moult and higher annual warmth sum values for the nine years for which data were available (1993–94, 1996, 2000–01, 2004–07), although this was not statistically significant (r = -0.54, *P* = 0.13, n = 9).

## Wing length for ageing and sexing

The wing lengths of 24 Marsh Tits with multiple measurements during one autumn–winter period showed a statistically significant decrease over that duration. However, the absolute difference between the means (± se) of the first and second measurements was negligible (respectively 62.5 mm ± 0.32, and 62.2 mm ± 0.35, n = 24; one-tailed paired t-test, $t_{23}$ = 2.77, $P < 0.01$). The effect of wear and sampling date on wing-length measurement was therefore thought to be minimal, enabling measurements from throughout the sampling periods to be included in the analyses. In addition, repeat wing-length measurements of adults over subsequent years showed no clear evidence of a consistent change in wing length with age after the first complete moult (two-tailed t-test, $t_{17}$ = 1.59, *P* = 0.07, n = 18). Although the *P* value was suggestive of a possible effect with such a small sample, and despite six of the 18 birds showing an increase in wing length (mean = 1.67 mm ± 0.21), three birds showed a decrease in wing length (all of -1 mm) and nine birds showed no change. Thus wing-length measurements of adults of all ages were included in analyses.

The mean (± se) wing length of male Marsh Tits was significantly longer than that of females (age classes combined, males: 64.2 mm ± 0.09, n = 130; females: 61.2 mm ± 0.10, n = 100; two-tailed t-test, $t_{217}$ = 21.94, $P < 0.001$), and significantly longer for adults than for first-year birds (sexes combined, adults: 63.6 mm ± 0.17, n = 103; first-years: 62.4 mm ± 0.15, n = 127; two-tailed t-test, $t_{213}$ = 5.44, $P < 0.001$).

The frequency distributions of wing lengths for the age and sex classes are shown in Fig 4. Empirical probability analyses indicated that, by classifying birds with wing lengths of ≤ 62 mm as females and those of ≥ 63 mm as males, only 8.0% of females and 5.4% of males would be wrongly classified. Such a classification would, therefore, assign 93.5% of unknown birds to the correct sex. Table 1 shows the probability of a bird of a given wing length belonging to a specific age/sex class, and the probability of an individual in that class having a specific wing length. This shows, for example, that while a bird with a wing length of 66 mm had a very high probability of being an adult male (91.7%), the probability of an adult male having a wing length of 66 mm was rather low (17.7%). Table 1 indicates that approximately half of all individuals in each

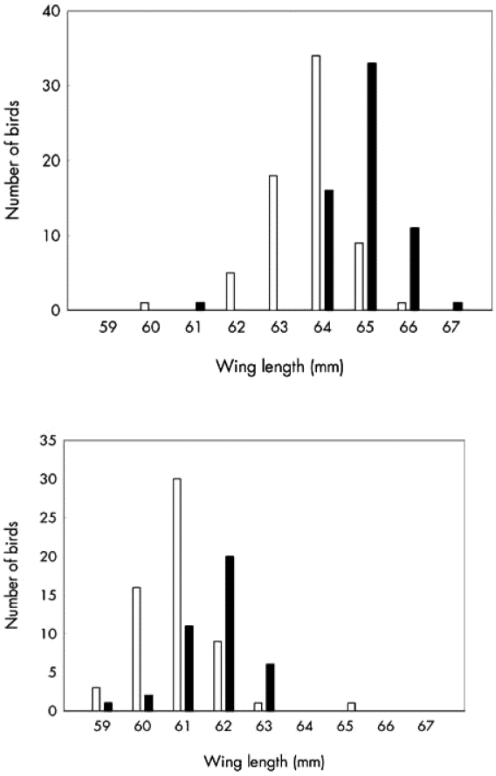

**Figure 4.** Wing lengths of first-year (white) and adult (black) Marsh Tits: (a) males, (b) females.

age/sex category displayed the same wing length: first-year female = 61 mm (50.8%), adult female = 62 mm (48.8%), first-year male = 64 mm (50.0%) and adult male = 65 mm (53.2%). In addition, the probability of assigning an individual to the correct age/sex class using wing length alone was between 58.8% and 100%, depending on class. These age and sex classifications and cut-off points may, therefore, be applied to birds displaying these wing lengths, albeit with varying degrees of caution.

The low incidence of rectrix replacement among first-years, with only one bird having replaced the whole tail, and the high incidence of a moult limit in the greater coverts, meant that all individuals could be aged independently of wing length. Table 2 indicates that most birds of known age and specified wing length could be sexed with an enhanced probability of success, due to birds of the wrong age class being excluded from consideration. Only first-years with a wing length of 62 mm remained problematic; first-years displaying any other wing length could be correctly assigned to the appropriate sex with a probability of 94.1% or more. Known adults could be correctly sexed with a probability of 91.7% or more, using wing length alone. Where sex was known but age was undetermined, however, the probability of assigning individuals to the correct age class was generally lower (Table 3). This was particularly true for females, where the maximum probability of correct ageing was 88.9% when discounting the outlying individual (with a wing length of 65 mm). The probability of a male or female being an adult nevertheless increased with wing length, though outliers were present in both sex categories.

## DISCUSSION

Nearly all (93.0%) juvenile Marsh Tits examined in the Monks Wood area had some retained JGCs, in contrast to the findings of King & Muddeman (1995) in another English population, who found JGCs in just one bird (2.0% of their sample). The moult limit is subtle yet distinctive and was unlikely to have been missed or misinterpreted in either study. In addition, King & Muddeman (1995) found that 14% of their sample appeared to have replaced the entire tail during the post-juvenile moult, whereas our study found that only one bird (1.7%) had replaced the entire tail, and only 29.4% had replaced any rectrices at all. These differences are notable, as King & Muddeman (1995) collected their data less than 15 years before the period of our study and approximately 100 km (at similar latitude) from our study site. Both studies may, therefore, have failed to detect annual variation in the extent of greater covert and rectrix moult due to data collection occurring in a small number of years. The extent of post-juvenile moult in the greater coverts and rectrices varies for the Blue Tit *Cyanistes caeruleus* and Great Tit *Parus major*, both between years and between regions (Ginn & Melville 1983, Cramp & Perrins 1993). Some of this variation has been explained by differences in hatching dates (*eg* Rymkevich & Bojarinova 1996), although annual variation in hatching dates for Monks Wood Marsh Tits was low across 2005–08, and breeding is single-brooded and highly synchronised within populations (our unpublished data, Wesołowski 1998). There is evidence that laying dates for British Marsh Tits have become earlier over recent decades (Baillie *et al* 2007), which could be expected to produce an earlier and more complete post-juvenile moult in more recent birds. The suggestion from our study that post-juvenile moult is occurring later than previously recorded (Ginn & Melville 1983), and is less complete (King & Muddeman 1995), is contrary to this, and could imply that foraging conditions have deteriorated for the juvenile Marsh Tits we examined. Differences in relative hatching dates may have been present between our study and that of King & Muddeman (1995), or other factors may have been responsible for the discrepancy. Repeat studies over a longer period, and over

**Table 1.** Probability, as %, of assigning individual Marsh Tits to the correct age and sex class based on wing length, where age and sex are unknown. Figures in parentheses are the probability (%) of an individual in each class displaying a specified wing length.

| wing length (mm) | First-year females | | Adult females | | First-year males | | Adult males | | n |
|---|---|---|---|---|---|---|---|---|---|
| 59 | 75.0 | (5.1) | 25.0 | (2.4) | 0 | (0) | 0 | (0) | 4 |
| 60 | 84.2 | (27.1) | 10.5 | (4.9) | 5.3 | (1.5) | 0 | (0) | 19 |
| 61 | 71.4 | (50.8) | 26.2 | (26.2) | 0 | (0) | 2.4 | (1.6) | 42 |
| 62 | 26.5 | (15.3) | 58.8 | (48.8) | 14.7 | (7.4) | 0 | (0) | 34 |
| 63 | 4.2 | (1.7) | 24.0 | (14.6) | 72.0 | (26.5) | 0 | (0) | 25 |
| 64 | 0 | (0) | 0 | (0) | 68.0 | (50.0) | 32.0 | (25.8) | 50 |
| 65 | 0 | (0) | 2.3 | (2.4) | 20.9 | (13.2) | 76.7 | (53.2) | 43 |
| 66 | 0 | (0) | 0 | (0) | 8.3 | (1.5) | 91.7 | (17.7) | 12 |
| 67 | 0 | (0) | 0 | (0) | 0 | (0) | 100.0 | (1.6) | 1 |
| *n* | 59 | | 41 | | 68 | | 62 | | 230 |

**Table 2.** Probability, as %, of assigning individual Marsh Tits to the correct sex class based on wing length, when age is known.

| Wing length (mm) | First-year females | First-year males | n (first-years) | Adult females | Adult males | n |
|---|---|---|---|---|---|---|
| 59 | 100.0 | 0 | 3 | 100.0 | 0 | 1 |
| 60 | 94.1 | 5.9 | 17 | 100.0 | 0 | 2 |
| 61 | 100.0 | 0 | 30 | 91.7 | 8.3 | 12 |
| 62 | 64.3 | 35.7 | 14 | 100.0 | 0 | 20 |
| 63 | 5.3 | 94.7 | 19 | 100.0 | 0 | 6 |
| 64 | 0 | 100.0 | 34 | 0 | 100.0 | 16 |
| 65 | 0 | 100.0 | 9 | 2.9 | 97.1 | 34 |
| 66 | 0 | 100.0 | 1 | 0 | 100.0 | 11 |
| 67 | - | - | 0 | 0 | 100.0 | 1 |
| n | 59 | 68 | 127 | 41 | 62 | 103 |

**Table 3.** Probability, as %, of assigning individual Marsh Tits to the correct age class based on wing length, when sex is known.

| Wing length (mm) | First-year females | Adult females | n (females) | First-year males | Adult males | n (males) |
|---|---|---|---|---|---|---|
| 59 | 75.0 | 25.0 | 4 | - | - | 0 |
| 60 | 88.9 | 11.1 | 18 | 100.0 | 0 | 1 |
| 61 | 73.2 | 26.8 | 41 | 0 | 100.0 | 1 |
| 62 | 31.0 | 69.0 | 29 | 100.0 | 0 | 5 |
| 63 | 14.3 | 85.7 | 7 | 100.0 | 0 | 18 |
| 64 | - | - | 0 | 68.0 | 32.0 | 50 |
| 65 | 0 | 100.0 | 1 | 21.4 | 78.6 | 42 |
| 66 | - | - | 0 | 8.3 | 91.7 | 12 |
| 67 | - | - | 0 | 0 | 100.0 | 1 |
| n | 59 | 41 | 100 | 68 | 62 | 130 |

a wider geographical area, would be required to address these questions.

The pattern of rectrix moult in juvenile Marsh Tits differed depending on whether replacement was symmetrical (feathers renewed in pairs) or asymmetrical (Fig 1). Asymmetrical moult involved the outer tail feathers much more frequently than in symmetrical moult. This may indicate that asynchronous replacement of outer rectrices may be due to accidental loss and not moult. In other British tits, partial tail moult appears to be symmetrical and centrifugal and tends to involve the central rectrices (Ginn & Melville 1983, Jenni & Winkler 1994). Aggression, including physical combat, is frequent among juvenile Marsh Tits during the post-dispersal settlement phase which occurs just prior to post-juvenile moult (Nilsson 1989, pers. obs.). It is possible that outer rectrices are lost during such aggressive encounters, particularly when birds may grapple with their claws during combat, and tails are fanned with the outer feathers exposed (Cramp & Perrins 1993). Such a hypothesis is difficult to prove once true moult is under way, however, and other mechanisms of accidental loss are also possible (attacks from predators or more dominant species), as is irregular or centripetal partial moult of the rectrices. The bird with a fully grown replacement outer rectrix on 14 July, and two birds with missing outer rectrices on 3 July and 23 October, had almost certainly lost them accidentally due to the disparity with the moult sequence.

The estimated duration of adult primary wing moult in Monks Wood, 67 days, is much shorter than the 80-day period given by Ginn & Melville (1983). This could be due to Ginn & Melville's (1983) choice of model (not correcting for feather mass grown), or to data being pooled from a national database and therefore incorporating clinal or local effects on moult onset and duration (Silverin *et al* 1993). We found evidence that the onset of moult was closely linked to the timing of the breeding cycle in our population, although our sample was small, and also some indication of a link to spring temperatures. Combined data from across Britain, incorporating populations at different altitudes and latitudes, may therefore miscalculate the duration of moult. However, more information is needed to establish a firm link with spring temperatures for the timing of moult and breeding in this species.

The date of mean onset of adult wing moult, 27 May, was 6–8 weeks before the estimated onset of post-juvenile moult (early to mid July), and was during the period when successful breeders were still feeding dependent fledglings (earliest date of brood dispersal: 29 May to 9 June in 2006–08, our data). All birds caught during June until mid July could, therefore, easily be aged based on presence of wing moult or whether first-years still retained recognisable characteristics of juvenile plumage (EURING code 3J, moult code J or P). Even after the post-juvenile moult, however, virtually all first-years in our population could be aged until at least March, based on the presence of JGCs and juvenile rectrices. After March, and into the breeding period, abrasion could limit the usefulness of these features in identifying first-year birds.

Our results support those of Nilsson (1992) and Gosler & King (1989) in finding wing length to be a reliable method of sexing full-grown Marsh Tits, and validate King & Muddeman's (1995) discriminant wing length of ≤ 62 mm for females and ≥ 63 mm for males in English birds. These measurements may apply to all British birds, although large samples of birds of known age and sex from a much wider geographical range in Britain would be needed to eliminate the possibility of any clinal variation in these traits. Caution should therefore be used when applying these classifications to untested populations, and care should be taken to avoid measurement error. If adopting the wing-length classifications reported in this paper, however, retained JGCs and rectrices should also be looked for in order to refine the age and sex determination with increased reliability. Wing length was found to be useful as an additional indicator of age, with first-years having significantly shorter wings than adults, and with approximately half of all birds that shared a wing length being of the same age and sex. Although there was overlap in wing length between classes, where birds could be independently sexed using, for example, behaviour or presence of a brood patch, then ageing using wing length was much more reliable. The use of genetic sexing techniques may be of use in this context for future population studies, in enabling birds lacking JGCs or juvenile rectrices to be aged retrospectively based on wing length and sex. Wing length was also indicative of sex where age was known, although the reliability of correct classification was limited.

These methods of ageing and sexing may also be tested on the closely related Willow Tit as, while there appears to be much more overlap of measurements for that species (Cramp & Perrins 1993), few data currently exist for birds of known age and sex of the British race.

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The authors thank Dr Alistair Dawson of the Centre for Ecology & Hydrology, Nigel Fisher (Conservator of Wytham Woods) and members of the Edward Grey Institute of Field Ornithology for additional Marsh Tit data, and Natural England for access to Monks Wood National Nature Reserve. We also thank the Editor and two anonymous referees for valuable comments on the manuscript. This work was funded by the Natural Environment Research Council (NERC).

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## APPENDIX 2

## CERTIFICATIONS OF AUTHOR’S CONTRIBUTION

Co-author certification of Richard K Broughton’s personal contribution to Paper I:

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

**From:** Bellamy, Paul [Paul.Bellamy@rspb.org.uk]
**Sent:** 06 July 2012 17:52
I certify that the statement below is an accurate representation of Richard K Broughton's contribution to the cited work: Paul Bellamy

**From:** jmandprothery [jmandprothery@talktalk.net]
**Sent:** 08 July 2012 11:19
I certify that the statement below is an accurate representation of Richard K Broughton's contribution to the cited work: Peter Rothery

**From:** Ross Hill [rhill@bournemouth.ac.uk]
**Sent:** 05 July 2012 17:26
I certify that the statement below is an accurate representation of Richard K Broughton's contribution to the cited work: Ross Hill

**From:** Hinsley, Shelley A. [sahi@ceh.ac.uk]
**Sent:** 05 July 2012 18:12
I certify that the statement below is an accurate representation of Richard K Broughton's contribution to the cited work: Shelley A. Hinsley

Richard K Broughton’s (RKB) personal contribution to this work involved the conception of the study in conjunction with S.A. Hinsley, and devising of the bird survey methodology, collecting approximately 90% of bird data, in addition to collection of approximately 30% of the ground-based vegetation data according to a methodology devised by S.A. Hinsley. RKB planned and executed all GIS mapping and spatial analyses of the bird data and the remote sensing data products, and performed all statistical analyses in consultation with P.E. Bellamy and P. Rothery. RKB drafted the text of the paper, incorporating the comments and suggestions of co-authors, and was ultimately responsible for approximately 85% of final content.

Co-author certification of Richard K Broughton’s personal contribution to Paper II:

Broughton, R.K., Hill, R.A., Freeman, S.N., Bellamy, P.E. & Hinsley, S.A. (in press). Describing habitat occupation by woodland birds using territory mapping and remote sensing data: an example using the Marsh Tit (*Poecile palustris*). The Condor.

**From:** Bellamy, Paul [Paul.Bellamy@rspb.org.uk]
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**From:** Ross Hill [rhill@bournemouth.ac.uk]
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**From:** Hinsley, Shelley A. [sahi@ceh.ac.uk]
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**From:** Freeman, Stephen N.
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Richard K Broughton’s (RKB) personal contribution to this work involved the conception of the study in conjunction with S.A. Hinsley, and devising of the bird survey methodology, collecting approximately 90% of bird data. RKB planned and executed all GIS mapping and spatial analyses of the bird data and the remote sensing data products, and performed all statistical analyses after consultation with S.N. Freeman. RKB drafted the great majority of the text, incorporating the comments and contributions of co-authors, and was ultimately responsible for approximately 85% of final content.

Co-author certification of Richard K Broughton’s personal contribution to Paper III:

Broughton, R.K., Hill, R.A., Henderson, L.J., Bellamy, P.E. & Hinsley, S.A. (2012) Patterns of nest placement in a population of Marsh Tits Poecile palustris. Journal of Ornithology 153:735-746.

**From:** Bellamy, Paul [Paul.Bellamy@rspb.org.uk]
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**Sent:** 05 July 2012 17:29
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**From:** Hinsley, Shelley A. [sahi@ceh.ac.uk]
**Sent:** 05 July 2012 18:14
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As lead author of this paper, Richard K Broughton (RKB) devised the study and collected 90% of field data after planning the bird survey methodology. RKB also carried out all GIS mapping and spatial analyses of the bird data and remote sensing data products. RKB conceived and supervised an MSc dissertation by L.J. Henderson which constituted an initial pilot study exploring a subset of this data, which determined the methodology adopted in this paper. RKB undertook all statistical analyses after consultation with a statistician. RKB drafted the text of the paper, incorporating the comments and suggestions of co-authors, and was ultimately responsible for approximately 95% of final content.

Co-author certification of Richard K Broughton’s personal contribution to Paper IV:

Broughton, R.K., Hill, R.A., Bellamy, P.E. &. Hinsley, S.A. (2011) Nest sites, breeding failure, and causes of non-breeding in a population of British Marsh Tits *Poecile palustris*. Bird Study 58:229-237.

**From:** Bellamy, Paul [Paul.Bellamy@rspb.org.uk]
**Sent:** 06 July 2012 17:50
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**From:** Ross Hill [rhill@bournemouth.ac.uk]
**Sent:** 05 July 2012 17:27
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**From:** Hinsley, Shelley A. [sahi@ceh.ac.uk]
**Sent:** 05 July 2012 18:13
I certify that the statement below is an accurate representation of Richard K Broughton's contribution to the cited work: Shelley A Hinsley

Richard K Broughton’s (RKB) contribution to this work involved the conception of the study and collection of 90% of nest-site data after devising the survey methodology, although co-authors and assistants helped in accessing and recording some nests. RKB conceived and supervised the MSc dissertation by Marchant (2006) that provided the vegetation survey data. RKB also designed and performed the data analyses, including all statistical analyses after initial consultation with a statistician (as noted in the acknowledgements). RKB drafted the text of the paper, incorporating the comments and suggestions of co-authors, and was ultimately responsible for approximately 95% of final content.

Co-author certification of Richard K Broughton’s personal contribution to Paper V:

Broughton, R.K., Hill, R.A., Bellamy, P.E. &. Hinsley, S.A. (2010) Dispersal, ranging and settling behaviour of Marsh Tits *Poecile palustris* in a fragmented landscape in lowland England. Bird Study 57:458-472.

**From:** Bellamy, Paul [Paul.Bellamy@rspb.org.uk]
**Sent:** 06 July 2012 17:50
I certify that the statement below is an accurate representation of Richard K Broughton's contribution to the cited work: Paul Bellamy

**From:** Ross Hill [rhill@bournemouth.ac.uk]
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Richard K Broughton’s (RKB) personal contribution to this work involved the conception of the study and collection of approximately 90% of bird data after devising the survey methodology, with some assistance provided by co-authors and others in accessing high nests, processing nestlings, and general fieldwork. RKB designed and performed the spatial and statistical data analyses, the latter after consultation with a statistician as cited in the acknowledgements. RKB drafted the text of the paper, incorporating the comments and suggestions of co-authors, and was ultimately responsible for approximately 95% of final content.

Co-author certification of Richard K Broughton’s personal contribution to Paper VI:

Broughton, R.K., Hill, R.A. & Hinsley, S.A. (in review) Relationships between patterns of habitat cover and the historical distribution of the Marsh Tit, Willow Tit and Lesser Spotted Woodpecker in Britain. Ecological Informatics.

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This work was conceived by Richard K Broughton (RKB), who undertook all spatial and statistical analyses using the sourced data. RKB drafted the manuscript, incorporating the comments and suggestions of co-authors, and was ultimately responsible for 95% of content.