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Do Highly Modified Landscapes Favour Generalists at the Expense of Specialists? An Example using Woodland Birds.

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ABSTRACT Demands on land use in heavily populated landscapes create mosaic structures where semi-natural habitat patches are generally small and dominated by edges. Small patches are also more exposed and thus more vulnerable to adverse weather and potential effects of climate change. These conditions may be less problematic for generalist species than for specialists. Using insectivorous woodland birds (great tits and blue tits) as an example, we demonstrate that even generalists suffer reduced breeding success (in particular, rearing fewer and poorer quality young) and increased parental costs (daily energy expenditure) when living in such highly modified secondary habitats (small woods, parks, farmland). Within-habitat heterogeneity (using the example of Monks Wood NNR) is generally associated with greater species diversity, but to benefit from heterogeneity at a landscape-scale may require both high mobility and the ability to thrive in small habitat patches. Modern landscapes, dominated by small, modified and scattered habitat patches, may fail to provide specialists, especially sedentary ones, with access to sufficient quantity and quality of resources whilst simultaneously increasing the potential for competition from generalists.

KEYWORDS: Airborne remote sensing, habitat fragmentation, marsh tit, parkland, phenology

Introduction

The UK is a relatively small set of islands with a long history of habitat modification (Darby, 1951; Johnston & Doornkamp, 1982). The current human population is approximately 60.5 million (Office for National Statistics) and is predicted to reach 70 million by 2031 (Carvel, 2007). Thus modification of the landscape is only likely to increase as exemplified by a recently declared need to build 5 million new houses by 2027.

In terms of overall landscape structure, human habitat modification has had two large-scale contrasting effects. Initially, the natural land cover (mostly forest) was replaced and fragmented, increasing landscape heterogeneity (Rackham, 1986). More recently, agricultural intensification has decreased the heterogeneity of farmland by removing much of the remaining fragments of semi-natural habitat, increasing field sizes and promoting large-scale monoculture (Donald *et al.,* 2001; Robinson & Sutherland, 2002). About 65% of mainland UK and 75% of England is occupied by agricultural land and 50% of agricultural land in England is classed as arable/horticultural (Haines-Young *et al.,* 2000). Thus changes in agricultural land use and farming practices are major factors driving alterations in landscape structure in the UK (Benton *et al.,* 2003). Agricultural impacts on biodiversity have been well documented, especially in the case of the decline of farmland birds (Aebischer *et al.,* 2000; Vickery *et al* 2004). Measures to increase farmland biodiversity and ecological productivity include habitat creation as well as changes in management practices and hence also contribute to restoring structural heterogeneity. However, crop production remains the primary purpose of farmland and therefore, although the uptake of agri-environment schemes may eventually occur on a national scale, individual habitat patches and margins are relatively small and the resulting structure is fine-grained.

Where land is at a premium in heavily populated modern landscapes, habitat patch sizes are likely to be small and connectivity high. This creates mosaics with a high proportion of edge-habitat and a lack of large areas of single habitat types. Such edge-dominated, small-patch landscapes tend to favour generalist species at the expense of specialists (Lovejoy *et al.,* 1984; Askins *et al.,* 1987; Simberloff & Cox 1987, Saunders *et al.,* 1991; With & Crist 1995). Habitat fragmentation may also be more severe than is apparent from the presence of physical gaps alone. Many semi-natural habitats, especially parks and gardens, are dominated by exotic plant species which may support few invertebrates and hence create functional foraging gaps for higher taxa such as birds (Reichard *et al.,* 2001). Exotic plant species may also present birds and other animals with phenological gaps – even if they support significant invertebrate populations, their timing of flowering or leafing may be inappropriate for native species. In addition, climate change (both long term and acute events) may interact with the above factors increasing habitat instability to which specialists may be more vulnerable than generalists. Recent work on the effects of climate change and increasing spring temperatures in Europe has also identified the possibility of a temperature-induced mismatch between timing of breeding in birds and the timing of the peak availability of their food supply (Visser *et al.*, 1998; Visser *et al.,* 2004).

In this paper, we investigate the consequences of habitat fragmentation for two generalist species of arboreal insectivorous birds which feed their young principally on tree-dwelling caterpillars. Great tits *Parus major* and blue tits *Cyanistes caeruleus* were originally forest birds, but now also breed in a range of secondary habitats including farmland, parks and gardens. In the UK with its long history of deforestation, virtually all deciduous woodland could be regarded as secondary. Thus, we use the terms primary and secondary habitat within a UK context, where large

woods constitute the least modified and best available "primary" woodland habitat and small woods, parks and farmland comprise more highly fragmented and modified "secondary" habitats. We demonstrate that even these apparently adaptable tits have reduced breeding success and higher parental costs in secondary habitats due to fragmentation and gap effects. We also examine how climate interacts with bird ecology and habitat suitability. The implications of these results for the persistence of habitat specialists compared to generalists in highly modified landscapes are discussed with reference to a third parid, the marsh tit *Poecile palustris* which is still largely confined to mature deciduous woodland. Although the terms "generalist" and "specialist" imply a dichotomy, in reality species will comprise a continuum depending on their responses to the availability and quality of particular key resources. The effects of fine-grained landscape-scale habitat variation are also considered in relation to heterogeneity within a single habitat type using woodland (Monks Wood National Nature Reserve, NNR) as an example.

Methods

Habitat heterogeneity

Monks Wood NNR (52°24' N, 0°14' W) comprises 157 ha of mixed deciduous woodland in Cambridgeshire in eastern England (Gardiner & Sparks, 2005) (Figure 1). The boundaries of the NNR are as shown in Figure 1b and 1d. The additional block of woodland across the road to the south (Figure 1a and 1c) is a privately owned conifer plantation (Bevill's Wood). A tree species map of Monks Wood was derived from supervised classification of Airborne Thematic Mapper (ATM) multi-spectral data from 2003 (George, 2005). Different types of vegetation cover including different tree species have characteristic reflectance spectra due to differential

reflection of solar radiation (Carleer & Wolff, 2004). Tree species also differ in leaf phenology, e.g. timing and rate of senescence, increasing the differences in reflectance spectra. Thus, using ATM data from five images of the wood, the six most abundant tree species (55% common ash *Fraxinus excelsior*, 21% English oak *Quercus robur*, 14% field maple *Acer campestre*, 7% aspen *Populus tremulus*, 2% silver birch *Betula pendula* and 1% elm *Ulmus* spp.) in the top canopy (minimum height threshold of 8 m) were mapped with an accuracy of 89%.

Top canopy height and sub-canopy understory height were mapped using airborne Light Detection And Ranging (LiDAR). Airborne LiDAR can describe vegetation structure at both high resolution (sub-metre) and at a landscape-scale (Lefsky *et al.,* 2002; Lim *et al.,* 2003; Vierling *et al.,* 2008) and thus has particular value in ecological applications (Hill *et al.,* 2004; Bradbury *et al.,* 2005; Hinsley *et al.,* 2006, 2008). LiDAR uses a laser range finder to measure the height of points beneath the flight-path of an aircraft. Short duration pulses of near infrared laser light are fired at the ground and the return signals reflected from the ground and surface features such as trees and buildings are recorded (Wehr & Lohr, 1999). The timing of the returns, combined with measurement of the aircraft's orientation and position, allow the 3D position of the points to be calculated and geo-referenced. Digital models of the surface of the ground and of vegetation canopy height can then be derived from these measurements (Hill *et al.,* 2002; Gaveau & Hill, 2003; Hill & Thomson, 2005). The LiDAR data for the Monks Wood top canopy model were acquired on June 10th 2000 using an Optech Airborne Laser Terrain Mapper (ALTM) 1210 scanner with a 10 kHz laser pulse repetition rate, scan angle of ± 10^{o} and a post spacing of one hit per 4.83 m^{2}. For the understory model, data were acquired on 14th April 2003 and 26th June 2005 using an Optech Inc. ALTM-3033 with a 33 kHz laser pulse repetition rate. The

April (leaf-off) data were acquired at an average flying altitude of 980 m, with a scan half angle of 15^{o} generating 1 laser hit per 1 m^{2}, whilst the June (leaf-on) data were acquired at an average flying altitude of 1,125 m, with a scan half angle of 20^{o} generating 1 laser hit per 2 m^{2} (Hill, 2007).

Fragmentation and reproductive success

Reproductive performance of great tits and blue tits was monitored for pairs breeding in nest boxes in large woods, small woods, urban parkland and farmland. The large woods comprised Monks Wood (36 boxes) and Brampton Wood (52^{o}19' N, 0 ^{o}16' W, 132 ha, 22 boxes) in Cambridgeshire. Both are mixed deciduous woodlands in which the dominant tree species are common ash, English oak and field maple, with Brampton Wood also having some areas of spruce *Picea* spp. and pine *Pinus* spp. The understory in both is predominantly hawthorn *Crataegus* spp., blackthorn *Prunus spinosus* and hazel *Coryllus avellana* (Collins *et al.,* 2005). Up to 53 boxes were located in up to 36 small woods (0.1-1.39 ha) in Cambridgeshire and south Lincolnshire. All are mixed deciduous woods with the same dominant tree and understory species as the two large woods, but with additional small numbers of a wide range of species. All these woods are part of a long-term study of woodland bird ecology in eastern England (e.g. Hinsley *et al.,* 1999, 2006). The landscape in this area is dominated by intensive arable agriculture.

Breeding performance in parkland was monitored in up to 26 boxes in Bute Park (51^{o}29' N, 3 ^{o}11' W, c. 53 ha) in the centre of Cardiff, south Wales and in up to 42 boxes in the Cambridge Botanic Gardens (52^{o}12' N, 0 ^{o}08' E, c. 25 ha). Bute Park comprises a mixture of mown grassland, sports pitches, an arboretum, plant nurseries and areas of more natural woodland dominated by sycamore *Acer pseudoplatanus,*

Norway maple *Acer platanoides* and common lime *Tilia europaea*. The Cambridge Botanic Gardens, in the centre of the city, is a formally managed arboretum with garden displays, mown grass, water features, greenhouses and visitor facilities, plus some small areas of less heavily managed vegetation. At both sites, tree species diversity is high with many exotics (broadleaves and conifers) often planted in broad taxonomic groups within which many species and varieties are represented. The park and gardens are both heavily used by the public.

Farmland breeding tits were monitored in 75 tit boxes and 15 sparrow boxes (each with three compartments) making a total of 120 "boxes". The boxes were located in hedgerow trees, hedges and the occasional small clump of trees across about 9 km^2 of intensive arable farmland in Buckinghamshire, east central England (51^{o}57' N, 1 ^{o}00' W). The trees were mostly English oak and common ash and the hedges mixed hawthorn, blackthorn, hazel and elm plus small amounts of other species.

At all sites, boxes were visited approximately weekly from the end of March until July. Parameters defining breeding success were recorded as follows: (i) first egg date, (ii) clutch size, (iii) mean chick weight (g) at 11 days of age, (excluding runts) and (iv) the number of young fledged. Chicks were weighed to 0.1 g using a spring balance. Mean chick body mass provided an estimate of territory quality because it integrates the availability and abundance of food in the territory with the adults' abilities to collect it and deliver it to the young (Hinsley *et al.,* 2002, 2006). Previous work has also shown that heavier young are those most likely to survive to breed (e.g. Perrins & McCleery, 2001).

Results were examined for three years (2005 to 2007) for all sites except farmland for which data were available only for 2007. In total, data were available for two large woods, about 30 small woods, two urban parks but only one farmland site. Thus to

facilitate analysis between habitat types, the farmland data were divided by an arbitrary east/west division of the site into two approximately equal parts. To test for differences in performance in the different habitat types, a mixed model with fixed effects for habitat type, year and type x year interaction, and random effects for site, site x year interaction and nest box was used. The model allowed for correlation between observations on nest boxes from the same site, in a particular year and/or in different years, and thereby avoided the pseudo-replication problem of treating observations on all boxes as statistically independent. The model was fitted by the method of residual maximum likelihood (REML) using the statistical package Genstat 7 (Patterson & Thompson, 1971).

Structural and functional gaps

The influences of structural and functional gaps on breeding success were examined by monitoring birds breeding in the four different habitats as described above. The effects of such gaps on the adults themselves were investigated in two habitat types (large wood and park) by measuring the daily energy expenditure (DEE) of adults feeding large (10-11 days of age) nestlings (Hinsley *et al.,* 2008). Adults foraging in patchy habitat waste time and energy simply crossing gaps to reach suitable foraging locations (Hinsley, 2000). Increased adult energy expenditure may be detrimental for long-term adult survival (Daan *et al.,* 1996) and in the shorter term may reduce food delivery to the nest if adults spend more time foraging for themselves.

In Bute Park, structural gaps in the tree canopy were common. The percentage of gap in the canopy within a 30 m radius of each nest box was calculated from a LiDAR top canopy model (data acquired in June 2004, Hinsley *et al.*, 2008) derived as described above for Monks Wood (Figure 1c). In Monks Wood, structural gaps were

rare, but functional gaps were created by the patchy availability of oak trees (Figure 1b) which comprise a prime source of the caterpillars essential for rearing young (Fischbacher *et al.,* 1998). Thus, the percentage of oak in the canopy within 30 m of each box was calculated from the Monks Wood tree canopy map (Figure 1b). English oak was uncommon in the park and largely absent within 30 m of any box.

The DEE of free-living great tits and blue tits feeding young was measured in Bute Park and Monks Wood using doubly labelled water (Speakman, 1997). This technique uses the differential turnover of oxygen-18 (excreted from the body in water and carbon dioxide) and deuterium (excreted in water) to measure carbon dioxide production which can then be converted to energy expenditure. The two isotopes are stable, but being heavier than the commonly occurring forms of oxygen and hydrogen can be measured in blood (or urine) samples using a mass spectrometer. The technique has been used on a wide range of animals, including humans, and provides the best means of measuring energy expenditure in free-living animals performing their normal activities.

Energy expenditure was measured in both great tits and blue tits in Bute Park and in great tits only (too few boxes were occupied by blue tits) in Monks Wood in 2003 and 2004. Measurements were also made in 2005 in the park to compensate for the small sample size (one bird) in 2003. Full details are given in Hinsley *et al.*, (2008). All procedures were carried out under licence (see acknowledgements). The relationships between DEE and the presence of structural gaps (percentage canopy gap) in Bute Park and of functional gaps (percentage of the tree canopy which was not oak) in Monks Wood were described using quadratic regression.

Timing, temporal gaps and climate effects

In Monks Wood and Bute Park, the timing and progression of tree leafing was scored on a scale of 0 to 6 as follows: 0 = tightly closed dormant buds, 1 = swollen buds, no green showing between scales, 2 = swollen buds, green showing between scales, 3 = leaf beginning to emerge from bud, 4 = leaf half open, 5 = leaf fully open, but not fully expanded, 6 = leaf fully expanded. Six English oak and six common ash were recorded at both sites; in addition, six sycamore and six Norway maple were recorded in the park because they were abundant and early. The overall state of bud burst/leaf expansion for the bottom half of each tree was scored at least once a week. Results were expressed as an average per species for oak and ash, and for the two *Acer* spp. combined.

Timing of breeding of great tits and blue tits in all four habitat types was assessed using the date on which each female laid her first egg, recorded by monitoring nest boxes as described above. Timing of breeding in tits can vary quite widely between years (e.g. Perrins, 1970) and thus results are shown for two years to illustrate the pattern across the four habitats in both a relatively early (2007) and relatively late (2006) year (although data were only available for farmland in 2007). Results for 15 years (from 1993 to 2007) for Monks Wood, Brampton Wood and the small woods were used to demonstrate the influence of local climate on the timing of breeding and how this relationship was influenced by habitat fragmentation. The mean first egg date for great tits in each of the two large woods and for all the small woods combined were calculated for each of the 15 years. In general, warm springs are more favourable for breeding success in tits than cold ones (Slagsvold, 1976, Hinsley *et al.*, 1999). The warmth sum, calculated as the sum of the maximum daily temperature from March 1st to April 25th (McCleery & Perrins, 1998), was used as an index of

local spring warmth. Maximum daily temperatures were obtained from a Meteorological Office weather station located about 100 m from Monks Wood and *c.* 9 km from Brampton Wood. The relationships between egg dates and the warmth sum were described using linear regression and the slopes and elevations of the lines for Monks Wood, Brampton Wood and the small woods were compared by ANCOVA.

The interaction of climate with habitat structure and the consequences for breeding success were illustrated using data for Monks Wood from two years with contrasting spring weather. In 1997, spring was early and warm (mean first egg date 9th April, warmth sum = 759) whereas in 2001 it was late and cold (mean first egg date 27th April, warmth sum = 568). The relationships between mean chick body mass, i.e. chick quality, and canopy height (obtained from the LiDAR top canopy model for Monks Wood, Figure 1c) around the nest box were compared in these two years using linear regression (Hinsley *et al.,* 2006).

Results

Habitat heterogeneity

The heterogeneity of Monks Wood in terms of both structure and tree species composition is illustrated in Figure 1. Aerial photography (Figure 1a) provided information about relatively large features such as fields and the main glades and rides, and some qualitative indication of canopy evenness or closure. The tree species map derived from ATM reflectance data (Figure 1b) showed that species composition is dominated by common ash. Despite this, the six main species are well mixed across the wood, but with heterogeneity tending to be greater in the centre and the east. The canopy height model provided by LiDAR (Figure 1c) showed that top canopy height was highly heterogeneous across the wood, with the tallest trees concentrated more

towards the edges and tending to reflect the distribution of ash trees (Figure 1b). The lower and more open character of the canopy in the centre of the wood is not apparent in the aerial photograph (Figure 1a). The sub-tree canopy understory model (Figure 1d) also showed considerable variation in structure across the wood with the tallest shrub layer in the west and central eastern parts of the wood.

Fragmentation and reproductive success

Overall, reproductive success in both great tits and blue tits declined with declining habitat patch size (e.g. from large woods to small woods) and with increasing fragmentation (e.g. from woods to park/farmland) (Figure 2). Both fewer (Figure 2c, & f) and poorer quality (i.e. lower body mass, Figure 2b & e) young were reared in secondary habitats. The models showed that the declining trend from large to small to park/farmland was significant for both species for all three parameters of breeding success except numbers fledged for great tits where some effect was suggested by the *P* value of <0.10 (Table 1). For great tits there was a Type x Year interaction for chick mass and the number fledged indicating differences between habitat types between years (Figure 2). There were no such interactions for blue tits. The declining trends suggested that farmland and parkland were similarly poor, but to determine the relative status of farmland will require more data.

Structural and functional gaps

Despite their reduced breeding success, great tits in Bute Park worked harder than those in Monks Wood (Park: DEE = 86.3 ± 12.3 kJ day^{-1}, $n = 12$; Wood: DEE = 78.0 ± 11.7 kJ day^{-1}, $n = 23$; $t = 1.97$, $P = 0.058$) and because of the smaller brood sizes, nearly twice as hard for each chick reared (Park: DEE per chick = 14.6 ± 4.8 kJ day^{-1};

Wood: DEE per chick = 8.9 ± 1.7 kJ day^{-1}; $t = 5.12$, $P < 0.001$). The parental costs of rearing young increased as the amount of gap around the nest site increased (Figure 3a). In Bute Park, the tits that were working harder than the average for all the birds measured in the park were those with more than about 35% gap around their boxes. In Monks Wood, there was no relationship between parental DEE and the presence of structural gaps around the boxes because the amount of gap was small (less than 1% for 21 out of 36 boxes and less than 10% for 26 boxes) and less than that in the park (Wood: Gap = 1 ± 4%, n = 22; Park: Gap = 33 ± 23%, $n = 26$, $t_{26} = 7.02$, $P < 0.001$). However, a functional gap effect was evident in that females with less than about 30% oak around their boxes (i.e. about 70% "non-oak") were working harder than the average for all birds measured in the wood (Figure 3b) (Hinsley *et al.*, 2008).

Timing, temporal gaps and climate effects

Signs of leafing, i.e. bud swelling, in oak and ash started a little earlier in Bute Park than in Monks Wood, but timing of leaf emergence and expansion were similar (Figure 4). However, overall timing of leafing in the park was earlier due to the much larger number of tree species; leaf expansion in the maples started about 20 days before that in oak and ash in the wood (Figure 4).

Previous work has shown timing of breeding in both great tits and blue tits to be later in small woods compared to large woods (Hinsley *et al.,* 1999), whereas urban great tits, but not blue tits, tend to be early (Perrins, 1979, Cowie & Hinsley, 1987). These same trends were found at our sites (Table 2). Farmland birds were late compared to large woods, but unlike woodland where blue tits tend to start breeding a little earlier than great tits, timing was similar in both species on farmland (Table 2).

However, as shown here (and see below), timing of breeding in tits can vary substantially between years and data were only available for farmland for one year.

Local climate, summarised as a simple temperature index, the warmth sum, influenced timing of breeding in great tits such that egg laying started earlier in warmer springs (Figure 5). Over the 15 years from 1993 to 2007, the mean first egg date varied by 22 days in the two large woods, Brampton and Monks Wood, and by 30 days across large and small woods. The interaction between site and warmth sum was not significant in an ANCOVA of first egg date on these two variables, and hence the regression lines did not differ in slope between sites ($F_{2,39} = 0.08$, $P > 0.200$). However, the lines did differ significantly in elevation ($F_{2,41} = 17.0$, $P < 0.0005$), the common slope (± SE) being -0.0687 ± 0.0092. The mean first egg dates (± SD) for the three sites were Brampton Wood: 18.5 ± 5.8, Monks Wood: 20.0 ± 6.6 and small woods: 26.4 ± 5.6. Therefore, the significant difference in elevation was almost entirely a consequence of the difference in timing of breeding between small and large woods.

Climate also influenced great tit breeding performance in Monks Wood in relation to habitat selection; mean chick body mass increased with canopy height in warm springs, but decreased with height in cold springs (Figure 6).

Discussion

Great tits and blue tits are common and widespread inhabitants of secondary habitats, but even as generalists, the birds pay costs in terms of both reduced breeding success and higher parental energy expenditure in comparison to their performance in continuous woodland. Even in woodland, an effect of functional gaps, i.e. “non-oak” foraging habitat, was detected. There was little or no English oak near the nest boxes

in Bute Park and exotic tree species were common, as they are in many secondary habitats. Therefore, both structural and functional gaps, and their concomitant ill effects, are likely to be widespread in secondary habitats. For example, as urbanisation increases, small arboreal insectivores are typically the first to disappear (Clergeau *et al*., 1998); urban avifaunas are characterised by medium-sized, ground-feeding granivores (Marzluff *et al.,* 2001). In addition to rearing fewer and poorer quality young, adult survival in secondary habitats may also be reduced. Increased energy expenditure and late breeding have both been linked to lower adult survival (Thomas *et al.,* 2001; Nilsson & Svensson, 1996), but other factors (such as artificial food and warmer urban temperatures) associated with some secondary habitats may have a positive influence on survival (see below).

Evidence from blue tits breeding in adjacent forest types in the south of France (Dias & Blondel, 1996) and from other studies (van Noordwijk *et al.,* 1981, Lambrechts & Dias, 1993) has shown that timing is partly under genetic control. Immigrants may mistime their breeding attempts relative to the local food supply and suffer reduced success, increased parental costs and lower survival (Thomas *et al.,* 2001). Timing is also profoundly affected by climate at both local and geographical scales (Slagsvold, 1976; McCleery & Perrins, 1998). Given that timing differs between habitat types (Table 2, Figure 5) as well as forest types, the potential for climate change to cause mismatching between rates of plant and insect development, bird reproductive condition and the cues birds use to initiate breeding is substantial (Visser *et al.,* 1998; Sanz, 2003). Single-brooded species may be most at risk, but climate factors can also affect multi-brooded species, especially by reducing the number of broods produced each year (Peach *et al.,* 2004). Small and modified habitat

patches may be particularly vulnerable to climatic effects, for example, due to exposure and drying of soils under drought conditions (Saunders *et al.,* 1991).

Paradoxically, although great tits and blue tits breed less well and at greater cost in secondary habitats, the national UK populations of both have increased (British Trust for Ornithology, 2006). As small, hole-breeders, tits can be limited by nest site availability (e.g. East & Perrins, 1988) and the major cause of annual mortality is starvation/predation in cold winter weather (Newton, 1998). Many secondary habitats, especially gardens, (but also primary woodland sites) are now supplied with nest boxes and a majority of households provide food for birds, especially in winter (Cowie & Hinsley, 1988; Cannon *et al.*, 2005). The national success of these two species may therefore depend at least in part on the fortuitous provision of both nest sites and food by humans and a trend in the UK towards milder winters. However, the success of great tits and blue tits in exploiting these new resources may be detrimental for other, less adaptable species, and those limited by other factors. For example, usurpation of willow tit *Poecile montanus* nest holes by great tits and blue tits has been implicated in the long-term decline (*c.* 80% in last 40 years) of this species (Maxwell, 2002; Gregory *et al.,* 2002).

By definition, habitat specialists are likely to be more vulnerable to loss, fragmentation and modification of their primary habitat, less likely to exploit secondary habitats and prone to competition/predation from increasing numbers of generalists. Sedentary species and poor dispersers will be at particular risk. Marsh tits are sedentary, hole-breeding, arboreal insectivores similar in size to blue tits, but seldom occur in secondary habitats. They maintain year-round, relatively large (*c.* 4-5 ha) territories in mature deciduous woodland and require the presence of a well-developed shrub layer (Broughton *et al.,* 2006; Hinsley *et al.,* 2007). Unlike great tits

and blue tits, they do not commonly exploit human-provided food and rarely use nest boxes. Also unlike great tits and blue tits, the national UK population of marsh tits has declined by more than 50% in the last 25 years (Gregory *et al.,* 2002) and declines have been greater in smaller woods set in less wooded landscapes (Amar *et al.,* 2006). In recent years, the Monks Wood marsh tit population has been stable at about 22 pairs, whereas numbers in smaller, surrounding woods fluctuate from one (or none) to five pairs (R. Broughton, unpubl. data). In 2006, immigrants from these smaller woods comprised about 65% of juveniles present in the autumn in Monks Wood. In 2007, conditions during chick rearing were poor (cold, wet and windy), and probably disproportionately so in these smaller woods, and the proportion of immigrant juveniles fell to about 50%, raising a real possibility of inbreeding. It also highlights the vulnerability of sedentary specialists to the loss of particular key sites. Without Monks Wood, the marsh tit populations in the surrounding small woods would probably collapse. Thus habitat fragmentation in this landscape where woodland is sparse and highly fragmented (Bellamy *et al.,* 1998) has at least the potential to be more detrimental for the specialist marsh tit than for the more generalist great tit and blue tit. However, as discussed above, even these two adaptable species fare less well in secondary habitats, which bodes ill for less mobile, more specialist species.

Within a particular habitat type, such as Monks Wood in Figure 1, heterogeneity contributes to diversity. For example, the numbers of nightingales *Luscinia megarhynchos* in Monks Wood has declined to 0-2 pairs in recent years as the wood has matured and the habitat structure required by this species has become rare (Gardiner & Sparks, 2005). Conversely, re-growth after widening of some rides has increased the availability of low bushy vegetation allowing whitethroats *Sylvia communis* to colonise these interior patches. In addition to the numerous biotic and

abiotic differences between large and small habitat patches (Saunders *et al.,* 1991), a key factor in the ability of a species to exploit heterogeneity at any scale is mobility. A poorly dispersing woodland specialist can traverse unsuitable woodland habitat, but may have less success in moving between landscape elements (Gjerde & Wegge, 1989; Matthysen & Currie, 1996). The provision under agri-environment schemes of relatively small and dispersed habitat patches across a large proportion of UK farmland has a good chance of success for at least some species of farmland birds because they are relatively mobile and adept at exploiting localised and shifting food resources (Newton, 1972). Conversely, small, dispersed woods will not maintain marsh tits. The lesser spotted woodpecker *Dendrocopos minor* is another woodland species in steep decline (Gregory *et al.,* 2002). In contrast to the sedentary marsh tit, it is highly mobile with a home range size of several hundred hectares (Wiktander *et al.,* 2001), but for specialists, habitat quantity goes hand-in-hand with habitat quality (Olsson *et al.,* 2001). If modern landscapes are to provide for specialists as well as generalists, they will need to contain certain minimum quantities of good quality habitat. Given the conflicting and wide-ranging pressures on land use in modern landscapes, this presents a considerable challenge.

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Figure 1. Illustration of habitat level heterogeneity using Monks Wood NNR as an example. a) aerial photograph, b) tree species distribution: light green = common ash, red = English oak, dark green = field maple, purple = aspen, pink = silver birch and yellow = elm spp., c) top canopy height: tallest trees, *c*. 16-23 m = orange and reds, medium heights, *c*. 8-16 m = light blue, greens and yellow, lower levels *c*. 1-8 m = purple and dark blues; surface of the ground, < 1 m = pale yellow, d) sub-canopy understory height: increasing height indicated by darker shading.

Figure 2. Reproductive success of great tits and blue tits breeding in different habitats. Mean values are shown for each habitat type for each year (2005-2007); note: data only available for farmland for 2007. For clarity, for each habitat type, the standard error (SE) of the mean is shown only for the year with the largest SE. Closed circles, solid lines = 2005, open circles, dotted lines = 2006, closed triangles, dashed lines = 2007.

Figure 3. The influence of a) structural gaps in the tree canopy in Bute Park and b) functional gaps in the tree canopy in Monks Wood on the DEE of great tits and blue tits feeding nestlings. Lines fitted using quadratic regression, a) structural gaps: % deviation from average DEE = -1.868 – 0.506 % gap + 0.013 % gap^2, $r^2 = 0.42$, $P = 0.008$, $n = 20$, note: fitted line omitted the results for the blue tit with the greatest negative deviation from the mean because this bird probably failed to restart feeding young promptly after experimental manipulation; b) functional gaps: % deviation from average DEE = 19.998 – 1.249 % non-oak + 0.014 % non-oak^2, $r^2 = 0.60$, $P = 0.001$, $n = 19$. Figure redrawn using data first published in *Landscape Ecology*

(Figures 3 and 4, Hinsley *et al*. 2008), with kind permission of Springer Science and Business Media.

Figure 4. Phenology of leaf development in Bute Park (open symbols) and Monks Wood (closed symbols) in 2004. Circles = English oak, triangles = common ash and squares = maple spp.

Figure 5. The influence of local climate (an index of spring warmth) on the timing of breeding (first egg date) of great tits in two large woods and in small woods. Results are for 15 years (1993 to 2007). For each wood or habitat type, each point represents the mean date for about 17 broods each year. Lines fitted using linear regression, Monks Wood: first egg date = 70.3 – 0.074 warmth sum, $r^2 = 0.56$, $P = 0.001$; Brampton Wood: first egg date = 63.4 – 0.066 warmth sum, $r^2 = 0.57$, $P = 0.001$; small woods: first egg date = 71.2 – 0.066 warmth sum, $r^2 = 0.62$, $P = 0.001$.

Figure 6. The interaction of climate (cold and warm springs) with habitat structure (tree canopy height around the nest site) and its effects on breeding success in great tits. Chick body mass is positively correlated with survival and thus is an indicator of chick quality. Lines fitted using linear regression. 2001, cold spring: mean chick body mass = 21.4 – 0.260 canopy height, $r^2 = 0.82$, $P < 0.001$, $n = 11$; 1997, warm spring: mean chick body mass = 12.9 + 0.323 canopy height, $r^2 = 0.45$, $P = 0.069$, $n = 8$.

Table 1. Comparison of breeding success between habitat types (large wood, small wood, parkland, farmland): summary of fitted mixed model with fixed effects for Habitat Type, Year and Type x Year interaction, and random effects for Site, Site x Year interaction and Nest Box. *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, $^{+}$ = $P < 0.10$.

		Wald tests for fixed effects			Estimated components of variance		
Species	Variable	Habitat type	Year	Type x Year interaction	Between sites	Site x Year interaction	Between boxes within sites/years
Great tit	Clutch size	41.1***	7.7*	2.9	0.013	0	2.29
	Mean chick mass	143.4***	9.3**	17.3**	0	0	1.93
	No. fledged	107.8*	4.4*	9.9^{+}	0	0.073	3.38
Blue tit	Clutch size	31.2***	0.03	1.2	0	0	2.44
	Mean chick mass	31.6***	3.0	6.1	0.033	0.004	1.22
	No. fledged	57.7***	3.8	2.8	0	0	5.57

Table 2. Timing of breeding by great tits and blue tits in different habitats. Data for farmland available only in 2007; April 1st = 1; *n* refers to numbers of nests; sites comprise two large, *c.* 30 small woods, two parkland sites and one farmland site.

	2006				2007			
	GREAT TIT		BLUE TIT		GREAT TIT		BLUE TIT	
	Date	*n*	Date	*n*	Date	*n*	Date	*n*
Large woods *c.* 150 ha	26.7 ± 4.6	43	24.0 ± 4.0	7	16.3 ± 3.1	46	15.2 ± 2.1	6
Small woods *c.* 1 ha	28.8 ± 5.0	20	26.3 ± 3.4	11	19.2 ± 4.1	20	16.4 ± 4.9	9
Urban parkland	20.1 ± 4.2	22	24.6 ± 3.5	21	15.3 ± 5.6	24	18.8 ± 3.8	23
Farmland	-	-	-	-	20.7 ± 4.0	33	20.9 ± 3.6	31

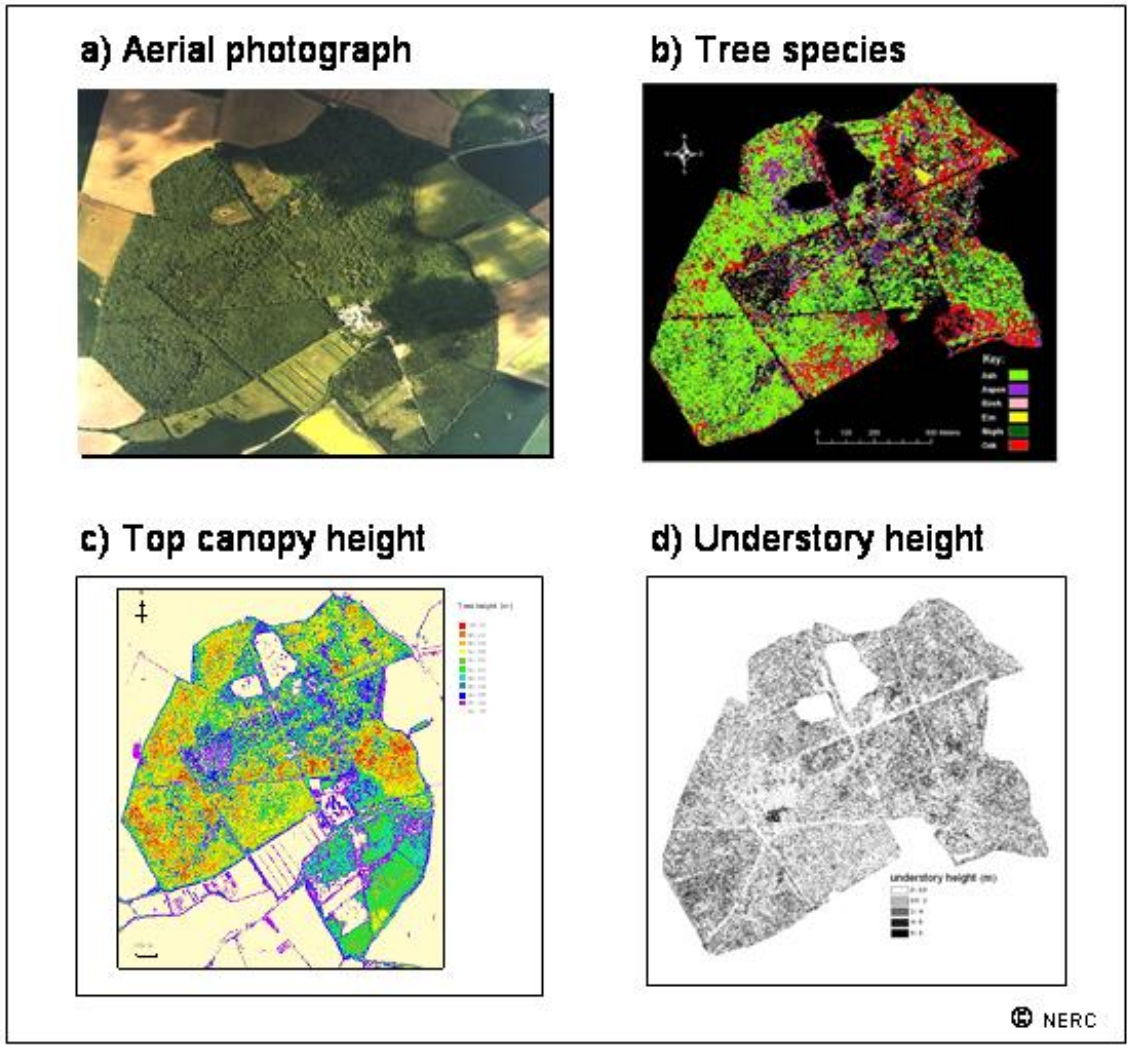

a) Aerial photograph
b) Tree species
c) Top canopy height
d) Understory height
NERC

Fig. 1

Fig. 2

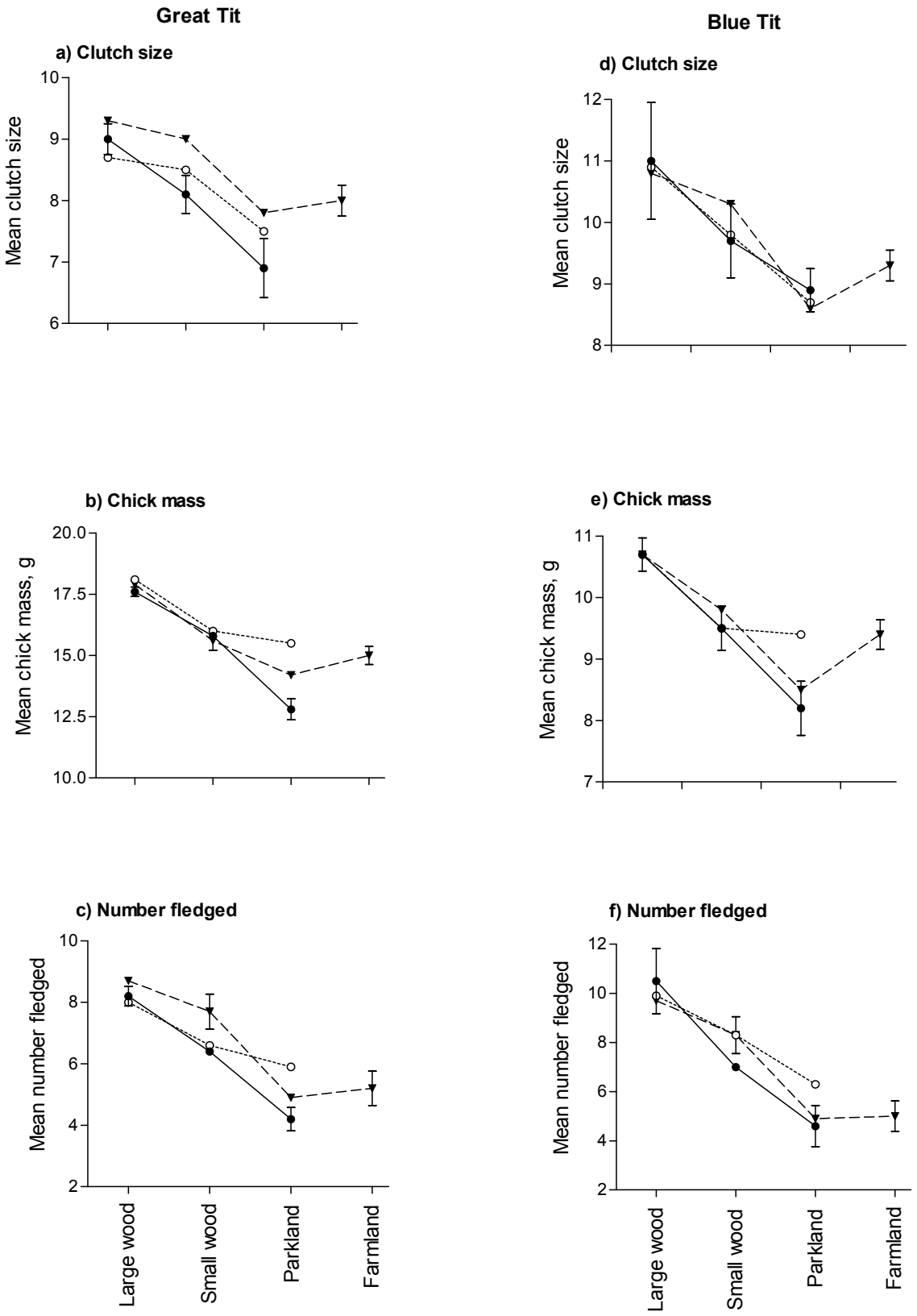

Great Tit
a) Clutch size
Mean clutch size
10
9
8
7
6
Blue Tit
d) Clutch size
Mean clutch size
12
11
10
9
8
b) Chick mass
Mean chick mass, g
20.0
17.5
15.0
12.5
10.0
e) Chick mass
Mean chick mass, g
11
10
9
8
7
c) Number fledged
Mean number fledged
10
8
6
4
2
Large wood
Small wood
Parkland
Farmland
f) Number fledged
Mean number fledged
12
10
8
6
4
2
Large wood
Small wood
Parkland
Farmland

Fig. 3

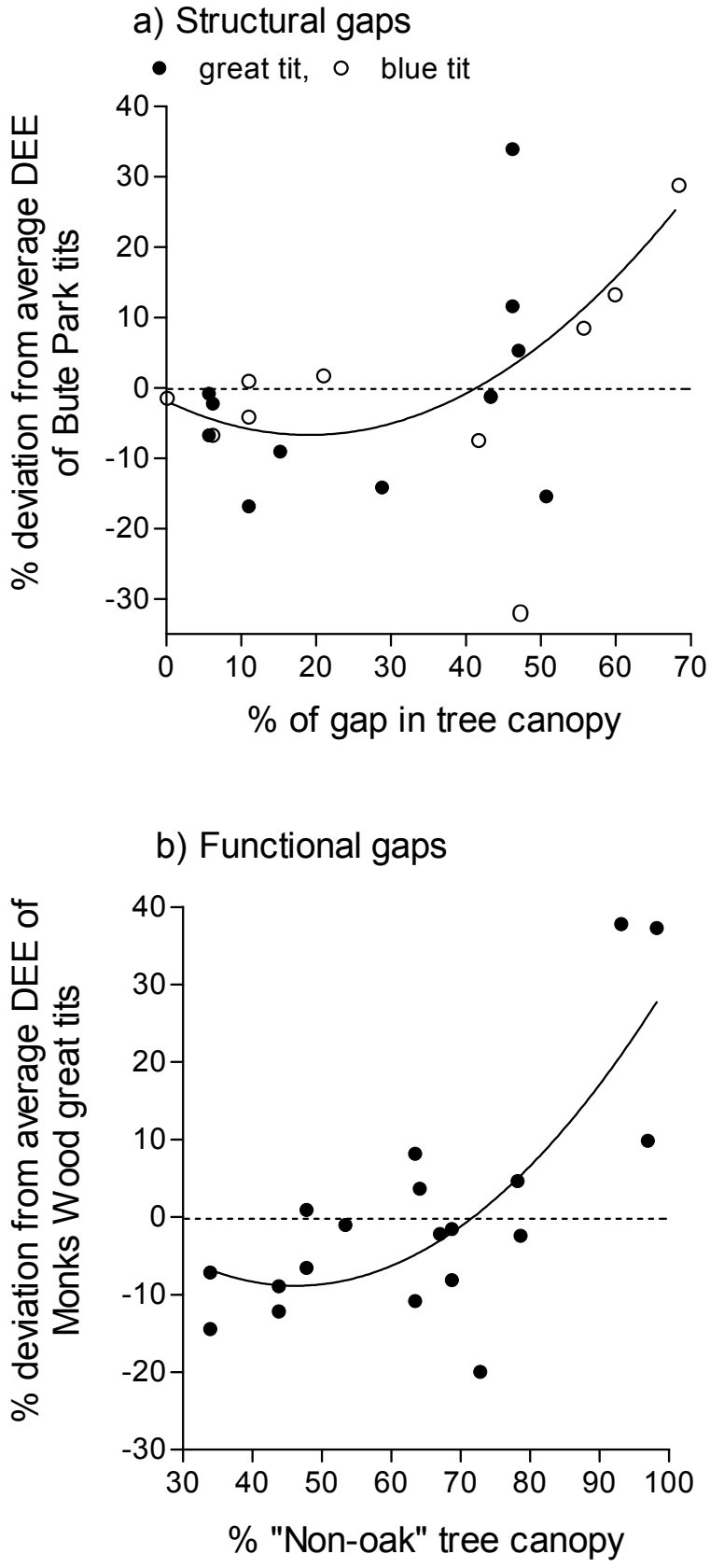

a) Structural gaps
great tit,
blue tit
% deviation from average DEE of Bute Park tits
% of gap in tree canopy
b) Functional gaps
% deviation from average DEE of Monks Wood great tits
% "Non-oak" tree canopy

Fig. 4

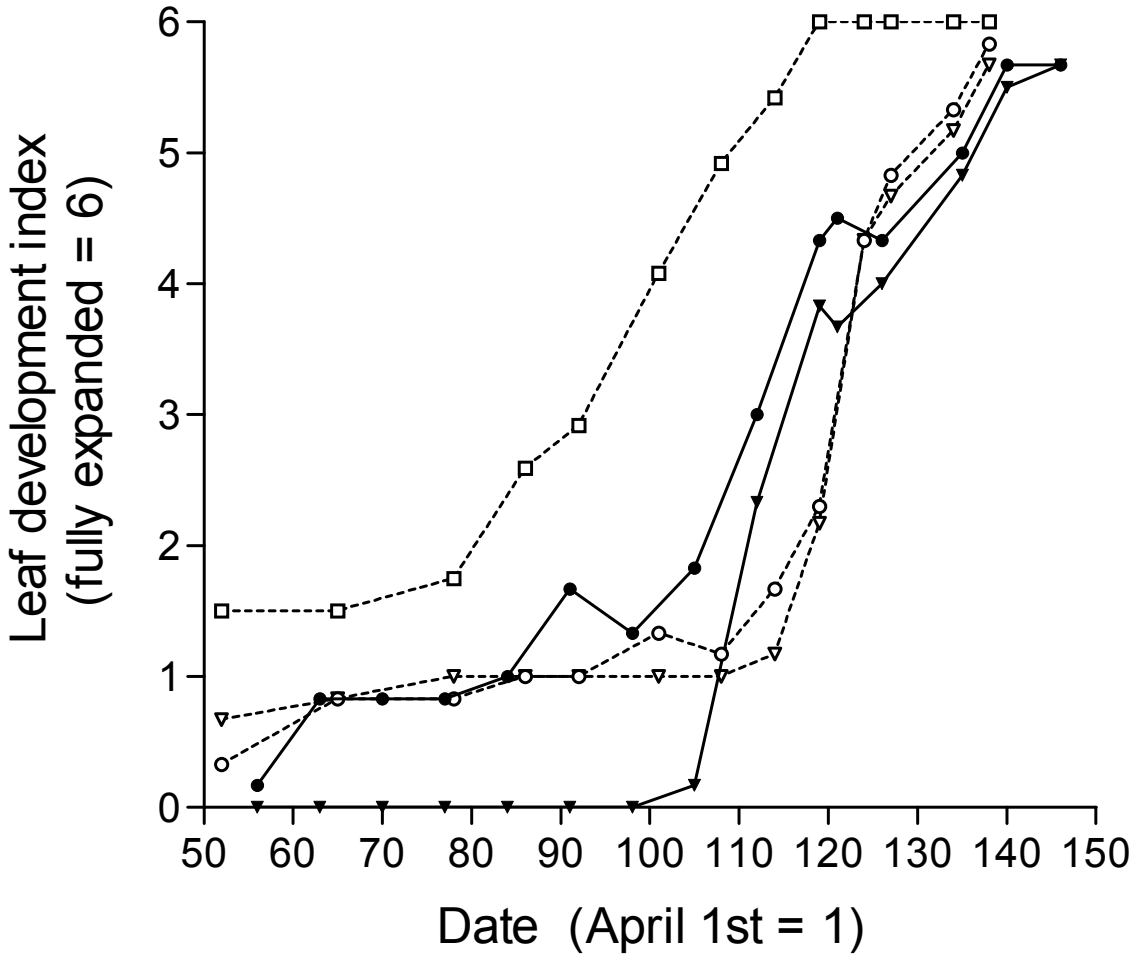

Leaf development index
(fully expanded = 6)
0
1
2
3
4
5
6
50
60
70
80
90
100
110
120
130
140
150
Date (April 1st = 1)

Fig. 5

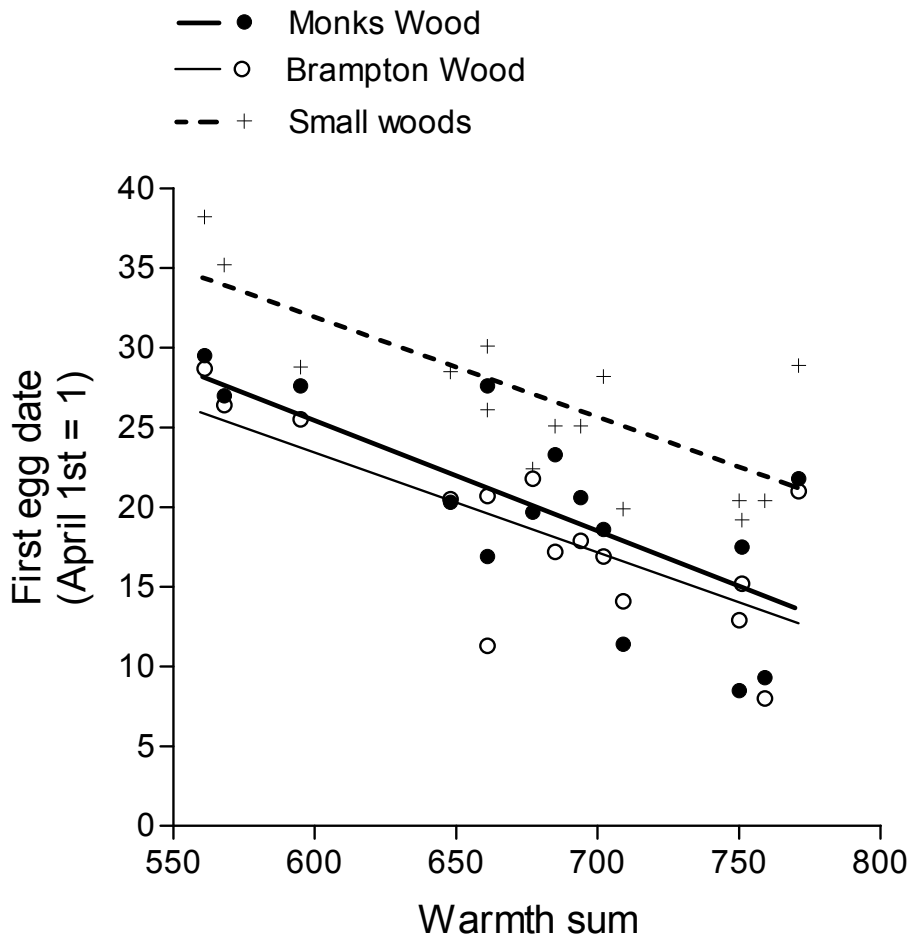
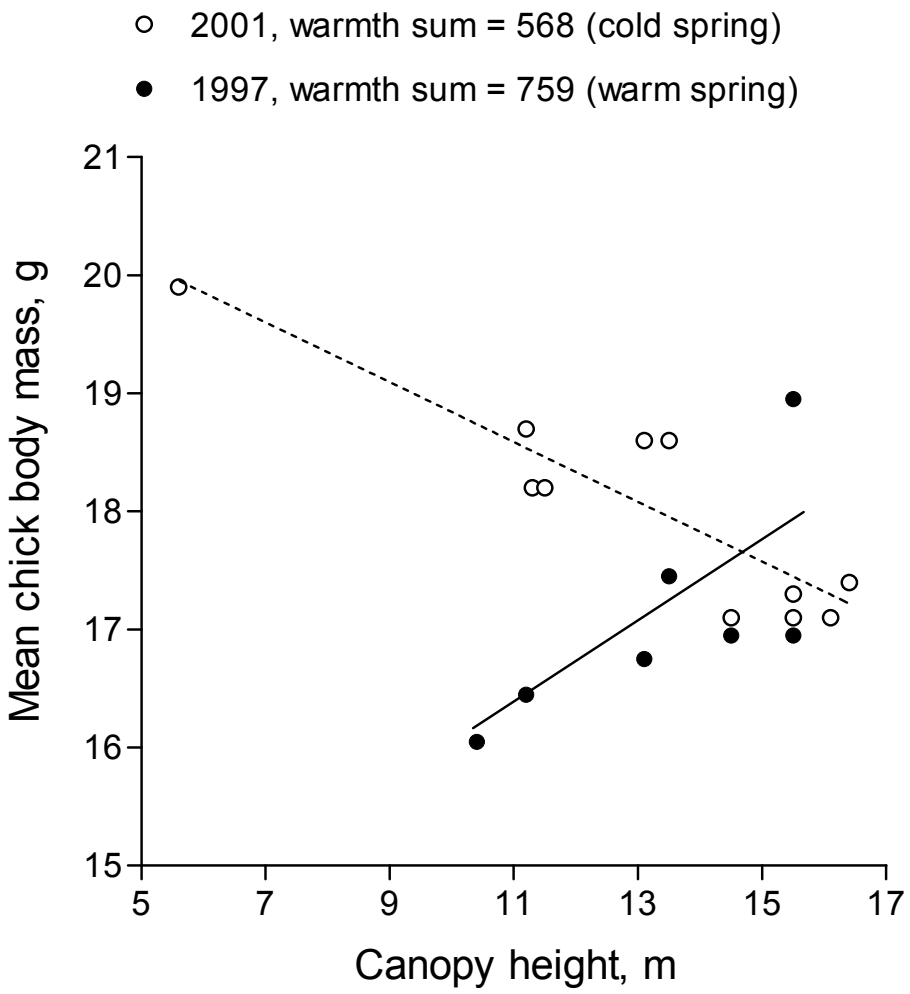

Monks Wood
Brampton Wood
Small woods
First egg date
(April 1st = 1)
0
5
10
15
20
25
30
35
40
550
600
650
700
750
800
Warmth sum

Fig. 6


2001, warmth sum = 568 (cold spring)
1997, warmth sum = 759 (warm spring)
Mean chick body mass, g
21
20
19
18
17
16
15
5
7
9
11
13
15
17
Canopy height, m