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Effects of structural and functional habitat gaps on breeding woodland birds: working harder for less

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Abstract The effects of habitat gaps on breeding success and parental daily energy expenditure (DEE) were investigated in great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) in urban parkland (Cardiff, UK) compared with birds in deciduous woodland (eastern England, UK). Tree canopy height, the percentage of gap in the canopy and the percentage of oak (in the wood only) within a 30 m radius of nest boxes were obtained from airborne remote-sensed data. Breeding success was monitored and parental DEE (great tits: both habitats; blue tits: park only) was measured using doubly labelled water in birds feeding young. In the park, mean (± SD) tree height (7.5 ± 4.7 m) was less than in the wood (10.6 ± 4.5 m), but the incidence of gaps (32.7 ± 22.6%) was greater (9.2 ± 14.7%). Great tits and blue tits both reared fewer young in the park and chick body mass was also reduced in park-reared great tits. Park great tits had a higher DEE (86.3 ± 12.3 kJ day^{-1}) than those in the wood (78.0 ± 11.7 kJ day^{-1}) and, because of smaller brood sizes, worked about 64% harder for each chick reared. Tits in the park with more than about 35% gap around their boxes had higher DEEs than the average for the habitat. In the wood, great tits with less oak around their boxes worked harder than average. Thus structural gaps, and functional gaps generated by variation in the quality of foraging habitat, increased the costs of rearing young.

Introduction

Habitat fragmentation and loss are two of the major causes of current worldwide declines in biodiversity (Ehrlich and Wilson 1991; Heywood 1995). The extent of fragmentation in the UK (Fuller et al 1994) and elsewhere means that substantial proportions of many species populations now live in such habitat (Vane-Wright et al 1991). For birds and other wildlife, small patches, whether rural or urban, may constitute sub-optimal habitat. For example, small patches may lack food resources and be more exposed to poor weather conditions and certain predators (Andrén 1992; Burke and Nol 1998; McCollin 1998). In urban parkland, structural patchiness can be exacerbated by functional patchiness due to high proportions of exotic plant species which may support relatively few invertebrates, reducing the foraging opportunities for birds (Mills et al 1989; Reichard et al 2001, Stauss et al 2005). The wider diversity of plant species may also generate temporal patchiness when differing phenologies create mismatches in timing between food supply and demand (Dias and Blondel 1996; Schoech and Bowman 2001; Thomas et al 2001). Thus birds living in patchy habitat may have to travel more widely in search of food, increasing their workload (Eybert et al 1995; Hinsley 2000). Continuous woodland has fewer physical gaps, but food resources vary between both tree species and individual trees of the same species resulting in functional patchiness and a patchy use of territory by foraging birds (Naef-Daenzer 2000; Stauss et al 2005; Tremblay et al 2005).

In this paper, we investigate the effects of structural and functional habitat gaps (quantified using airborne remote sensing) on parental energy expenditure (measured using doubly labelled water) and breeding success in great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) feeding young in urban parkland and in continuous woodland. Structural gaps are defined as physical spaces in the tree canopy; functional gaps are defined as arising from differences in the quality of different plant species as foraging habitat (Kennedy and Southwood 1984; Peck 1989; Lambrechts et al 2004; Alexander *et al.* 2006). For altricial nestlings, all food must be carried to the nest and thus breeding success may be affected by the amount of time and energy the adults expend in crossing gaps.

Similarly, the presence of gaps may increase travel times and distances if adults take longer routes around gaps to reduce potential exposure to aerial predators (Hinsley et al 1995; Desrochers and Hannon 1997). Although principally forest birds, in the UK, great tits and blue tits are common breeders in secondary habitats such as small woods, farmland hedgerow-tree networks and suburban-urban gardens and parks. All these secondary habitats are characteristically patchy and reproductive success in both species is known to be reduced compared with continuous woodland (e.g. Schmidt and Steinbach 1983; Cowie and Hinsley 1987; Riddington and Gosler 1995; Hinsley et al 1999). Both species also feed their young principally on tree-dwelling lepidopteran larvae (Perrins 1979; Perrins 1991) and the availability of caterpillars influences many aspects of tit breeding ecology including chick growth, survival and recruitment (Haywood and Perrins 1992; Keller and van Noordwijk 1994; Tremblay et al., 2003). The abundance and distribution of the food supply available to adults when feeding young can also affect adult body condition and survival by increasing the time and energy demands of foraging (Tinbergen and Dietz 1994; Moreno et al 1995; Merilä and Wiggins 1997; Sanz et al 1998; Thomas et al 2001). If structural and functional gaps influence foraging habitat quality, then we hypothesize that parental energy expenditure should correlate with the availability and quality of trees around the nest site. Thus birds in patchy habitat may suffer the double penalty of having to work harder for a reduced reproductive success (Daan et al 1996).

Methods

Study sites

The two study sites were Bute Park (51°29' N, 3°11' W) in Cardiff, south Wales, UK, and Monks Wood National Nature Reserve (NNR) (52°24' N, 0°14' W) in Cambridgeshire, eastern England, UK. Bute Park comprises about 53 ha and is located in the centre of the city of Cardiff, lying more or less north-south along the east bank of the River Taff (Fig. 1). The southern end includes Cardiff Castle, formal gardens, mown grass and an arboretum while the northern end has sports pitches and

some more extensive areas of woodland. Tree species diversity is high with many exotics often planted in groups of closely related species and varieties. The most abundant native species are common lime (*Tilia europaea*) and sycamore (*Acer pseudoplatanus*), plus smaller amounts of common ash (*Fraxinus excelsior*) and occasional English oaks (*Quercus robur*). The most frequently occurring species overall, including exotics, are limes (*Tilia* spp.), maples (*Acer* spp.), oaks (*Quercus* spp.) and pines (*Pinus* spp.). Conifers constitute about 15% of all formally planted trees. The park is heavily used by the public for recreation, sports, concerts and other events.

#Figure 1 approximately here#

Monks Wood comprises 157 ha of mixed deciduous woodland (Gardiner and Sparks 2005) (Fig. 1). It occupies a shallow north facing slope of maximum angle 14.5º and elevational range 6-46 m. The dominant tree species, in order of abundance, are common ash, English oak and field maple (*Acer campestre*) and are well mixed throughout the wood. Other tree species include small-leaved elm (*Ulmus minor*), silver birch (*Betula pendula*) and aspen (*Populus tremula*), and the main shrub species are hawthorn (*Crataegus* spp.), blackthorn (*Prunus spinosa*) and common hazel (*Corylus avellana*). These are all native species. The field layer is dominated by grasses and sedge (*Carex pendula*). There is a network of paths and rides, some wide enough to create gaps in the canopy, two open fields (4.3 ha and 1.7 ha), a number of smaller glades and several ponds. On part of its southern boundary, the wood is adjoined across a minor road by a mature 37 ha conifer plantation.

Site data

In Bute Park, a total of 26 sites throughout the centre and north of the park were provided with wooden nest boxes, with a hole-diameter of 32 mm, allowing access by both great tits and blue tits. Each year, 19 boxes were available during the breeding season (typically late March to the end of

June), the additional seven sites arising through replacement of vandalized/stolen boxes. Boxes were located randomly with a spacing of about 40-100 m. The position of each nest box was recorded by differential GPS Real Time Kinematic survey (Topcon Hiper+ GPS receiver and Legacy-E Base Station) during winter, leaf-off conditions. Breeding success and energy expenditure of great tits was measured in Bute Park in 2003-2005, and in blue tits in 2004-2005. The extension of the project into 2005 in the park (but not in the wood, see below) was to compensate for a low sample size (one bird) in the park in 2003. In the park, in 2003-2005, the numbers of boxes in which great tits reached the chick-rearing stage were two, eight and five respectively, and energy expenditure was measured successfully at one, six and five of these. In 2004-2005, the numbers of boxes in which blue tits reached the chick-rearing stage were nine and six respectively, and energy expenditure was measured at six and four of these.

In Monks Wood, 36 nest boxes similar to those used in the park, and similarly located, were available each year. The position of each box was recorded during winter, leaf-off conditions using an electronic total station (Pentax R-125N), surveying from an established Ordnance Survey benchmark. Breeding success and energy expenditure of great tits was measured in Monks Wood in 2003 and 2004, and breeding success of blue tits in 2004 and 2005. Energy expenditure was only measured in great tits in the wood because too few boxes were used by blue tits (great tits, being larger, could out-compete blue tits for boxes). The numbers of boxes in which great tits reached the chick-rearing stage were 23 and 25 in 2003 and 2004 respectively and energy expenditure was measured successfully at 15 and nine of these. The numbers of boxes in which blue tits reached the chick-rearing stage in Monks Wood were five and two in 2004 and 2005 respectively. To obtain an adequate sample for blue tit breeding success in woodland, results from five boxes in another, similar, wood in Cambridgeshire were also used (Brampton Wood, 132 ha, mixed ash, oak, field maple, 9 km south of Monks Wood). No other data for Brampton Wood were used here. Ambient temperature was recorded in both Monks Wood and Bute Park using automatic loggers (Micro-T-log temperature datalogger, F.W. Parrett Ltd.) recording every 4 hours.

Canopy height and habitat patchiness were measured using airborne Light Detection And Ranging (LiDAR). Airborne scanning LiDAR is a remote sensing technique which can provide finely resolved data describing vegetation structure (Lim et al 2003; Næsett 2004) of particular value for ecological applications (Lefsky et al 2002; Hill et al 2004; Bradbury et al 2005; Broughton et al 2006; Hinsley et al 2006). It uses a laser range finder to measure the elevation of points in a swath beneath the flight-path of an aircraft. Short duration pulses of near infrared laser light are fired at the ground and the return signals backscattered from the ground itself and/or surface features such as trees and buildings are recorded (Wehr and Lohr 1999). The timing of the returns, combined with measurement of the aircraft's orientation and position, allow the 3D position of the ranged points to be calculated and geo-referenced (Ackermann 1999). Digital models of the surface of the ground and of vegetation canopy height can then be derived from these measurements (Hill et al 2002). Further details of the analysis of the LiDAR data are given in the supplementary material.

LiDAR data for Bute Park were acquired on June 14th 2004 using an ALTM 3033 scanner, and for Monks Wood on June 10th 2000 using an Optech ALTM 1210 scanner. The ALTM is a small footprint (20-25 cm on the ground for these data sets), discrete return system supplying the first and last significant return per laser pulse. The ALTM 3033 had a 33 kHz repetition rate, and data were acquired with a scan angle of $\pm 20^o$ and a post spacing of one hit per 1.66 m^2. The ALTM 1210 had a 10 kHz laser pulse repetition rate, and data were acquired with a scan angle of $\pm 10^o$ and a post spacing of one hit per 4.83m^2.

For Monks Wood, a tree species map was also available, produced from supervised classification of time series Airborne Thematic Mapper (ATM) multi-spectral data from 2003 (George 2005). Different types of vegetation cover, and at a finer scale, different tree species, have characteristic reflectance spectra due to differential reflection of solar radiation (Treitz and Howarth 2000; Carleer and Wolff, 2004). Such differences between species can also be increased by differing leaf phenologies, e.g. rates of development and senescence (Wolter et al 1995; Mickelson et al 1998). Thus, using ATM data from five images of the wood, the six dominant tree species (see above) in

the top canopy were mapped with an assessed accuracy of *c.* 89%. The tree species map had a minimum height threshold of 8 m, which masked out areas of shrubs and young trees.

Bird breeding performance

All boxes were visited approximately weekly from the end of March until July. The following parameters were recorded (i) first egg date, (ii) clutch size, (iii) hatching date, (iv) number of young alive in the nest at 11 days of age where day of hatching = 0, (v) mean chick weight (g) at 11 days, excluding runts (runts were defined as chicks too small to be ringed at age 11 days and were rare), (vi) total live biomass (g) of young in the nest at 11 days (including runts), (vii) number of young fledged, and (viii) overall success calculated as the percentage of eggs producing fledged young. Chicks were weighed to 0.1 g using a spring balance, and were also ringed with a uniquely numbered ring of the British ringing scheme run. After the young had fledged, the nest was removed from the box and searched for dead chicks and unhatched eggs.

Bird energy expenditure

Energy expenditure of birds feeding young was measured using doubly labelled water (DLW). This technique uses the differential turnover of oxygen-18 (^{18}O) (excreted from the body in water and carbon dioxide) and deuterium (^{2}H) (excreted in water) to measure carbon dioxide production which can then be converted to energy expenditure (Speakman 1997). 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 (Speakman 1998). Adults feeding c. 11 day-old young were trapped at the nestbox, injected intraperitoneally with approximately 0.1 ml of DLW and a baseline blood sample collected after allowing 0.5 h for equilibration with the body water. Birds were then released to continue feeding the young and were retrapped about 24 hours later to collect a final

sample. To reduce disturbance at the nest, only one member of each pair was trapped. This was usually the female, but a few male blue tits were also trapped due to the greater difficulty of distinguishing the sexes. Further details of the DLW methodology and analysis are given in the supplementary material.

Of a total of 51 measurement attempts, 45 were successful, five failed (four great tits were not retrapped, one final sample dried out, all Monks Wood birds) and one park blue tit deserted and her brood of four died. The broods of all the other 50 birds fledged. All trapping, sampling and storage procedures were carried out under licence (see acknowledgements) and all operators were experienced and licenced bird ringers.

Bird-habitat analysis

Data on mean tree canopy height and the percentage of gap (defined as canopy < 1 m tall) in the canopy were extracted from the digital canopy height models of Monks Wood and Bute Park for 30 m radius circles centred on the nest box locations. In addition, for 22 of the 36 Monks Wood nest boxes, the percentage of oak tree canopy was also extracted per 30 m radius circle. This information was extracted from the tree species map and was expressed as a percent of tree canopy rather than as a percent of the whole 30 m circle. However, given the low incidence of gaps in the wood, these two measures were similar for most boxes. Oak canopy could not be obtained for the remaining 14 Monks Wood boxes because the tree map did not include some woodland which lay outside the boundary of the NNR. A 30 m radius sample plot was used because this distance was representative of the typical foraging distances of tits (see discussion) (Stauss et al 2005; Tremblay et al 2005). Foraging distances may be greater (e.g. 40-50 m) in lower quality habitat, but the amounts of gap for radii of 30 m and 50 m were highly correlated (Bute Park: $r = 0.957$, $P < 0.001$, $n = 26$; Monks Wood: $r = 0.960$, $P < 0.001$, $n = 36$), and using 30 m for both study sites minimised assumptions concerning likely quality.

Breeding performance and parental DEE were summarised for each species and compared between the park and wood using two sample t tests. The effects of habitat structure (expressed as mean canopy height and percentage gap within 30 m in both the park and the wood, and as the percentage of oak canopy within 30 m in the wood) on parental DEE were examined using linear or quadratic regression analysis as appropriate to obtain best fit. Parental DEE was expressed as kJ day^{-1}, and also as the percentage deviation from the mean DEE for each site calculated as (DEE – mean for the year)/mean for the year. All analyses were done using Minitab Release 12.

Results

In the park ($n = 26$), the mean canopy height within 30 m of each nest box was less than in the wood ($n = 36$) (mean ± SD canopy height: park = 7.5 ± 4.7 m; wood = 10.6 ± 4.5 m; $t_{60} = -2.62$, $P = 0.011$). In particular, there were many more gaps in the tree canopy in the park (% gap: park = 33 ± 23%; wood = 9 ± 15%; $t_{60} = 4.96$, $P < 0.001$). In Monks Wood, the amount of gap was less than 10% for 26 of the 36 boxes (Fig. 2), and less than 1% for 21 of them. The occurrence of gaps in the wood was related to the presence of large rides and proximity to the edge of the wood.

#Figure 2 approximately here#

Great tits in the park bred earlier than those in the wood, but all measures of breeding performance were significantly reduced (Table 1). Female DEE was greater in the park (and the difference close to significance at $P = 0.058$), but the smaller brood sizes and fledging success increased the females' costs per chick by about 64% (Table 1). These differences between the park and the wood remained when comparing within the same year, i.e. 2004 (DEE: $t_{13} = -2.47$, $P = 0.028$; DEE per chick: $t_{13} = -3.58$, $P = 0.003$, Table 1). In blue tits, there was no difference between the park and the wood in the timing of breeding or clutch size, but fewer chicks were reared to fledging (Table 2). However, the quality of the young, measured as mean chick body mass (Lloyd 1987; Slagsvold et al 1995), was comparable with that of woodland chicks. Earlier timing of

breeding by urban great tits, but not blue tits, has been noted in previous work (Perrins 1979; Cowie and Hinsley 1987) and may be related to differential use of artificial food (Dhondt et al 1984).

#Tables 1 and 2 approximately here#

In the park (great tit, $n = 12$; blue tit, $n = 10$), we predicted that DEE would decrease with canopy height and increase with the amount of gap around the box, and while these trends were evident for both species, the relationships were not significant. However, when DEE was expressed as the percentage deviation from the mean DEE for the year, females working harder than average were found to have more patchy habitat around their nest boxes (great tits and blue tits combined, one outlier omitted, Fig. 3). Daily energy expenditure, relative to the mean, decreased with increasing canopy height and increased with increasing amounts of gap. The quadratic relationship (Fig. 3, % gap) showed that DEE, relative to the mean, was not linearly related to the amount of gap, but showed an increasing trend above about 35% gap.

#Figure 3 approximately here#

In the wood (great tit, $n = 23$), two females had relatively high DEEs in 2003 (as apparent in Fig. 4, see below). Without the results from these two birds, both DEE and the percentage deviation from the mean DEE for the year declined linearly with increasing canopy height (as found in the park), but the former relationship was weak ($r^2 = 0.17$, $P = 0.061$, $n = 21$) and the latter non-significant and they are not shown. Gaps were relatively rare in Monks Wood (Fig. 2), and there were no relationships with the amount of gap. However, both DEE and the percentage deviation declined as the percentage of oak canopy around the nest box increased (Fig. 4). Similar to the pattern of results for canopy gaps in the park, as the percentage of oak decreased below about 30%, birds worked increasingly harder. There was also an indication of a year effect. Both the females

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with the highest DEEs in 2003 had little oak within 30 m of their boxes, whereas the influence of

oak appeared to be less in 2004 (Fig. 4).

#Figure 4 approximately here#

Mean and minimum ambient temperatures for the 24 hours during which DEE was measured did

not differ between Bute Park and Monks Wood (park: mean ± SD = 14.4 ± 1.7 ^{o}C, minimum = 11.6

± 1.7 ^{o}C, n = 22; wood: mean = 15.1 ± 1.9 ^{o}C, minimum = 11.7 ± 2.1 ^{o}C, n = 23. Mean: t_{43} = -1.26,

P = 0.213; minimum: t_{43} = -0.21, P = 0.837).

Discussion

In the park, the reproductive success of great tits was reduced compared with the wood, and yet

female energy expenditure was higher, despite the smaller brood sizes. Thus great tits in the park

worked harder for less return. We did not measure food abundance directly (the high tree species

diversity in parkland makes frass trapping ineffective [Zandt 1994]), but the increase above average

DEE in birds whose territories had more than about 35% gap indicated that the availability of trees

per se had a direct effect on the costs of rearing young. Work on great tits in the Netherlands

(Verhulst and Tinbergen 1997; Tinbergen and Verhulst 2000) has suggested that adults feeding

young are constrained by time, rather than by intrinsic (e.g. phylogenic or physiological) limits to

energy expenditure, due to a shortage of daylight for foraging. Our results for the park birds are

consistent with this because, despite their higher work rate compared with Monks Wood birds, their

DEE was similar or slightly less than values reported for great tits in various woodland sites in the

Netherlands (Tinbergen and Dietz 1994; Tinbergen and Verhulst 2000) and were not excessive in

terms of average (Daan et al 1990; Bryant and Tatner 1991) or maximal suggested limits for

sustainable energy expenditure (Lindström and Kvist 1995; Hammond and Diamond 1997).

Tinbergen and Verhulst (2000) also suggested that ambient temperature might impose an extrinsic limit to energy expenditure (an "energetic ceiling"), but temperatures during the measurement of DEE did not differ between Bute Park and Monks Wood.

The results for the blue tit indicated by the arrows in Figure 3 were omitted from the calculations of the fitted lines because the value of DEE for this bird was low compared to the rest of the data set. In a study of marsh tits (*Poecile palustris*), Nilsson (2002) found that six out of 12 females took 4-10 h to resume feeding their young after the initial procedures of the DLW method and that this reduced their DEE by an average of 46% compared with the others which resumed within one hour. Although such adverse reactions are unusual (Speakman 1997), it is possible that the park blue tit was slow to resume normal feeding behaviour resulting in the low value. Results for great tits and blue tits in the park were combined by expressing DEE as the deviation from the mean because the breeding ecology of both species is well known to be particularly dependent on the spring abundance of tree-dwelling caterpillars (e.g. van Balen 1973; Perrins 1979; Perrins 1991). The use of alternative food supplies by either species would tend to obscure relationships with tree canopy height and gaps and the data for the two species showed no sign of segregation by species across the relationships (Fig. 3).

In Monks Wood, the relationships between both DEE and the percentage deviation from the mean for the year and the availability of oak around the nest box were analogous to that between the percentage deviation and amount of gap in Bute Park (Figs. 2 & 3). In the wood, birds with less oak around their boxes worked harder than average, while in the park, birds with fewer trees worked harder. In the park, English oak was rare within 30 m of any experimental box and thus the prime problem for the park birds appeared to concern quantity, rather than quality, of trees. Obviously, the non-oak species in Monks Wood do provide the birds with foraging opportunities, but the relationship with oak highlights its importance as a source of caterpillars as found in other studies (e.g. Perrins 1991; Fischbacher et al 1998; Naef-Daenzer et al 2004) and suggests that functional gap effects may commonly influence bird foraging behaviour. Tinbergen and Verhulst (2000) found

an unusually high DEE for one female great tit which spent much of her time flying to a relatively distant oak with a high density of small caterpillars. Thus, the two females in Monks Wood with little oak canopy within 30 m and high DEEs in 2003 may have been travelling further than average to find oak trees. Other work has also shown that functional gap effects may operate at a landscape scale due to a heterogeneous distribution of forest patch sizes and tree species composition (e.g. Lambrechts et al 2004).

The difference between the years in Figure 4 suggested that the importance of oak to territory quality may differ between years (Lõhmus 2003; Hinsley et al 2006). In blue tits breeding in suburban gardens, the amount of oak and rowan (*Sorbus acuparia*) within 25 m of the nest explained 21% of the variation in fledging success in one out of three years (Cowie and Hinsley 1987). In this one year, but not the other two, the time of peak chick demand (age 10-11 days, Perrins 1991) coincided with days of heavy rain.

Thomas et al. (2001) reported that a mismatch between the timing of breeding and peak caterpillar abundance could double the cost of rearing young in blue tits breeding in evergreen holm oak (*Quercus ilex*) forest in southern France (but also see Verhulst and Tinbergen 2001). For the most badly timed birds, DEE was in the region of 120-130 kJ day^{-1}, which raises the question of why the Bute Park birds did not work harder, if such work rates are possible? If the evergreen oak habitat was more continuous than that of the park, then possibly the park tits were more constrained by the time taken to cross, or avoid, gaps than the additional energy expenditure. In a study of blue tits on Corsica (Tremblay et al 2005), birds at a site with low caterpillar abundance, had average foraging distances from the nest of more than twice that of birds where caterpillar abundance was high (53 m versus 25 m). However, total flight distances per hour were similar because the birds in poor habitat made longer, but fewer, trips and fed their young a similar total biomass of caterpillars comprising fewer, larger prey. Tremblay et al. (2005) suggested that foraging costs, although not measured directly, would therefore be similar in both habitats because the costs of longer, but fewer, foraging trips would be offset by lower costs whilst searching more selectively within

particular trees for large prey, i.e. the costs of searching would be less than the costs of flight (Goldstein 1990; Hinsley 2000). This was in contrast to the shorter, but more frequent, foraging trips and shorter search times of the birds in the good habitat. Similarly, starlings (*Sturnus vulgaris*) rearing experimentally enlarged broods, were able to maintain food delivery rates per chick without increasing DEE by adjustments in foraging and social behaviour and prey selection (Wright et al 1998). Thus parkland birds might be able to minimise overall DEE by adopting a selective, large prey, strategy.

A study of foraging distances in blue tits in Germany (Stuass et al 2005), again found shorter foraging distances in high quality habitat (deciduous woodland, 22 m) compared with low quality habitat (mixed woodland, 40 m). Prey size was not measured, but unlike the Corsican birds, feeding rates did not differ between the two habitats, suggesting that parental costs in the poor habitat should have been greater. In both Corsica and Germany, clutch and brood sizes were smaller in the poor habitats, whereas chick body mass was also lower in Corsica, but not in Germany. The lower body mass in poor habitat in Corsica was thought to be due to infestation of the young by blow-fly larvae (*Protocalliphora* spp.) because the total amount of prey delivered was the same as in the high quality habitat. In Bute Park, blue tits reared fewer young than in Monks Wood, but chick body mass did not differ. In contrast, great tits in the park reared both fewer and lighter young. Juvenile survival and recruitment into the breeding population is positively correlated with fledging mass (Tinbergen and Boerlijst 1990; Lindén et al 1992); thus blue tits appeared to cope better in the park than great tits, as has been found for these two species in other secondary habitats such as suburban gardens (Cowie and Hinsley 1987) and small woods (Hinsley et al 1999). Blue tits are smaller than great tits (*c.* 10 g versus 18 g) and feed their young proportionately smaller prey items. Therefore, they may have an advantage over great tits in the application of a foraging strategy involving the selection of larger prey and fewer nest visits.

Habitat gaps, both structural and functional, can increase the costs of rearing young, and may also reduce breeding success. Given these effects on parental DEE of gaps in the park and of oak

trees in the wood, it is clear that habitat quality for breeding tits, and other arboreal insectivores, could be improved. In parks and other secondary habitats, and especially where space to increase total habitat area is limited, this could be done by increasing the proportion of native tree species. In woodland, increasing the proportion of oak, and other tree species with rich invertebrate faunas, is one possibility, but would have to be balanced against additional requirements of both the birds and other taxa.

Table 1 Breeding performance of great tits, and female DEE when feeding young, in Bute Park and Monks Wood. Values are: mean ± SD. First egg date assumes April 1st = 1. Overall success was calculated as the percentage of eggs which produced fledged young.

Location and year	First egg date	Clutch size	Brood size at 11 days	Mean chick mass (g)	Total biomass at 11 days (g)	Number fledged	% overall success	DEE (kJ day^{-1})	DEE per chick (kJ day^{-1})
BUTE PARK									
2003 ($n = 1$)	19.0	5.0	4.0	13.9	55.6	2.0	40	72.8	18.2
2004 ($n = 6$)	9.2 ± 4.7	9.3 ± 1.8	7.7 ± 1.4	16.6 ± 1.1	126.4 ± 21.7	7.5 ± 1.4	82 ± 18	88.3 ± 15.8	11.7 ± 2.1
2005 ($n = 5$)	15.4 ± 13.1	8.0 ± 2.7	5.5 ± 1.9	13.4 ± 0.5	72.4 ± 24.5	4.8 ± 1.1	64 ± 22	86.6 ± 7.4	17.2 ± 5.8
Mean ($n = 12$)	12.6 ± 9.3	8.4 ± 0.7	6.5 ± 0.6	15.0 ± 1.8	98.0 ± 36.5	5.9 ± 2.2	71 ± 22	86.3 ± 12.3	14.6 ± 4.8
MONKS WOOD									
2003 ($n = 14$)	22.2 ± 2.3[1]	9.6 ± 1.2	9.0 ± 1.2	17.3 ± 0.5	154.9 ± 19.3	9.0 ± 1.2	95 ± 8	80.2 ± 14.2	9.0 ± 2.0
2004 ($n = 9$)	21.2 ± 4.2	10.0 ± 1.3	8.6 ± 1.2	17.7 ± 0.7	151.4 ± 24.0	8.6 ± 1.2	86 ± 13	74.5 ± 5.1	8.8 ± 1.0
Mean ($n = 23$)	21.8 ± 3.2[2]	9.7 ± 1.3	8.8 ± 1.2	17.4 ± 0.6	153.5 ± 20.8	8.8 ± 1.2	91 ± 11	78.0 ± 11.7	8.9 ± 1.7
t, park vs wood	-4.27	-2.16	-4.50	-5.82	-5.76	-5.23	-3.68	1.97	5.12
P	< 0.001	0.038	< 0.001	< 0.001	< 0.001	< 0.001	0.001	0.058	< 0.001

Note: to increase the sample size, data were pooled across years when comparing performance between parkland and woodland, but for the park there were significant differences between 2004 and 2005 for brood size at 11 days of age ($t_9 = 2.22$, $P = 0.053$), mean chick body mass ($t_9 = 5.81$, $P < 0.001$), total biomass at 11 days of age ($t_9 = 3.87$, $P = 0.004$), the number of young fledged ($t_9 = 3.54$, $P = 0.006$) and DEE per chick ($t_9 = -2.21$, $P = 0.055$). [1]$n = 13$; [2]$n = 22$.

Table 2 Breeding performance, and DEE when feeding young, of blue tits in Bute Park, and comparison with breeding performance in Monks Wood and Brampton Wood (see text). Values are: mean ± SD. First egg date assumes April 1st = 1. Overall success was calculated as the percentage of eggs which produced fledged young.

Location and year	First egg date	Clutch size	Brood size at 11 days	Mean chick mass (g)	Total biomass at 11 days (g)	Number fledged	% overall success	DEE (kJ day^{-1})	DEE per chick (kJ day^{-1})
BUTE PARK									
2004 ($n = 6$)	18.8 ± 2.1[1.]	9.8 ± 1.0	8.0 ± 0.6	10.0 ± 1.2	80.7 ± 13.4	8.0 ± 0.6	82 ± 13	50.6 ± 10.2	6.4 ± 1.7
2005 ($n = 4$)	22.8 ± 6.1	8.8 ± 1.0	6.5 ± 1.9	8.7 ± 0.5	56.8 ± 17.3	5.0 ± 2.6	58 ± 32	64.3 ± 6.2	10.5 ± 3.1
Mean ($n = 10$)	20.8 ± 4.7[2.]	9.4 ± 1.1	7.4 ± 1.4	9.5 ± 1.1	71.1 ± 18.8	6.8 ± 2.2	73 ± 24	56.0 ± 11.0	8.1 ± 3.0
WOODLAND (data from 2004 and 2005 combined)									
Mean ($n = 12$)	18.2 ± 7.5[3.]	10.6 ± 2.0[3.]	10.3 ± 2.0	10.1 ± 1.1	103.3 ± 20.9	10.3 ± 2.0	96.3 ± 4.8	-	-
t, park vs wood	0.87	-1.75	-3.76	-1.31	-3.76	-3.84	-3.29	-	-
P	0.393	0.095	0.001	0.204	0.001	0.001	0.004	-	-

Note: to increase the sample size, data were pooled across years when comparing performance between parkland and woodland, but for parkland there were significant differences between 2004 and 2005 for total biomass at 11 days of age ($t_8 = 2.48$, $P = 0.038$), the numbers of young fledged ($t_8 = 2.80$, $P = 0.023$), DEE ($t_8 = -2.38$, $P = 0.044$ and DEE per chick ($t_8 = -2.77$, $P = 0.024$). [1]$n = 4$; [2]$n = 8$; [3]$n = 13$.

Fig. 1. LiDAR first return Digital Surface Model of Bute Park, Cardiff (area shown is 1.4 km x 1.8 km) and Monks Wood, Cambridgeshire (area shown is 1.8 km x 1.7 km). The boundaries of the study areas are shown by dashed lines. Lighter shades of grey denote higher elevations, e.g. the northerly slope of Monks Wood is shown by the transition from light to darker shading from the bottom to the top of the image. Map of mainland UK shows site locations.

Fig. 2. Percentage frequency distributions of (a) mean canopy height (m) and (b) the amount of gap (%) in the canopy for 30 m radius sample areas around 36 nest boxes in Monks Wood (dark bars) and 26 nest boxes in Bute Park (hatched bars).

Fig. 3. Percentage deviation from mean daily energy expenditure (DEE) of great tits (closed circles) and blue tits (open circles) rearing young in Bute Park in relation to (a) mean canopy height (m) and (b) the amount of gap (%) measured within 30 m radius sample areas around the nest box. Regression equations are (i) canopy height: % deviation $= 25.197 - 5.800$ canopy height $+ 0.252$ canopy height^2, $r^2 = 0.32$, $P = 0.031$, $n = 21$; (ii) gap: % deviation $= -1.868 - 0.506$ % gap $+ 0.013$ % gap^2, $r^2 = 0.42$, $P = 0.008$, $n = 21$. Deviations were calculated separately for 2004 and 2005, and an overall mean used for 2003. Arrows indicate an outlier which was omitted from the calculations of the fitted lines, see discussion.

Fig. 4. Daily energy expenditure (DEE) (a) and percentage deviation from mean daily energy expenditure (b) of female great tits rearing young in Monks Wood in relation to the presence of oak canopy (as percentage of the canopy area of all trees ≥ 8 m in height) within a 30 m radius of the nest box. Regression equations are (i) DEE $= 101.893 - 1.189$ % oak $+ 0.0113$ % oak^2, $r^2 = 0.56$, $P = 0.001$, $n = 19$; (ii) % deviation $= 30.267 - 1.145$ % oak $+ 0.0135$ % oak^2, $r^2 = 0.60$, $P = 0.001$, $n = 19$. Closed triangles show results for 2003 and open triangles results for 2004.
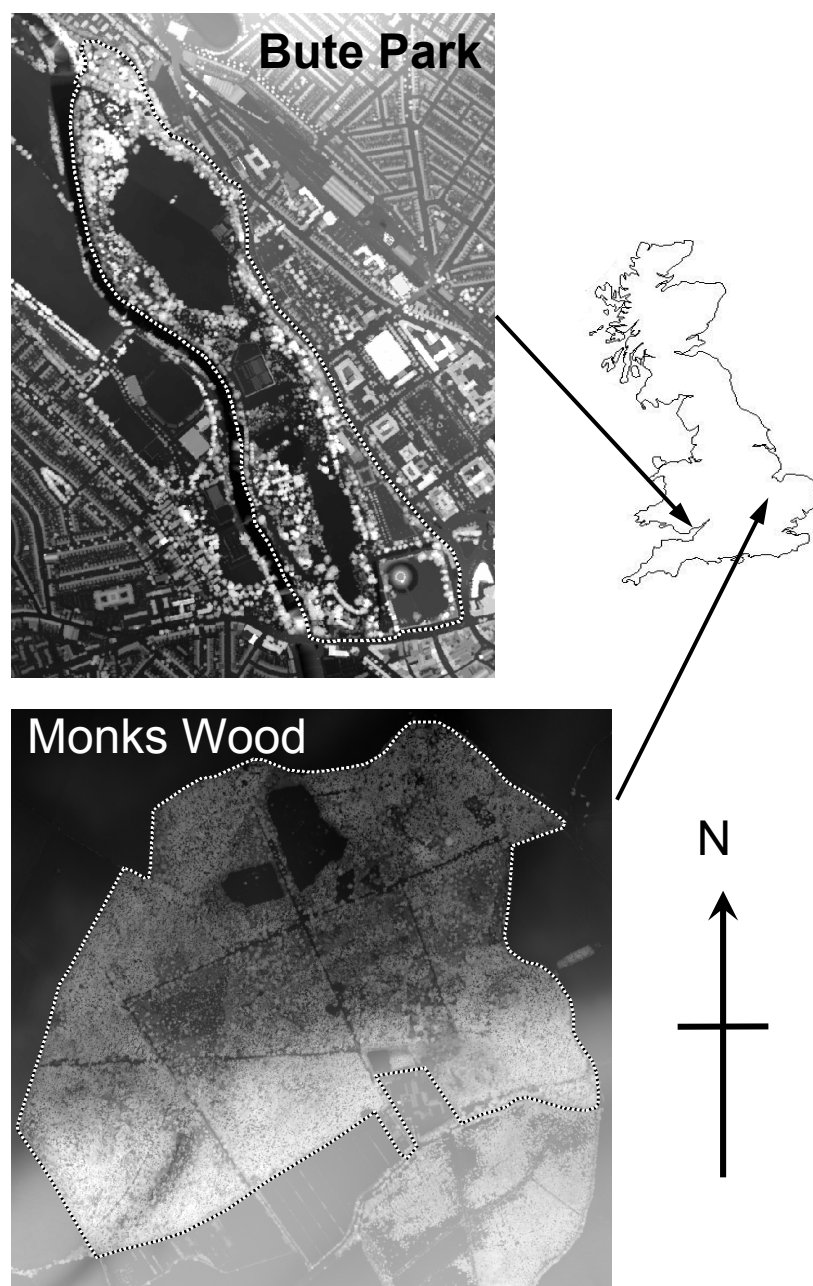
Fig. 1

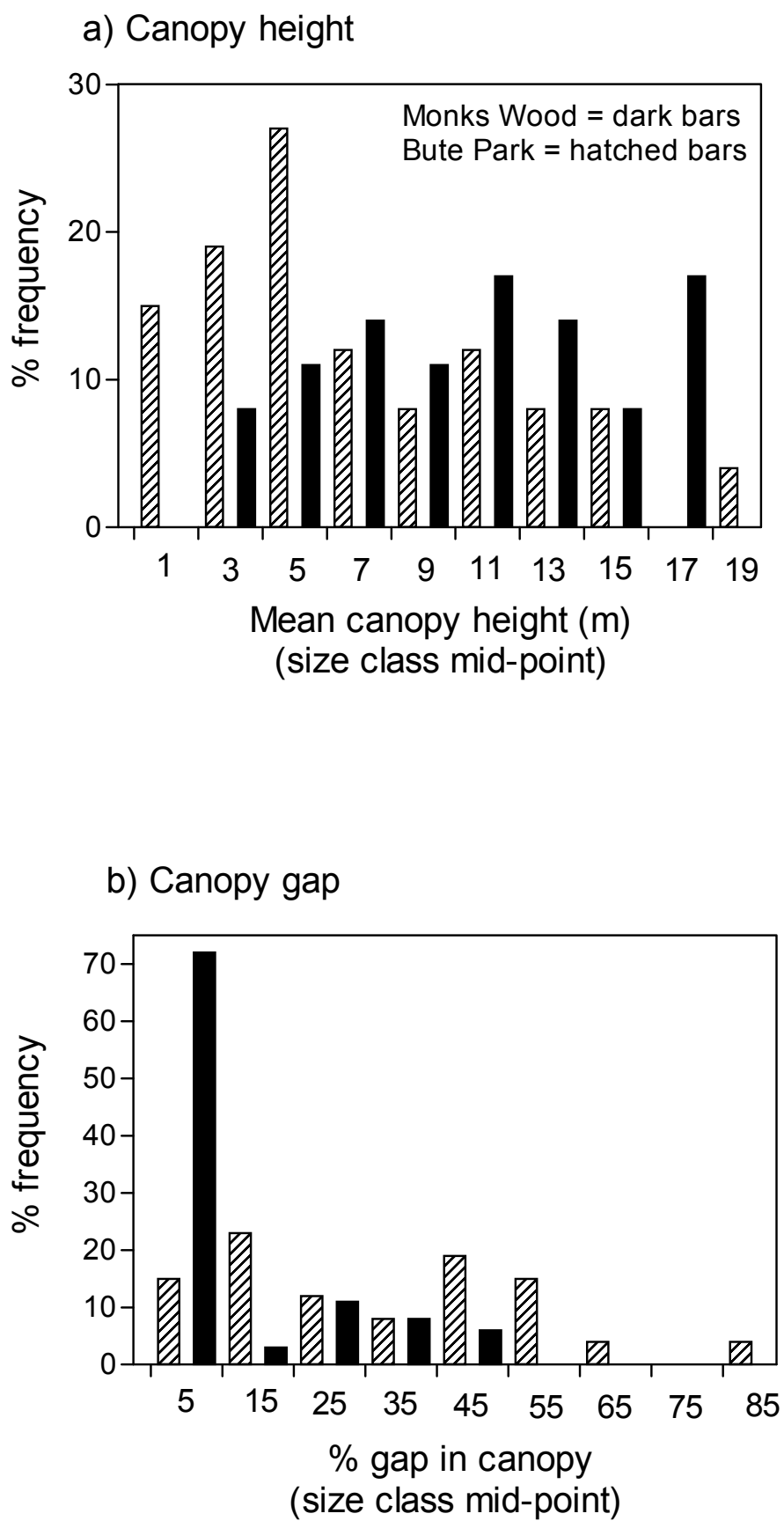## a) Canopy height

b) Canopy gap

Fig .2

a) Canopy height

b) Canopy gap
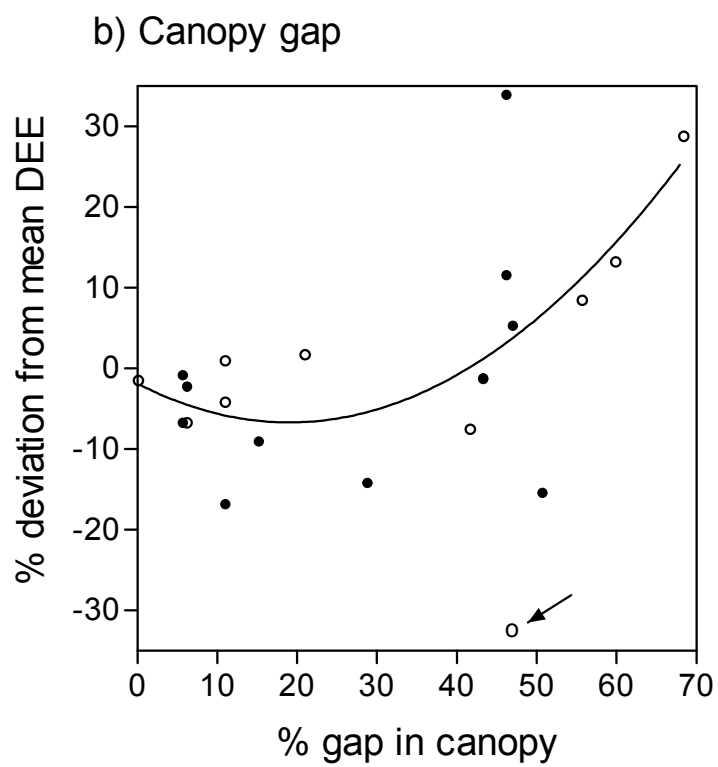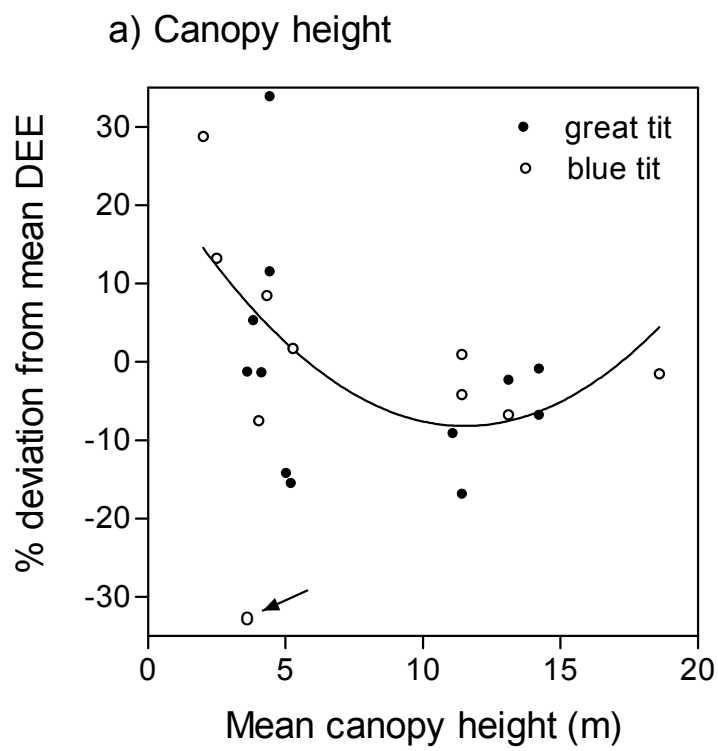
Fig. 3

a) DEE

b) Deviation from mean DEE

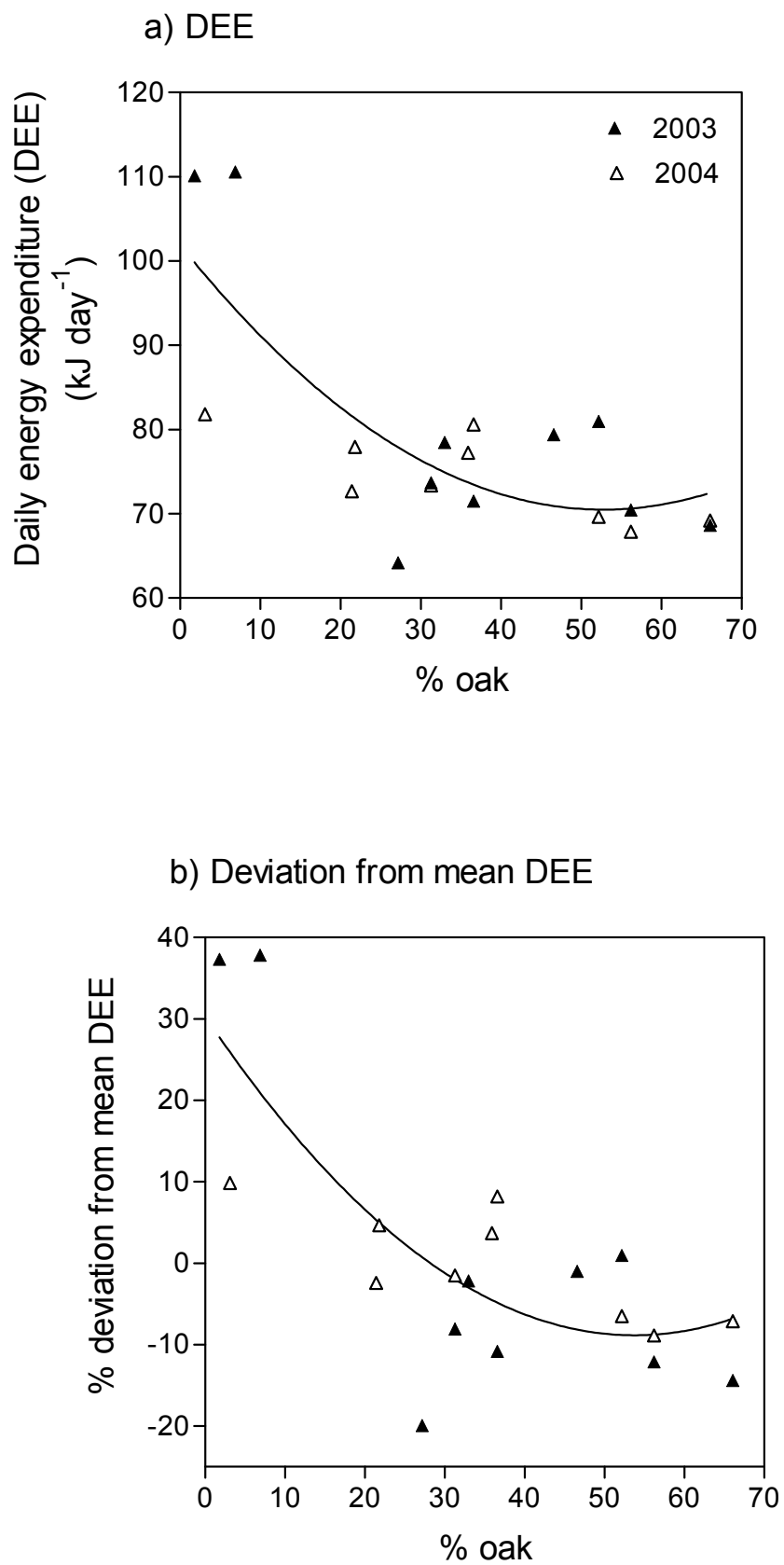
Fig. 4

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Effects of structural and functional habitat gaps on breeding woodland birds: working harder for less

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Supplementary Material

Measurement of bird energy expenditure using doubly labeled water (DLW)

We measured the daily energy expenditure (DEE, kJ day^{-}1) using the doubly labelled water (DLW) technique (Lifson and McClintock 1966; Speakman 1998). This method has been previously validated by comparison to indirect calorimetry in a range of small birds (Visser and Shekkermann 1999) and provides an accurate measure of daily energy expenditure over periods of several days (Speakman et al. 1994; Berteaux et al. 1996).

All the nest boxes were equipped with an internal trap door allowing the operator to trap the individual bird required. Once caught, the bird was ringed, or the ring number recorded if already present, sexed, aged as a first year or older using plumage characteristics (Svensson 1992) and the length (maximum chord) of one wing was measured. Body mass was measured to 0.01g using a portable top pan balance (Adam Equipment Co. Ltd., ACB 300) and the tip of the tail marked with a small amount of white correction fluid to facilitate identification when retrapping. The bird was then injected intraperitoneally with approximately 0.1 ml DLW and placed in a cloth bag for 30 minutes (Thomas et al 2001) to allow the injectate to equilibrate with the body water. After equilibration, a blood sample, maximum volume 70 μl for great tits and 40 μl for blue tits, was collected from the brachial vein in one wing using non-

heparinized capillary tubes (Hirschmann 100 μl ringcaps), and the bird returned to the

bag for a few minutes to ensure that all bleeding had stopped. The tubes were

immediately flamed-sealed using a portable butane gas burner (RS Components Ltd.,

mini gas torch) and stored in larger, screw-topped glass tubes. The condition of the

bird was checked and it was then released in the nest box to continue feeding the

young. The whole procedure from capture to release took about one hour. The bird

was retrapped as near to 24 hours later as possible (Speakman and Racey 1988) and a

second blood sample collected from the brachial vein in the other wing before again

releasing it in the box. The measurement procedures were carried out at a distance

from the box to allow the untrapped partner to continue feeding the young. Most

nestlings were 11 days old on the first day of capture and thus they were ringed and

individually weighed during the equilibration period, reducing disturbance at the nest.

The syringes (1 ml disposable, 0.3 x 13 mm needle) of DLW were prepared

immediately prior to going into the field or occasionally the night before, but no

longer than 15-18 hours before use. They were filled and weighed to 0.0001g in the

lab using an analytical balance and the exact volume of DLW injected calculated by

subtraction after reweighing the syringes on the same balance within a few hours of

use. An additional syringe was carried with those used and was weighed before and

after each field session to monitor possible evaporative losses, but these were

negligible. Blood samples were also collected from non-experimental birds at both

sites in all years (minimum six birds per species per site per year as appropriate) to

determine background levels of ^{18}O and ^2H (Speakman and Racey 1987: method C).

All blood samples were stored at 4ºC until analysis.

The blood samples were vacuum distilled into glass Pasteur pipettes (Nagy 1983)

and the water obtained used for isotope-ratio mass spectrometric analysis of ^2H and

^{18}O. The ^2H analysis was performed on hydrogen (H_2) gas, produced by on-line chromium reduction of water (Morrison et al 2001). For analysis of ^{18}O enrichment in blood samples, water distilled from blood was equilibrated with carbon dioxide (CO_2) gas using the small sample equilibration technique (Speakman et al 1990).

For estimation of the injectate enrichment, the original injectate was diluted with tap water (five different solutions, $\pm$ 0.0001 g), in proportions similar to those expected in the injected birds. Mass spectrometric analysis of ^2H and ^{18}O was performed on five sub-samples of each solution and five sub-samples of tap water. The enrichment of the injectate was calculated for the five different solutions (Prentice 1990, Speakman 1997), and then averaged. Isotopically characterized gases of H_2 and CO_2 (CP grade gases BOC Ltd) were used in the reference channels of the isotope ratio mass spectrometers. Reference gases were characterized every three months relative to SMOW and SLAP (Craig 1961) supplied by the International Atomic Energy Agency. Each batch of samples was run adjacent to triplicates of three laboratory standards to correct for day-to-day differences in mass spectrometer performance. All isotope enrichments were measured in δ per ml relative to the working standards and converted to ppm, using the established ratios for these reference materials. The measures of isotope enrichment in blood samples were based on analysis of five sub-samples (^2H) or two sub-samples (^{18}O); all subsequent calculations were performed on the mean values.

Isotope enrichment were converted to values of daily energy expenditure using a single pool model as recommended for this size of animal by Speakman (1993). There are several alternative approaches for the treatment of evaporative water loss in the calculation (Visser and Schekkermann 1999). We chose the assumption of a fixed evaporation of 25% of the water flux (Speakman 1997: equation 7.17) which has been

established to minimise error in a range of conditions (Visser and Schekkerman 1999; van Tright et al. 2002).

Analysis of remote sensed data

The LiDAR data for Monks Wood and Bute Park were supplied as ACSII data sets of x-, y-, and z- co-ordinates (and intensity) for the first and last return of each laser pulse. The x- and y- location of each scanned point was supplied in British National Grid co-ordinates, whilst the z- elevation was supplied in metres above the Ordnance Survey of Great Britain 1936 Datum. For ease of data processing, the point cloud data sets were each interpolated into raster Digital Surface Models (DSMs). Separate DSMs were created for the first and last return elevation measurements of each data set. The selected pixel size was 1m for Monks Wood and 0.5 m for Bute Park; the higher sampling density allowing for the interpolation of a finer spatial resolution DSM for the park. The last return DSMs had a higher proportion of ground hits than the first return DSMs and so were used to model the underlying terrain. In both cases, modelling of the terrain was based on local minimum filtering, extracting ground hits as local elevation minima, but varying the kernel size depending on canopy heterogeneity and openness. As a more open site, smaller kernel sizes were used at Bute Park than at Monks Wood. Terrain modelling was an iterative process involving manual editing and the retention of a higher proportion of last return data per iteration, resulting in the interpolation of increasingly detailed terrain surfaces. A thin-plate spline interpolation was used to render a Digital Terrain Model (DTM) from the final set of extracted ground hits per site. By the per-pixel subtraction of the DTM from the first return DSM, and the removal of buildings within digitised areas of

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interest, a Digital Canopy Height Model (DCHM) was created for each site in which canopy height was expressed in metres above the ground. Further details of the LiDAR processing method as applied to Monks Wood are available in Hill and Thomson (2005), whilst accuracy assessment of the DTM and DCHM for Monks Wood are available in Gaveau and Hill (2003) and Patenaude et al. (2004).

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