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Parid foraging choices in urban habitat and the consequences for fitness

JULIA A. MACKENZIE,[1*] SHELLEY A. HINSLEY[2] & NANCY M. HARRISON[1]

[1]*Animal and Environmental Research Group, Department of Life Sciences, Anglia Ruskin University, East Road, Cambridge, Cambridgeshire, CB1 1PT, UK*

[2]*Centre for Ecology and Hydrology, Maclean Building, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, UK*

[*]Corresponding author.

Email: Julia.Mackenzie@anglia.ac.uk

Urban environments are habitat mosaics, often with an abundance of exotic flora, and represent complex problems for foraging arboreal birds. In this study, we used compositional analysis to test how Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major* used heterogeneous urban habitat, with the aim of establishing whether breeding birds were selective in the habitat they used when foraging and particularly how they responded to non-native trees and shrubs. We also tested whether they showed foraging preferences for certain plant taxa, such as oak *Quercus*, which are important to their breeding performance in native woodland. Additionally, we used mixed models to test the impact these different habitat types had on breeding success (expressed as mean nestling mass). Blue Tits foraged significantly more in native than non-native deciduous trees during incubation and when feeding fledglings, and significantly more in deciduous than in evergreen plants throughout the breeding season. Great Tits used deciduous trees more than expected by chance when feeding nestlings, and a positive relationship was found between availability of deciduous trees and mean nestling mass. Overall, the breeding performance of both species was poor and highly variable. Positive relationships were found between mean nestling mass and the abundance of *Quercus* for Great Tits, but not for Blue Tits. Our study shows the importance of native vegetation in the complex habitat matrix found in urban environments. The capacity of some, but not all, species to locate and benefit from isolated patches of native trees suggests that species vary in their response to urbanisation and this has implications for urban ecosystem function.

Keywords: Blue Tit, breeding success, compositional analysis, exotic flora, foraging behaviour, Great Tit, habitat preferences, urbanisation

Avian ecologists are increasingly concerned about the effects of urbanisation on structure and composition of bird communities because it causes loss and degradation of bird habitat and often involves introduction of exotic plant species (Bowman & Marzluff 2001, Chace & Walsh 2006). The planting of exotics may be detrimental to some bird species, particularly when combined with reduction and fragmentation of native vegetation (Donnelly & Marzluff 2006), and it is predicted that the species most likely to disappear as urbanisation increases are small arboreal insectivores (Clergeau *et al*. 1998, Crooks *et al*. 2004).

Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major* are small arboreal insectivores which often breed in urban environments, but whose optimal habitat in the United Kingdom (UK) is mature oak woodland (see Perrins 1979 for a general account of tit ecology in woodland). Lack (1958) found that the reduced availability of nestling food in certain habitats was associated with reduced breeding success in both species. For example, Blue Tits and Great Tits have over 95% fledging success in broadleaved woodland but only 60-70% in pine woodland. In woodland, tits primarily feed their young on tree-dwelling caterpillars (Cholewa & Wesołowski 2011). However, in urban environments, where both Blue Tits and Great Tits now commonly breed, caterpillar availability is likely to be much lower because there are fewer trees, and this may reduce reproductive success (Cowie & Hinsley 1988, Riddington & Gosler 1995). Rates of nestling mortality due to starvation are higher in Blue Tits and Great Tits nesting in gardens compared to those nesting in woodland (Lack 1955, Perrins 1979, Cowie & Hinsley 1987) suggesting that adults struggle to find food for their broods. For example, energy expenditure of female Great Tits breeding in urban parkland was 64% higher per nestling than in woodland because foraging habitat was more patchily distributed (Hinsley *et al*. 2008). Habitat may be physically patchy and/or functionally patchy because trees and shrubs are present but for various reasons do not provide suitable foraging habitat. These reasons include the presence of exotic plant species which are common in parks and gardens but typically exhibit low abundances of the arthropod prey favoured by birds (Southwood *et al*.

1982, Burghardt *et al*. 2008, Tallamy & Shropshire 2009). The fact that non-natives plants are more likely to be unpalatable to local herbivorous insects may explain, at least in part, why they are preferentially planted (Tallamy 2004). Additionally, exotic plants often leaf and flower at different times of year than native plants; herbivorous insects often time their reproduction to coincide with bud burst (Buse & Good 1996) and thus create a mismatch between the nestling period and the peak abundance of invertebrate prey.

In parids, fledgling condition is positively correlated with post-fledging survival (Naef-Daenzer *et al*. 2001) and recruitment (Both *et al*. 1999). Because fledgling condition is often dependent upon parental food supply (e.g. Naef-Daenzer & Keller 1999, Mägi *et al*. 2009), parents are expected to maximise their foraging efficiency by selecting invertebrate-rich trees, and there is empirical evidence to support this (Naef-Daenzer 2000, Hino *et al*. 2002). Studies of other birds have found clear foraging preferences for particular tree species, which may also be related to the availability of invertebrate prey (Holmes & Robinson 1981, Peck 1989, Gabbe *et al*. 2002). However, previous studies have been conducted in continuous woodland, whereas much of the habitat available to birds in urban environments comprises parks and gardens (Cannon *et al*. 2005, Hinsley *et al*. 2009) where habitat is usually extremely patchy and heterogeneous.

In this study, our aim was to test whether Great Tits and Blue Tits showed specific foraging preferences for particular trees or habitats, such as native or exotic flora, deciduous versus evergreen plants or for particular taxa (e.g. *Quercus, Acer, Betula*), and whether habitat composition and foraging preferences influenced their breeding success. To do this we used the highly heterogeneous environment of the Cambridge University Botanic Garden (CUBG), located in the centre of the city of Cambridge, UK, as a study site. The CUBG has a high plant species diversity (over 8000 species) including an abundance of exotic flora, and a varied structure of trees and shrubs interspersed with open lawns and herbaceous areas. We made repeated observations of foraging bouts by known individuals in a range of defined habitat types and compared the frequency of use with habitat availability using compositional analysis.

METHODS

Study site

The study was conducted from April-June of 2003-2009 on Blue Tits and Great Tits nesting in the CUBG, a large landscaped garden (~16.5 ha) situated less than a mile from Cambridge city centre (52° 12' N, 0° 08'E). The CUBG is surrounded by a mixture of residential housing, shops and offices, and busy roads. The CUBG contains many plant species with a wide variety of origins (Hinsley *et al*. 2009, Mackenzie 2010). It is consequently an ideal study site in which to examine the responses of native birds to exotic flora in the fragmented habitat typical of urban environments. In addition, the CUBG is open to the public and attracts a large number of visitors, and consequently the resident tits are habituated to the presence of humans, thus enabling us to observe foraging behaviour at close range and reduce the likelihood of habitat-specific variation in bird detectability.

Collection of habitat data

The available habitat in the CUBG was categorised using aerial photographs and ground survey. Presence and absence of flora across a fine-scale grid was used to establish structure (e.g. tree/shrub/gap) and composition (e.g. native/non-native) of the vegetation; this was the basis of the calculation of availability of different habitat types. A grid of 5 x 5 m squares was created using Grid Maker within the Tool Manager option of the GIS software package MapInfo Professional 8.5 (MapInfo Corporation 2006) and laid over an aerial photograph of the CUBG. The approximate number of squares within the study area was 4585, which represented approximately 82% of the total area of the CUBG. The study area excluded the lake and the northern extreme of the garden, where the unusual configuration of the habitat made it difficult to map the flora and observe the birds. Within each square, we recorded the presence or absence of habitat types used by foraging tits, namely an herbaceous layer, shrub layer and/or tree canopy. If a square lacked any such habitat it was recorded as a 'gap'. Thus gaps were both physical (e.g. buildings, paths) and functional (e.g. non-shrubby planted areas/grassed areas that were rarely used by the tits). For the shrub layer and tree canopy we also recorded the following data: 1) genus, 2) leaf type (evergreen versus deciduous) and 3) origin of plant (native and/or northern/central European, Mediterranean or southern European, Asian, American or 'other'). Note that plants categorised as 'garden variety' were, if possible, attributed to an origin based on the ancestral species or otherwise designated as 'other'. If a vegetation patch spanned two squares, but was only equivalent to one square in size then it was only recorded as available in one of the squares (selected randomly) to avoid inflating availability.

The herbaceous layer was defined as any ground-covering, wild-growing plants such as Cow Parsley *Anthriscus sylvestris* or Common Ivy *Hedera helix*. A shrub was defined as a woody plant less than 5 m high and a tree defined as a woody plant greater than 5 m high.

Because the habitat available in a single square could occupy several levels in a 3 dimensional space (e.g. tree canopy, shrub layer and herbaceous layer), each habitat type within a square was counted as '1'. For example, if an area was completely covered with tree canopy and shrubbery, the total habitat available would be twice that of an area covered with either just tree canopy or just shrub and was given a count of '2'. The maximum score a square could have was '3'.

The scores for each of the squares were then summed making it possible to calculate the proportions of different habitat types. The habitat survey (taking account of the 3-D habitat space) showed that 14.0% of the study area was composed of native trees and shrubs (11.7% of which were deciduous and 2.3% evergreen) and 27.4% of non-native trees and shrubs (15.9% of which were deciduous and 11.5% evergreen). The remaining area was made up of herbaceous layers (26.2%) and 'gaps' (32.4%).

Observations of foraging behaviour and habitat use

We observed the foraging behaviour of colour-ringed Blue Tits and Great Tits from late March to mid-June during the 2006-2008 breeding seasons. Between December and March, mist-nets baited with peanut feeders hung in nearby plants were used to capture Blue Tits and Great Tits at six areas around the CUBG. Most birds were ringed (under British Trust for Ornithology licence) with a numbered metal ring on one leg and a unique combination of two plastic coloured rings on the other. A few individuals had one colour ring on one leg and a second one on the other leg above the metal ring (Appendix 1). To avoid biasing observations to any particular part of the garden, it was split into five sections and each section was visited following a random rota. During these visits, each section was walked in such a way that the whole study area was covered once. We recorded the species, colour ring combination and foraging behaviour of any Great Tit or Blue Tit detected, along with the time, date and section of the garden in which it was located. We also noted if the focal bird was with another adult or fledgling(s). For each observation, we noted whether the bird was foraging in a tree, a shrub, the herbaceous layer or a 'gap'. If foraging in a tree or shrub, the species of plant and its origin (as described above in the habitat collection section) was noted. We observed each individual for as long as it was in sight. However, if a bird had not moved after five minutes, the observation was terminated to allow the survey to continue. Birds continued to be observed if they moved from one foraging site to another. Observations were made on 80 Blue Tits and 43 Great Tits over 3 consecutive breeding seasons (2006-2008). A small number of individuals of each species were observed in more than one year.

Measurement of reproductive performance

Both Great Tits and Blue Tits nested in boxes placed on trees throughout the CUBG (see Figure 1 for a map illustrating box placement) allowing their reproductive performance to be monitored from 2003 – 2009. Twenty boxes were present up to and including 2005, after which an extra 22 boxes were added. First egg dates were established by checking the nest boxes at least once per week beginning on approximately April 1st of each year, and then back-calculating from the number of eggs present in active nests (assuming one egg laid per day). Final clutch size was determined through repeated nest checks. The nest was checked for hatching two days before the estimated hatching date (typically 14 days after the day the last egg was laid) and every day thereafter until at least one egg had hatched (designated as day 0). On day 11, nestlings were ringed by licensed ringers and weighed to the nearest 0.1 g. The mean nestling mass (excluding runts) was then calculated for each brood. Because of the poor condition of many of the nestlings in the CUBG, we established objective criteria for categorising chicks as runts. We generated a frequency table of day 11 nestling masses for each species using data from all boxes and any nestling in the lowest 5% of these values (< 9.6 g for Great Tits and < 4.4 g for Blue Tit) was designated as a runt. This excluded an average of 4.5% of Great Tit nestlings and 4.2% of Blue Tit nestlings each year. For comparison, 11-day old Great Tit and Blue Tit nestlings reared in woodland habitats typically weigh 16 – 20 g and 9.0 – 11.5 g respectively (Hinsley *et al.* 1999).

Statistical analyses - foraging preferences

To test whether tits were using particular habitat types (native/non-native plants, deciduous/evergreen plants or specific plant genera) significantly more or less frequently than expected based on their abundance, a series of compositional analyses (Aitchison 1986, Aebischer *et al*. 1993) were carried out using the Compos Analysis v6.2+ software Excel Add-In tool (Smith 2005).

For these analyses the whole of the mapped study site was considered to be available habitat, as opposed to defining an expected foraging range for each bird based on its nest box location. We did not use the latter method because many foraging observations involved birds whose nest sites were not known (28/67 Blue Tits and 15/28 Great Tits in breeding period 1 and 18/57 Blue Tits and 12/30 Great Tits in breeding period 2 - see below for explanation of breeding periods). Furthermore, adults with fledged broods moved widely throughout the CUBG, as has been found in other studies of post-fledging habitat use in Parids (e.g. Van Overveld *et al*. 2011).

The proportion of foraging visits to each habitat by individual tits was categorised in the same way as the available habitat, and the square root of the number of foraging observations made from each bird was used as a weighting factor in the analysis (see Appendix 1 for numbers of observations per individual). Any zero values in the used habitat, corresponding to a habitat that was never used even though it was available, were replaced by a new value that was an order of magnitude smaller than the smallest observed non-zero value of either habitat use or availability (Smith 2005). The program ranks the habitat categories in order of use and determines any associated significance values between these categories by *t*-values.

Compositional analyses were carried out separately for each tit species and for each of three successive periods of the breeding season: period 1 (nest-building, egg-laying and incubation), period 2 (brood up to 17 days old) and period 3 (post-fledging; from 18 days old to the end of observations in late June). The dates of each period were selected by taking the mean of all nest boxes for each species during the focal year. This allowed us to include individuals whose nest locations were not known.

Foraging preference was analysed with respect to plant origin, plant type and selected plant genera (see numbered points below for details).. We ran a total of 18 separate compositional analyses, three tests per species on the three different habitat categorisations split by the three breeding periods. The habitat categories were:

1. Plant origin: a) native deciduous trees and shrubs, b) non-native deciduous trees and shrubs, c) native evergreen trees and shrubs, d) non-native evergreen trees and shrubs, e) herbaceous layers and f) ‘gaps’. Note ‘native’ indicates plant species native to Britain and northern and central Europe; non-native indicates pooled plant species originating from the Mediterranean or southern Europe, Asia, America or ‘other’.
2. Plant type: a) deciduous trees, b) deciduous shrubs, c) evergreen trees, d) evergreen shrubs, e) herbaceous layers and f) ‘gaps’. Note that in these tests all plants of a certain type (e.g. deciduous trees) are pooled regardless of their origin.
3. Selected plant genera: a) *Acer* (maples), b) *Betula* (birches) c) *Quercus* (oaks) (all genera were pooled regardless of their origin), d) all other deciduous trees and shrubs e) all other evergreen trees and shrubs f) herbaceous layers and g) ‘gaps’.

Blue Tits never foraged in a ‘gap’ and so this habitat category was always ranked significantly lowest. This may have biased the *P*-values of the remaining habitat comparisons and so it was removed and the analyses re-run. The MANOVA tests between the calculated log ratios of the remaining habitat categories were unaffected, and hence remained valid (Aebischer *et al*. 1993, Smith 2005). Great Tits sometimes foraged in the ’gaps’ category (on the ground and in leaf litter) and so this category was retained in the analysis for this species. Any unidentified vegetation, which amounted to approximately 0.33% of the trees and 0.69% of the shrubs in the CUBG, was excluded from the analyses.

Statistical analyses – reproductive performance

The influence of different habitat variables (habitat type) on reproductive performance was tested using mixed models in SPSS 16.0 (2007). Mean brood mass on day 11 was used as the response variable and the explanatory variables were habitat type within 25m of the nest, brood size (continuous variables), year and the interaction between habitat and year (categorical variables) . To explore the spatial scale of the effect of habitat, separate models were run with the habitat described within 100 m of the nest. Nest box identity was included as a random effect. Individual identity was not included as a random effect as few birds were present in more than one year and these usually occupied different nest boxes in each. Each habitat type was calculated as percentage of 5 x 5 m squares within a 25 m and 100 m radius of the nest box. These radii were chosen because 25 m is representative of foraging distances of Blue Tits in good quality habitat (Stauss *et al*. 2005, Tremblay *et al*. 2005) whereas 100 m is representative of foraging distances of both species in poor quality habitat (Blue Tits - Tremblay *et al*. 2005, both species - Redhead *et al*. 2013, pers. obs.).

Separate models were carried out for each of the different habitat variables. The habitat variables were 1) % of native trees and shrubs, 2) % of non-native trees and shrubs, 3) % of deciduous trees and shrubs, 4) % of evergreen trees and shrubs, 5) % of *Quercus* trees and shrubs (both deciduous and evergreen), 6) % of *Betula* trees and shrubs (all were deciduous) and 7) % *Acer* trees and shrubs (all were deciduous).

In the final reported model habitat type was always retained whether it was significant or non-significant because it was the variable of most interest, as was brood size (due to its influence on mean mass). Best models were chosen by calculating Akaike's Information Criterion (AIC). AIC values were then transformed to Akaike weights as per Burnham and Anderson (2002) and the model with the highest proportion compared to the other models was the one selected and reported. For all reported models, the three assumptions of normality, homogeneity and linearity were checked. The models were fitted by the method of restricted maximum likelihood (REML).

RESULTS

Foraging preferences

A total of 411 foraging observations was made of 43 individual Great Tits and 1182 observations of 80 individual Blue Tits (Appendix 1). The results of the compositional analyses are shown in Tables 1 to 3 and Figure 2. Because compositional analysis provides a weighted description of habitat use, the representation of the un-weighted data in the figure will not always exactly match the tables reporting the outcome of the compositional analysis. The foraging preference of each species in each of the three breeding periods is ranked according to habitat type. Great Tits were less selective than Blue Tits, but their foraging preference did vary through the breeding period (Fig. 2a). During period 1, Great Tits foraged significantly more frequently in native deciduous trees and shrubs compared with native evergreen trees and shrubs, although few other patterns were evident apart from the lack of use of gaps (Table 1). In period 2, they avoided native evergreens and gaps, relative to other habitat types. During the post-fledging period (breeding period 3) Great Tits used non-native trees and shrubs significantly more than other habitats and non-native trees and shrubs of both deciduous and evergreen varieties were preferred over their native equivalents.

For Blue Tits, throughout the breeding season, native deciduous trees and shrubs ranked as the preferred habitat followed by non-native deciduous trees and shrubs (Table 1, Fig. 2b). However, these differences were not significant during period 2. Both native and non-native deciduous categories were ranked significantly higher than native and non-native evergreen categories in all breeding periods. When plant type (tree or shrub) and leaf type (deciduous or evergreen) was considered irrespective of native or non-native status (Table 2, Fig. 2c & 2d) then, for Great Tits, deciduous trees were the most highly selected, especially in period 2. Deciduous trees were also the preferred foraging habitat for Blue Tits throughout the breeding season.

A final set of analyses tested for foraging differences between focal genera of host plants (Table 3, Fig. 2e & 2f). For Great Tits, there were no significant preferences for focal genera over non-focal deciduous trees and shrubs in periods 1 and 2 but in period 3 focal genera were used significantly less. In period 2, *Quercus* was used significantly less than all other habitat categories except gaps, and also significantly less than evergreens in period 3.

For Blue Tits, the only consistent patterns was that non-focal deciduous trees and shrubs were most highly selected throughout the breeding season (though not significantly more so than *Betula* in period 1) and the herbaceous layer was least selected. The focal deciduous genera tended to be more selected than evergreen trees and shrubs throughout the breeding season.

Breeding performance

We found considerable variation in nestling weight in the garden. Across all seven years, mean mass (± sd) of Great Tit nestlings on day 11 was 14.5 ± 2.3 g and mean brood size was 4.9 ± 2.0 (data from 50 broods). For Blue Tits mean mass of nestlings on day 11 was 9.0 ± 1.1 g and mean brood size was 5.7 ± 2.4 (data from 61 broods). Mean clutch size was 7.22 ± 1.30 for Great Tits and 8.53 ± 1.41 for Blue Tits with on average 54.3% and 50.7% respectively of the clutches producing fledged young (i.e. at least one fledgling).

For Great Tits, the habitat types that had a significant effect on mean nestling mass were the percentage of deciduous trees and shrubs and the percentage of *Quercus* within a 25 m radius of the box (both effects positive, parameter estimates 0.06 and 1.04 respectively) (Table 4). The percentage of native plants within a 25 m radius of the box had a marginal positive effect (parameter estimate 4.86, $P = 0.06$) (Table 4). For Blue Tits, mean nestling mass was significantly related to the percentage of *Quercus* within a 100 m radius (negative effect, parameter estimate 0.04) (Table 5). The percentage of *Betula* within a 100 m radius of the box had a marginally positive effect (parameter estimate 3.59, $P = 0.07$) (Table 5).

DISCUSSION

Compositional analyses of foraging observations of a colour-ringed population of Great Tits and Blue Tits in a diverse botanic garden, showed that Blue Tits foraged significantly more frequently in native plants than in exotics, even in areas where native plants were much less abundant. They fed more frequently in deciduous trees than in deciduous shrubs, but avoided evergreen trees and shrubs and the herbaceous ground layer. They also foraged significantly more on certain genera of trees, especially *Betula* (birch) and, to a lesser extent, *Acer* (maple). However, Blue Tits appear to be less selective in their choice of foraging habitat when rearing nestlings possibly because of the greater time constraints associated in bringing food back to the nest, an observation consistent with those of Grieco (2001).

In contrast, Great Tits showed little discrimination between native and non-native plant species and between specific plant genera, but were found feeding more on deciduous trees during the nestling period. This finding (as in Blue Tits) could be advantageous since insect species richness is found to be significantly greater in larger, mature trees rather than their smaller, younger congeners (Brändle & Brandl 2001, Brändle *et al*. 2008). Note that in the CUBG, woody plants were categorised as either trees or shrubs according to their height (≥ 5 m or < 5 m respectively) rather than by species.

We suspect that Blue Tits prefer to forage in native flora because these species represent a richer source of invertebrates than non-native flora. Native plants have a greater diversity and species richness of phytophagous insects than introduced plants (Kennedy & Southwood 1984, Tallamy & Shropshire 2009, Sugiura 2010). Introduced tree species also harbour fewer insect species in their non-native, compared to native, ranges perhaps because many insects, such as Lepidopteran larvae, have coevolved with their native hosts and are thus unlikely or unable to colonise an introduced species (Southwood 1961, Southwood *et al*. 1982). Whether the plant is deciduous or evergreen is also an important determinant of species richness (Kennedy & Southwood 1984). For example, Southwood *et al*. (2004) found that the evergreen Holm Oak *Quercus ilex* had a lower phytophage biomass and lower species richness than did deciduous oaks and argued that this could probably be attributed to features of evergreen oak leaves such as a dense covering of trichomes on their underside. Evergreen oaks also have slow-growing, tough leaves, most of which (70%) are retained between years (Blondel *et al.* 1991). This leads to a greater accumulation of tannins, which may repel feeding insects since these polyphenolic compounds inhibit their ability to digest the leaves (Feeny 1970). This may explain why other evergreen taxa such as *Taxus* and *Ilex* also have impoverished phytophage fauna (Kennedy & Southwood 1984, Brändle & Brandl 2001).

It is unclear however why we did not find a similar foraging preference for native deciduous plants in Great Tits, especially as we found a marginally positive relationship between the abundance of native plants within 25 m radius of the nest box and mean nestling mass. It is also of interest that the abundance of native plants had seemingly little effect on Blue Tit nestling mass despite their foraging preference for natives. In fact, Blue Tit nestling mass was not affected by the abundance of any particular plant type within a 25 m radius of the nest, the only positive, but non-significant, effect being the abundance of birch within a 100 m. In comparison, the mean mass of nestling Great Tits was positively influenced by a greater abundance of deciduous plants - which is consistent with their foraging preference during nestling provisioning - and by *Quercus* within a 25 m radius of the box. This suggests that Great Tit parents tended to forage relatively close to the nest while provisioning and closer to the box (within 25m) than Blue Tits. Thus the significance of the presence of good quality foraging habitat close to the box could be greater for Great Tits than for Blue Tits. Differences in prey size choice may also be important. Great Tits have been found to select larger prey items (caterpillars) than Blue Tits (Naef-Daenzer *et al*. 2000), and Blue Tits may significantly reduce the abundance of caterpillar prey before it can reach the larger sizes required for Great Tit nestlings (Minot 1981). This may impose an additional constraint on Great Tit breeding and foraging in the CUBG, and in urban habitats in general (Whitehouse *et al*. 2013).

Although the percentage of deciduous trees and shrubs and of *Quercus* within 25 m of the box had significant positive effects on Great Tit nestling mass, this was not directly reflected in the foraging observations, especially the apparent lack of preference for *Quercus*. However, if constrained by prey size and the need to forage relatively close to the nest, Great Tits may have been forced to use a wider range of foraging substrates due to a simple lack of potentially ‘best’ quality options. The foraging observations gave no information on search times or success rates in different foraging locations, but a shortage of good quality sites close to the nest could result in more time spent in sampling alternative plant species. As mainly single prey loaders (Naef-Daenzer *et al*. 2000), Great Tits may also be at a disadvantage in habitat where large prey is relatively scarce, again leading to foraging in a wider range of tree and shrub species.

Blue Tits preferred to forage in *Betula* compared to *Quercus* and *Acer*, but only during the early stage of breeding. This is probably because of the increased availability of insects on birch catkins early in the breeding season (Klemola *et al.* 2010). Gibb (1954) also found that Blue Tits fed in birches more frequently early in the season, with up to 20-29% of birds being recorded on birch catkins during March and April, whereas none were observed feeding in birches during May when they were presumably feeding nestlings. This is consistent with the finding that the peak in caterpillar abundance in birches occurs during late summer/early autumn (Niemelä *et al*. 1982), by which time Blue Tit nestlings have already fledged.

Blue Tits did not show a foraging preference for *Quercus* (oaks) in the heterogeneous habitat of the CUBG, and, unlike Great Tits, the abundance of oaks around the nest did not positively influence mean nestling mass. This was unexpected given that they are classified in some studies as oak specialists (Perrins 1991, Blondel *et al.*1992 1993). However, these studies were conducted in continuous woodland, where oak trees are more likely to support an abundance of Lepidopteran larvae and other insect prey. In fragmented urban habitats, such as the CUBG, the relative scarcity of oak can reduce insect colonisation rates and population growth (Southwood *et al.* 1982) and work by Yguel *et al.* (2011) has shown that, when surrounded by exotic trees of different taxa, phylogenetic isolation of oaks from neighbouring trees can strongly reduce phytophagy.

Acer species have a relatively low abundance of invertebrate species (Kennedy & Southwood 1984), but were used by Blue Tits more frequently than oaks in the CUBG during the post-fledging period. Peck (1989) found that Sycamores *Acer pseudoplatanus* have a high abundance of aphids, which would constitute a poor substitute for preferred caterpillar prey during breeding (Perrins 1979, 1991), but would be more accesible to fledged young. Overall, the use of maple by Blue Tits (9.6% of foraging observations) and observation (pers. obs.) of them feeding aphids to their offspring are likely to be indicative of a lack of high quality prey in the CUBG. Factors such as protection from predators, especially Sparrowhawks *Accipiter nisus*, may also influence brood and hence foraging locations.

It is noteworthy that the mean nestling mass of both species in the CUBG was low (14.5 g and 9.0 g for Great and Blue Tits respectively compared with 17.5 g and 10.6 g for nestlings of the same age in woodland habitats) (Hinsley *et al*. 2009). The birds produced not only lighter but fewer nestlings with only approximately half of the eggs laid in the CUBG producing fledglings (54.3% for Great Tits and 50.7% for Blue Tits) compared to about 80-90% in woodland habitat (Hinsley *et al*. 2009).Nestling mass in parids is a strong predictor of recruitment (Tinbergen & Boerlijst 1990, Cichon & Lindén 1995), thus low mass combined with a low success rate suggests that selection pressure for adaptive breeding/foraging strategies in urban environments could be high. Brood size was unrelated to nestling mass in Blue Tits, but was positively correlated with nestling mass in Great Tits. This finding for Great Tits was counterintuitive in that brood reduction could be expected to increase the quality, i.e. mass, of the smaller number of surviving chicks, and thus might be an indicator of a successful parental strategy. However, brood size can also influence nestling mass via thermoregulatory costs and effects on female time spent brooding versus feeding young (Mertens 1969).

It is possible that our results were biased to some extent because of the difficulty of detecting birds in some of the habitats surveyed, for example we may have missed birds at the top of the tallest trees. However, our protocols sought to minimise bias, and in practice birds were frequently detected initially by ear (both species are highly vocal) which would result in less bias than if we detected them by sight alone. The foraging preference of both species for trees over shrubs is opposite to the expectation if our observations were biased by detection probability. There is no indication that the comparisons between tree taxa would be flawed by any bias in detection of birds. Similarly, detection of birds in shrubs was facilitated by proximity to the observer and the bird's habituation to the close presence of people. Our data do suggest that the two species have very different foraging preferences, despite their broadly similar ecology. However, we caution that the sample sizes for the Great Tit analyses were substantially smaller than those of the Blue Tit analyses. We would also have liked to compare the invertebrate populations of both native and non-native flora found within the CUBG but this was beyond the scope of this project as over 8000 plant species were present. Indeed this comprises a major challenge in any urban foraging study where plant species diversity is high.

More people now live in cities than in rural areas (UNFPA 2007), and increasing urbanisation will lead to the loss of more natural and semi-natural habitats. Hence it is important to understand how insectivorous birds adjust their foraging decisions when faced with a decrease in overall habitat as well as a proportional increase in the number of non-native plants. Blue Tits, by preferential use of native deciduous trees, may be adopting a better foraging strategy compared with the less selective Great Tits, assuming that additional travel and search costs do not outweigh the advantages of the greater insect availability of the former. In urban environments, however, insect abundance and species richness are likely to be lower than in equivalent areas of woodland due to the lower abundance of plants, their higher spatial and compositional heterogeneity, and the higher ratio of exotics to natives. Urban pollution may also affect invertebrate abundance but there is no reason to assume this would correlate with particular vegetation types or provenances; proximity to the source of pollution would appear to have more potential influence (Eeva *et al*. 1997). Overall, foraging success in urban environments is likely to be poor compared with natural habitats, and thus may contribute to lower breeding success (Cowie & Hinsley 1987, Riddington & Gosler 1995). The current study highlights the need for greater consideration of foraging preferences of urban birds when designing floral landscapes.

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Appendix 1. Colour-ring combinations of Great Tits and Blue Tits studied in the Cambridge University Botanic Garden during the breeding seasons of 2006-2008 together with the number of foraging observations obtained from each individual.

Individual Great Tit	Number of foraging observations	Individual Blue Tit	Number of foraging observations	Individual Blue Tit	Number of foraging observations
B/M	8	B/B	17	P/W-M	2
B/O	17	B/M	22	P/Y	8
B/P	40	B/O	1	P+W	22
B/Y	4	B/P	10	R/B-Y	9
G/B	12	B/W	19	R/G	23
G/M	2	B/Y-B	8	R/M	42
G/O	2	B+P	6	R/R	1
G/R	9	B-Y/R	17	R/Y	5
G/W	2	G/B	16	R+B	24
N/O	2	G/R-B	11	R+G	28
O/M	10	G/R-W	7	R-B/G	29
O/O	23	G/W-R	21	R-B/O	69
O/Y	23	G+Y	1	R-B/P	28
P/B	21	G-O/B	40	R-B/Y	29
P/O	24	G-O/G	12	R-W/B	8
P/P	16	G-O/W	1	R-W/P	5
P/R-W	2	G-Y/B	2	R-W/R	26
P/W	37	M/G-O	14	R-W/Y	30
R/B-Y	9	M/M	7	W/B	33
R/R	6	M/O-G	4	W/B-R	2
R/W	11	M/R	19	W/G-O	32
R/Y	7	M/W	2	W/G-R	14
R-W/O	7	M/Y	5	W/N	5
W/B	2	M+O	3	W/R-B	1
W/O	3	N/B	1	W/Y-B	7
W/R	3	N/R	14	W+B	7
Y/B	25	N+R	11	W+Y	5
Y/N	32	O/G-B	25	Y/B	1
Y/P	20	O/N	1	Y/B-Y	3
B/B	1	O/R-W	32	Y/G-O	7
B/R-B	1	O/W-M	13	Y/G-R	10
B/W-R	2	O-G/R	1	Y/O	9
P/W-R	2	P/B	6	Y/O-G	18
P/Y	9	P/B-G	1	Y/R-B	1
R-W/Y	1	P/B-Y	1	Y/R-W	4
W/G-O	2	P/G	11	Y/W	11
W-R/P	1	P/G-B	25	Y/W-R	44
Y/B-Y	2	P/M	1	Y/Y	23
Y/O	1	P/R	34	Y+B	30
Y/R	3	P/R-B	79	Y-B/O	6
Y/W	5				
Y-B/P	1				

Y-B/Y	1				

B = dark blue, G = green, M = mauve, N = black, O = orange, P = pale blue, W = white, Y = yellow. A dash (-) indicates a striped colour ring, a slash (/) indicates two separate colour rings, one on top of the other on one leg of the bird. A plus (+) indicates two separate colour rings, one on each leg, with the second colour ring in the sequence being on top of the metal ring.

Table 1. Results of a compositional analysis of Great Tit and Blue Tit preferences for foraging from a variety of plants of different origins in the Cambridge University Botanic Garden, UK (non-native refers to any plant not found in Britain or north/central Europe). Variables are separated with > symbols, with those to the left of the symbol being of higher rank (greater usage during foraging) than those to the right of the symbol. A single symbol (>) indicates the difference in preference between the two consecutively ranked habitats is not significant whereas three symbols (>>>) indicates the difference is significant ($P < 0.05$). Significant differences between non-consecutively ranked variables (and any variables thereafter in the sequence) are indicated by * ($P < 0.05$) and ** ($P < 0.01$, calculated from univariate *t*-tests).

	Great Tits	Blue Tits
Breeding period 1	* ND > N-ND > HL > N-NEv > NEv >>> Gap N = 28	ND >>> N-ND >>> NEv > N-NEv >>> HL N = 67
Breeding period 2	** * * ND > N-ND > N-NEv > HL > NEv > Gap N = 30	ND > N-ND >>> NEv >>> N-NEv > HL N = 57
Breeding period 3	* * N-ND > N-NEv > ND > HL > NEv >>> Gap N = 29	ND >>> N-ND >>> N-NEv > NEv > HL N = 55

ND = native deciduous trees and shrubs, N-ND = non-native deciduous trees and shrubs, NEv = native evergreen trees and shrubs, N-NEv = non-native evergreen trees and shrubs, HL = herbaceous layer, Gap = ‘gaps’ category (see methods for description)

Table 2. Results of a compositional analysis of Great Tit and Blue Tit preferences for foraging from a variety of plant types in the Cambridge University Botanic Garden, UK. Variables are separated with > symbols, with those to the left of the symbol being of higher rank (greater usage during foraging) than those to the right of the symbol. A single symbol (>) indicates the difference in preference between the two consecutively ranked habitats is not significant whereas three symbols (>>>) indicates the difference is significant (P < 0.05). Significant differences between non-consecutively ranked variables (and any variables thereafter in the sequence) are indicated by * (P < 0.05), ** (P < 0.01) and *** (P < 0.001; calculated from univariate *t*-tests).

	Great Tits	Blue Tits
Breeding period 1	DT > DS > EvS > HL > EvT >>> Gap N = 28	DT >>> DS >>> EvS > EvT >>> HL N = 67
Breeding period 2	DT >>> HL > EvT > DS > EvS > Gap N = 30	DT>>>DS>EvS>EvT>HL N = 57
Breeding period 3	DT > DS > EvT > HL > EvS >>> Gap N = 29	DT >>> DS >>> EvS > HL > EvT N = 55

DS = deciduous shrubs, DT = deciduous trees, EvS = evergreen shrubs, EvT = evergreen trees, HL = herbaceous layer, Gap = 'gaps' category (see methods for description)

Table 3. Results of a compositional analysis of Great Tit and Blue Tit preferences for foraging from trees and shrubs of particular genera available in the Cambridge University Botanic Garden, UK. The genera were *Quercus* (including both deciduous and evergreen species), *Acer* and *Betula* (all species of both genera deciduous). Variables are separated with > symbols, with those to the left of the symbol being of higher rank (greater usage during foraging) than those to the right of the symbol. A single symbol (>) indicates the difference in preference between the two consecutively ranked habitats is not significant whereas three symbols (>>>) indicates the difference is significant (P < 0.05). Significant differences between non-consecutively ranked variables (and any variables thereafter in the sequence) are indicated by * (P < 0.05), ** (P < 0.01) and *** (P < 0.001; calculated from univariate *t*-tests).

	Great Tits	Blue Tits
Breeding period 1	DTS > *Ac* > EvTS > HL > *Be* >>> *Qu* >>> Gap N = 28	DTS > *Be* >>> *Ac* > *Qu* >>> EvTS >>> HL N = 67
Breeding period 2	*Ac* > DTS > *Be* > EvTS > HL >>> *Qu* >>> Gap N = 30	*** (*Be*–HL), ** (*Qu*–HL), *** (*Ac*–HL) DTS >>> *Be* > *Qu* > *Ac* > EvTS >HL N = 57
Breeding period 3	* (EvTS–*Qu*) DTS >>> EvTS > *Ac* > HL > *Be* > *Qu* >>> Gap N = 29	** (*Ac*–*Qu*), *** (*Be*–EvTS) DTS >>> *Ac* > *Be* > *Qu* > EvTS > HL N = 55

Ac = all *Acer* trees and shrubs, *Be* = all *Betula* trees and shrubs, *Qu* = all *Quercus* trees and shrubs, DTS = all other deciduous trees and shrubs, EvTS = all other evergreen trees and shrubs, HL = herbaceous layer, Gap = ‘gaps’ category (see methods for description)

Table 4. Summary of Mixed Models describing the relationships between mean body mass of 11-day old Great Tit nestlings produced within a given nest box within the Cambridge University Botanic Garden and the different habitat variables within a 25 m and 100 m radius of the box. For the variable 'Habitat' the direction of the relationship with mean nestling mass is shown by the symbols + and —; + indicates a positive parameter estimate and thus a positive effect on mean nestling mass and — indicates a negative parameter estimate and thus a negative effect on mean nestling mass. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, † variable omitted from the model based on AIC selection.

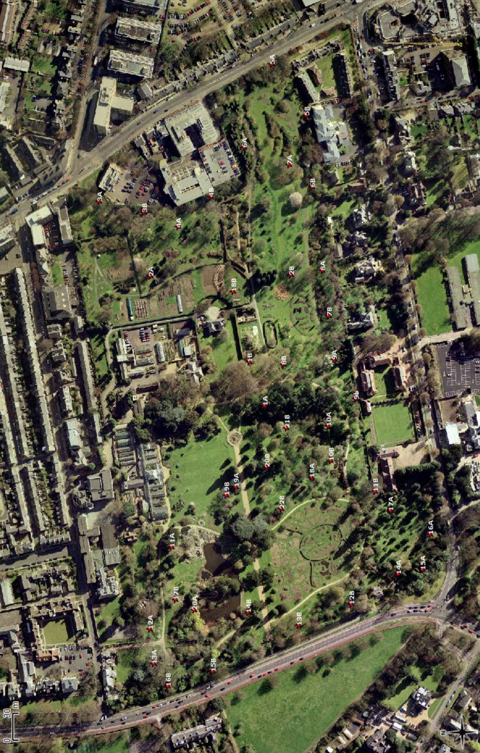
			F value of the predictor variables				Estimates of covariance parameters
Habitat type		Habitat radius	Habitat	Year	Habitat x year interaction	Brood size	Nest box
Non-native trees and shrubs		25 m	-1.15	6.11**	†	5.15*	1.95
		100 m	-3.53	0.67	0.47	4.77*	0.83
Native trees and shrubs		25 m	+4.86	6.59**	†	5.20*	1.10
		100 m	+2.17	6.19**	†	5.70*	1.54
Genera	*Quercus*	25 m	+6.23*	13.46***	6.21*	10.93**	3.02
		100 m	+0.37	1.57	0.16	2.55	1.74
	Betula	25 m	+2.66	3.59*	1.09	6.21*	1.37
		100 m	+3.32	3.57*	1.82	9.72**	1.56
	Acer	25 m	-0.24	4.37*	0.92	3.38	1.61
		100 m	-0.08	3.57*	1.45	6.13*	2.08
Evergreen trees and shrubs		25 m	-1.74	5.92**	†	5.92*	1.61
		100 m	-1.52	6.06**	†	5.74*	1.67
Deciduous trees and shrubs		25 m	+6.16*	6.42**	†	6.65*	0.84
		100 m	+1.11	5.95**	†	5.33*	1.80

Table 5. Summary of Mixed Models describing the relationships between mean body mass of 11-day old Blue Tit nestlings produced within a given nest box within the Cambridge University Botanic Garden and the different habitat variables within a 25 m and a 100 m radius of the box. For the variable ‘Habitat’ the direction of the relationship with mean nestling mass is shown by the symbols + and —; + indicates a positive parameter estimate and thus a positive effect on mean nestling mass and — indicates a negative parameter estimate and thus a negative effect on mean nestling mass. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, † variable omitted from the model based on AIC selection.

			F value of the predictor variables				Estimates of covariance parameters
Habitat type		Habitat radius	Habitat	Year	Habitat x year interaction	Brood size	Nest box
Non-native trees and shrubs		25 m	-0.40	1.13	†	0.72	0.11
		100 m	-0.27	1.29	1.25	1.15	0.00
Native trees and shrubs		25 m	+0.25	1.28	†	0.63	0.12
		100 m	+1.24	1.25	†	0.68	0.11
Genera	*Quercus*	25 m	+0.28	1.41	†	0.61	0.14
		100 m	-4.24*	1.61	1.15	0.15	0.47
	Betula	25 m	+0.74	1.40	0.85	0.34	0.29
		100 m	+3.59	1.50	0.77	0.40	0.38
	Acer	25 m	-0.35	3.38*	2.67	0.94	0.59
		100 m	-0.06	2.41	1.89	0.80	0.54
Evergreen trees and shrubs		25 m	-1.82	1.21	†	1.13	0.00
		100 m	-0.39	1.65	1.75	0.96	0.36
Deciduous trees and shrubs		25 m	+1.00	1.34	†	0.82	0.05
		100 m	+0.80	1.32	†	1.04	0.16

Figure 1. Map of the Cambridge University Botanic Gardens (Getmapping Plc © 2002) showing the locations of the 42 nest boxes used in this study. Nest boxes with an 'A' suffix were erected prior to 2006 and the size of their hole (approximately 28 mm) allows both Blue Tits and Great Tits to enter, although most were occupied by Great Tits. Nest boxes with a 'B' suffix were erected from 2006 onwards and the size of their hole (approximately 25 mm) allows only Blue Tits to enter. However, boxes 8B and 12B have a larger hole which allows both species to enter.

Figure 2. Great Tit and Blue Tit foraging use in relation to availability in the CUBG, UK during three periods of the breeding season of; (a and b) 4 different categories of plants (ND = native deciduous trees and shrubs, N-ND = non-native deciduous trees and shrubs, NEv = native evergreen trees and shrubs, N-NEv = non-native evergreen trees and shrubs); (c and d) plant type (tree or shrub) and leaf type (deciduous or evergreen) (DS = deciduous shrubs, DT = deciduous trees, EvS = evergreen shrubs, EvT = evergreen trees); (e and f) focal tree and shrub genera (Ac = all *Acer* trees and shrubs, Be = all *Betula* trees and shrubs, DTS = all other (than focal genera) deciduous trees and shrubs, EvTS = all other (than focal genera) evergreen trees and shrubs, Qu = all *Quercus* trees and shrubs) *Quercus* is represented by both deciduous and evergreen species while all representatives of *Acer* and *Betula* are deciduous. For all figures, data has been averaged over all individuals used in the compositional analyses. Two additional categories, herbaceous layers and 'gaps', were omitted for clarity. Error bars indicate standard deviations.


5A
5B
6A
7A
6B
3A
3B
4B
4A
8A
2A
2B
18B
7B
1B
8B
9A
9b
1A
21B
10A
20B
10B
18A
19B
19A
11B
22B
17A
16A
11A
14A
15A
17B
20A
14B
12B
12A
13B
13A
15B
16B
30 m


(a)
Great Tits
(b)
Blue Tits
Available
Used
(c)
(d)
(e)
(f)
(%) Habitat
Habitat type
Breeding period 1
Breeding period 2
Breeding period 3
ND
N-ND
NEv
N-NEv
DT
EvT
DS
EvS
DTS
Qu
Ac
Be
EvTS
0.00
20.00
40.00
60.00
80.00
100.00