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1 **Does the urban gradient influence the composition and ectoparasite load of nests of an urban**
2 **bird species?**

3

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13

14 **Abstract:** Urbanisation has profound impacts on birds via, for example, changes in activity budgets,
15 distributions and movements influenced by resource availability, and the connectedness of preferred
16 habitats. We live in an urbanising world and yet understand little about how urbanisation affects the
17 basic biology of organisms that share urban spaces with us. A case in point is nest construction and
18 nest maintenance behaviours that require significant investments of time and energy by birds early in
19 the breeding attempt. Here, we studied how position on an urban gradient in the city of Birmingham,
20 UK, influenced the composition and ectoparasite load of nests of Blue Tits (*Cyanistes caeruleus*). In
21 total, we deconstructed 131 nests removed from nestboxes at the end of the breeding season in 2014 at
22 30 different locations along an urban gradient. Nest composition varied significantly along this
23 gradient with significant relationships between feather content and built cover (negative), and
24 connected tree cover (positive). Notably, anthropogenic materials were found in 73% of nests but
25 their inclusion was unrelated to position on the urban gradient. The only identifiable ectoparasites in
26 nests were Siphonapterans (fleas) and although ectoparasite load was unrelated to position on the
27 urban gradient, it was positively related to nest mass. Taken together, we show that even for a
28 common species that is often referred to as an ‘urban adapter’, the urban gradient influences nest
29 composition and ectoparasite load, and thus potentially reproductive outcomes of small passerines.
30 The challenge is to roll out this approach over multiple years to test the applicability of our findings
31 over longer timeframes and their broader implications for a wide range of bird species that are
32 routinely found breeding in increasingly urbanised landscapes globally.

33

34 **1. INTRODUCTION**

35 We live in a rapidly urbanising world (United Nations, Department of Economic and Social Affairs,
36 Population Division, 2014) with 54% of the human population residing in urban areas in 2014. As a

37 result of urbanisation, many bird species have to adapt rapidly to the concomitant changes in habitat
38 structure (Rodewald *et al.*, 2013), predation risk (López-Flores *et al.*, 2009), food availability (Jones
39 and Reynolds, 2008), temperature regimes (Deeming *et al.*, 2012) and nest site availability (Chace
40 and Walsh, 2006). In recent years there have been a number of studies that have documented marked
41 changes in life-history strategies of birds co-existing with large (and ever increasing) human
42 populations (reviewed in Chace and Walsh, 2006). For example, Chamberlain *et al.* (2009) found that
43 when compared to non-urban birds, urban Great Tits (*Parus major*) and Blue Tits (*Cyanistes*
44 *caeruleus*) laid earlier, produced smaller clutches, reared lighter nestlings and had lower productivity
45 per nesting attempt. These effects were mediated through widespread availability of supplementary
46 food in urban areas resulting in birds in higher body condition laying eggs earlier than rural
47 conspecifics (Schoech and Bowman, 2001); lower availability of natural foods, however, resulted in
48 poorer provisioning of urban broods and thus ultimately reduced productivity. In another study
49 Rolshausen *et al.* (2009) described a migratory divide between sympatric Eurasian Blackcaps (*Sylvia*
50 *atricapilla*) that showed rapid changes in phenotype and reproductive isolation. This migratory divide
51 was established through increased anthropogenic food availability in urban centres, resulting in
52 changes in overwintering strategies of some birds and representing a possible mechanism for
53 speciation.

54 We know much about how urbanisation influences the behaviour and ecology of birds with
55 research findings summarised in a number of books (e.g. Bird *et al.*, 1996; Marzluff *et al.*, 2001;
56 Lepczyk and Warren, 2012; Gil and Brumm, 2013). Fuller *et al.* (2012) found that the availability of
57 food resources to birds breeding in urban areas was positively related to human population density
58 both at regional scales and within a single large city (i.e. Sheffield, UK). The population densities of
59 some small passerines such as the House Sparrow (*Passer domesticus*), the Common Blackbird
60 (*Turdus merula*) and the Common Starling (*Sturnus vulgaris*) were positively related to the density of
61 bird feeders in the city of Sheffield, UK. By contrast, other species that regularly visit bird feeders in
62 urban gardens, such as Great and Blue Tits, Common Wood Pigeons (*Columba palumbus*) and Winter
63 Wrens (*Troglodytes troglodytes*), they were not (Fuller *et al.*, 2012).

64 Compared with our knowledge of how urbanisation influences bird distribution and abundance,
65 our understanding of the nesting biology of birds in our towns and cities remains more limited
66 (reviewed in Deeming and Reynolds, 2015). This is surprising given that investment of time and
67 energy in nest building and maintenance is far from trivial in many species (Hansell, 2000; Stanley,
68 2002). Bird abundance is in part determined by their productivity but we now need to go beyond
69 studies that, for example, simply examine how the breeding performance of birds varies with
70 urbanisation (e.g. Tremblay *et al.*, 2003; Hedblom and Söderström, 2012; Partecke *et al.*, 2012).
71 There is a pressing need to investigate nest building and resultant nest composition in response to
72 urbanisation to allow us to understand in greater detail how such reproductive phases are shaped by
73 ecological context and how they explain life-history strategies of birds. Smith *et al.* (2013) examined

74 how food availability (as a proxy for urbanisation) influenced nest building of Blue and Great Tits and
75 found that food supplementation advanced the onset of nest construction and egg laying in both
76 species, and truncated the nest construction period of Blue Tits (but not Great Tits). However, the
77 nest-lining period was not influenced by food availability in either species. Nest composition has been
78 examined in relation to altitude (e.g. Kern and van Riper, 1984), latitude (e.g. Deeming *et al.*, 2012;
79 Mainwaring *et al.*, 2012), timing of laying (e.g. Mainwaring and Hartley, 2008; Britt and Deeming,
80 2011), and ectoparasite load (e.g. Petit *et al.*, 2002; Suárez-Rodríguez *et al.*, 2012), but not within an
81 urban context. In the case of nest defence against ectoparasites, we know that many species actively
82 select specific nest constituents to reduce the ectoparasite burden that if uncontrolled can dramatically
83 reduce offspring growth and/or survival (reviewed in López-Rull and Macías Garcia, 2015).

84 In this study we examine how the composition and ectoparasite load of nests of an urban
85 ‘adapter’ common passerine species, the Blue Tit (Crocì *et al.*, 2008), varied along an urban gradient
86 in the city of Birmingham, UK. First, we collected nests at the end of the 2014 breeding season from
87 clusters of identical nestboxes at various points along an urban gradient (as defined by two land cover
88 metrics) and deconstructed them to examine nest composition. Secondly, the same nests were
89 examined to quantify ectoparasite load. In this way it was possible to examine how nest composition
90 was related to the ectoparasite load experienced by the nest occupants.

91

92 2. METHODS

93 In January of 2014, 10 nestboxes were erected at each of 31 separate sites in the city of Birmingham
94 that provided a broad range of diversity along two urban gradients defined according to connected tree
95 cover and built cover. Descriptions of how the urban land cover measures were derived and a list of
96 the 31 sites identified in the study are provided in Appendix 1. Figure 1 shows the distribution of
97 some of these 31 sites throughout the city and representative photographs illustrate the habitat at each
98 of them.

99 At the end of the breeding season (i.e. August 2014) all nests (N = 163) were removed from
100 nestboxes and immediately placed in individual tin-foil containers with cardboard lids. Nests were
101 then stored in a domestic chest freezer (Space Max Whirlpool, Whirlpool UK Appliances Ltd,
102 Croydon, UK) prior to nest deconstruction. Nestboxes at one site (namely ‘Grand Union Canal’ – see
103 Appendix 1 for further details) contained no Blue Tit nests and so subsequent findings are based on
104 nests from the remaining 30 sites. All but three nestboxes, containing Great Tits, provided nests made
105 by Blue Tits. Of these 160 nests, 107 progressed beyond the egg stage.

106 Each nest was removed from the chest freezer, any eggs and dead chicks still contained in the
107 nest cup were removed and then it was weighed to the nearest 0.0001 g on an electronic balance
108 (Sartorius 1712, Göttingen, Germany). Each nest was then defrosted overnight at room temperature
109 for a minimum of 15 hours before processing. On average it took 1 hour and 34 minutes to process
110 each nest in the laboratory by deconstructing them and assessing ectoparasite load. Each nest was then

111 separated into cup and base components by one person (AW) to maintain consistency and each was
112 then weighed separately.

113 The cup and the base of each nest were deconstructed separately. Nest constituents were
114 separated using fine-point tweezers and placed into the following categories: moss, dry grass,
115 feathers, hair, fur, natural fibres and anthropogenic materials. Natural fibres consisted predominantly
116 of wool or wool-like material while anthropogenic materials were fibres that had undergone
117 processing such as plastics, dyed wool, cotton, *etc.*. Material of each constituent was weighed
118 separately to the nearest 0.0001 g on an electronic balance (see above for details) and then stored in
119 separate sealed Ziploc bags. The remaining material following separation of other nest constituents
120 was weighed and then examined to quantify ectoparasite load of each nest. It comprised dead skin
121 (from nestlings and tending adults), faeces, dust particles, invertebrates, pupae cases and any other
122 nest material not falling into the main nest constituents. It was searched methodically twice using
123 fine-point tweezers and a $\times 10$ hand lens for all ectoparasites which were removed and counted into
124 weighing boats. Following ectoparasite removal, all remaining material was stored in a sealed Ziploc
125 bag. Subsequent identification of larvae removed from nest materials as being ectoparasites proved
126 inconclusive and thus they were excluded from subsequent statistical analysis.

127 Statistical analysis of nest composition data treated the nest constituents separately but in the
128 case of ectoparasite load, we combined hair, fur and natural fibres into a new category called ‘animal
129 fibres’; these nest materials are functionally alike in acting in a similar manner as substrate for
130 ectoparasites in nests (Hansell, 2000). All statistical analysis was carried out using SPSS (SPSS 23 for
131 Windows 7, IBM Corporation, New York, New York, USA). The sampling unit for analyses was the
132 nest site location and thus all data from analyses of nest composition and ectoparasite load are
133 presented as site averages (range: 1-9 nestboxes). This approach attempts to control for statistical non-
134 independence of nests from the same site where habitat and microclimatic variables were likely
135 shared across all nestboxes. However, summary data for nest mass and nest composition in terms of
136 masses of the different are provided in Appendix 2.

137 Nests were categorised along the urban gradient into ‘low’ (0-33%), ‘medium’ (34-66%) and
138 ‘high’ (67-100%) connected tree cover and built cover. This inevitably resulted in unequal sample
139 sizes between categories for statistical comparisons. Proportional (bound) data were not normally
140 distributed and thus were normalised using arcsine square-root transformation prior to one-way
141 analyses of variance (ANOVA). Significant ANOVA outputs were followed by *post hoc* Tukey’s
142 tests. Ectoparasite loads were count data, were not normally distributed and so we used Mann-
143 Whitney *U*-tests and Kruskal-Wallis tests for statistical comparisons. Linear regression analysis was
144 used to elucidate relationships between variables where one could be established as a dependent
145 variable. In all cases statistical analyses were conducted using an alpha threshold of 0.05.

146

147 3. RESULTS

148 In total 131 Blue Tit nests were deconstructed with 107 of them having contained live chicks during
149 the breeding season and 24 of them having failed at the egg stage.

150

151 **3.1 Nest composition**

152 All nests were composed of a base of moss with the nest lining comprising dry grass, feathers, natural
153 fibres, anthropogenic materials and fur (Appendix 2). The composition of nests according to the
154 relative masses of each of these components did not differ significantly in nests from low, medium
155 and high connected tree cover categories of the urban gradient (Fig. 2a; $F_{2,27} = 0.15$, $P = 0.86$).
156 However, the composition of nests from low, medium and high built cover categories of the urban
157 gradient was significantly different (Fig. 2b; $F_{2,27} = 5.70$, $P = 0.009$) with more natural fibres found in
158 nests in high built cover ($P < 0.05$).

159 If urban land cover is treated as a continuous (rather than a categorical) variable, few
160 statistically significant changes in nest composition were found along the urban gradient. Feathers
161 were the only nest component to be significantly positively correlated with connected tree cover (Fig.
162 3a; $R = 0.41$, $df = 28$, $P = 0.02$), and they were negatively correlated with built cover (Fig. 3b; $R = -$
163 0.42 , $df = 28$, $P = 0.02$). Natural fibre content of nests was marginally negatively correlated with
164 connected tree cover (Fig. 3c; $R = -0.33$, $df = 28$, $P = 0.07$), but it was marginally positively
165 correlated with built cover (Fig. 3d; $R = 0.32$, $df = 28$, $P = 0.08$). Although anthropogenic materials
166 were found in 73% of all nests, their contribution to overall nest composition did not differ
167 significantly in relation to the location of nest sites along the urban gradient.

168

169 **3.2 Ectoparasite load**

170 Fleas (Siphonaptera) were the only ectoparasites discovered in the nests and on average each of the
171 131 nests that were deconstructed contained 184 fleas. The 107 nests that contained live pulli during
172 the 2014 breeding season contained many more fleas than the 24 nests that did not ($U = 380$, $n_1 = 107$,
173 $n_2 = 24$, $P < 0.0001$). As a result all subsequent analyses were performed on nests that only contained
174 pulli. Flea counts did not differ significantly in nests from low, medium and high connected tree cover
175 categories of the urban gradient ($H = 0.93$, $df = 2$, $P = 0.63$), and nor did they differ between built
176 cover categories of the urban gradient ($H = 0.77$, $df = 2$, $P = 0.68$).

177 Flea count did not appear to be dependent on the relative proportions of the different
178 components of nests (all R^2 s < 0.07 , all P s > 0.05). The only nest trait that was related to flea
179 abundance was nest mass, with the two variables being positively related (Fig. 4; $R^2 = 0.27$, $df = 28$, P
180 $= 0.004$).

181

182 **4. DISCUSSION**

183 Compared with other reproductive phases, the nest phase (including its construction and ongoing
184 maintenance) is under-studied, especially in relation to the urban gradient. Therefore, our study was

185 based upon the general reproductive behaviour of small passerines in urban environments in response
186 to habitat connectivity, foraging resource and activity budgets, rather than on the specifics of their
187 nesting biology *per se*. Thus, we might have expected that birds in urban areas would construct nests
188 of similar insulative property to those constructed by birds in more rural areas providing benefits to
189 the former as a result of the urban heat island (UHI) effect translating into a warmer nest
190 microclimate. Alternatively, we might have expected that birds nesting in more urban environments
191 would have less well insulated nests because of the nest microclimate being warmer (Deviche and
192 Davies, 2014). However, both expectations are accompanied by the caveat that there is little evidence
193 to suggest that increases of even a few °C in ambient temperature associated with the UHI effect
194 influence the recrudescence of reproductive systems of birds and thus nest building, timing of egg
195 laying *etc.*. We also expected that in nests from more urban areas, the proportion of anthropogenic
196 materials might increase while that of more natural nest components might decrease, simply based
197 upon predicted changes in their relative availabilities along the gradient. Similarly, we also suspected
198 that Blue Tit nests might incorporate less natural aromatic plants (based upon their availability) at
199 more urban nest sites and thus that ectoparasite loads of such nests might increase (Mennerat *et al.*,
200 2009). However, with the study of Mennerat *et al.* (2009) having taken place in Corsica, we know
201 little about the presence of aromatic plants along our urban gradient and, if available, the propensity
202 of birds in the city to use them as nest constituents.

203 We found similar nest components to other studies of Blue Tit nests here in the UK and in
204 western mainland Europe (see Table 4.1 in Deeming and Mainwaring, 2015) with the exception that
205 nests at some sites such as RSPB Woodland – Cannon Hill Park and Soho Pool Wharf contained large
206 amounts of anthropogenic materials (see Appendix 2 for further details). Nevertheless, we found few
207 statistically significant effects of the urban gradient on the composition (Figs 2 and 3) and ectoparasite
208 loads (Fig. 4) of nests. The feather content of nests varied significantly in relation to connected tree
209 cover (positive) and built cover (negative), perhaps reflecting the availability of feathers to nest-
210 building birds. In Blue Tits we know that feathers are an important nest component (Britt and
211 Deeming, 2011) but Mainwaring *et al.* (2015) found that they may serve a signalling function in the
212 detection of intrusions by competitive birds into nestboxes of resident males, rather than providing a
213 thermoregulatory benefit during incubation and/or chick rearing as has been found in other species
214 (Møller, 1984). Nests of conspecifics either in artificial nestboxes or in natural tree cavities represent
215 sources of feathers to intruding birds that can be incorporated into their own nest contents. We would
216 predict that breeding density of tits is probably higher in areas of the city with less built cover
217 (reviewed by Marzluff, 2001), and more connected tree cover, but we lack such empirical data
218 currently from the city of Birmingham to investigate this hypothesis further. Further studies along the
219 urban gradient in the city might include assessments of: the usage of breeding sites other than
220 nestboxes we provided by tits in urban areas; the availability of natural and anthropogenic nest

221 materials at breeding sites; and how breeding density across the gradient influences the composition
222 and ectoparasite load of individual nests.

223 We found that the relationships between natural fibre content of nests, and urban built cover
224 and connected tree cover, were only marginally significant and our findings suggest that we need
225 more data from more cities and over more breeding seasons before we can reach firmer conclusions.
226 We understand very little about how far birds will travel to obtain such natural nest components in
227 urban habitats but if they travel as extensively as they do in searching for micronutrients such as
228 calcium in the pre-laying phase (e.g. Wilkin *et al.*, 2009), then birds might cross many breeding
229 territories of conspecifics and heterospecifics, risking many agonistic encounters, and flying many
230 hundreds of metres, also risking elevated predation risk, in doing so. Given that Wilkin *et al.* (2009)
231 examined birds breeding in a woodland outside of a city, further initial work is needed to study search
232 efforts of birds nest building in cities and their investment in sourcing nest materials.

233 A surprise finding of the study was the presence of anthropogenic material (e.g. plastics, dyed
234 wool, cotton) in most nests (73% of all nest deconstructed) irrespective of their position on the urban
235 gradient. We had predicted that birds in areas with more built cover and less connected tree cover
236 would have more ready access to such nest material. The inclusion of such materials in the majority of
237 deconstructed nests suggests that birds may obtain significant benefits from them which may
238 contribute to reducing energetic costs of incubating adults (Cresswell *et al.*, 2003), and increasing
239 chick growth rates (Lombardo *et al.*, 1994), and ultimately fitness (Hepp *et al.*, 2015). Surgey *et al.*
240 (2012) provided artificially dyed wool of different colours to four tit species (Paridae) nesting in rural
241 woodland and found that while the collection of it (as examined by nest deconstruction) appeared
242 opportunistic, some birds travelled extensively to many different sources to collect it as valuable nest
243 material. It is clear that we still know relatively little about the relative contributions of different nest
244 constituents to breeding performance of birds in urban habitats. Until we know more, it is difficult to
245 understand how such nest materials shape life-history strategies of urban birds.

246 Finally, we examined the relationship between the ectoparasite load of nests that had
247 contained chicks during the breeding season and their position on the urban gradient; the only
248 ectoparasites found were fleas. We know that nestboxes are more prone to infestations of fleas than
249 natural cavities (Wesołowski and Stańska, 2001), but we were surprised that other nest ectoparasites
250 (reviewed by López-Rull and Macías Garcia, 2015) were not detected during nest deconstruction. We
251 found no indication that nesting Blue Tits had employed plant aromatics (Mennerat *et al.*, 2009),
252 cigarette butts (Suárez-Rodríguez *et al.*, 2012) *etc.* as defence against ectoparasites. Of course,
253 extensive further work is required in the city to assess the availability of both to nesting birds across
254 the gradient. Furthermore, there was no significant relationship between ectoparasite load and feather
255 content of nests as we might have expected. Winkler (1993) found that removal of feathers from the
256 nests of Tree Swallows (*Tachycineta bicolor*) depressed the growth of nestlings and resulted in them
257 carrying greater ectoparasite burdens than nestlings in unmanipulated nests. The only significant

258 relationship was between ectoparasite load and overall nest mass (Fig. 4). To fleas and other
259 ectoparasites in nests, those containing chicks represent the peak of food availability provided by
260 brooding adults, growing chicks, faeces and undigested food in the nest lining (Heeb *et al.*, 1996; Lea
261 and Klandorf, 2002). Despite the criticisms of Wesołowski and Stańska (2001) of nestboxes and their
262 inherent biases in studies such as ours, newly established nestboxes contained no material prior to the
263 2014 breeding season and thus ectoparasites counted in our study were associated with the current
264 breeding attempt. Therefore, they had not burrowed into materials from previous seasons in order to
265 enter diapause (Tauber *et al.*, 1986).

266 There is an urgent need for further research to investigate the nesting biology of birds in
267 urban habitats. Specifically, we need to know how changes in the built cover and connected tree cover
268 brought about by land clearance and construction of roads and buildings, for example, influence the
269 breeding performance of birds. Cavity nesters such as Blue Tits are an ideal study species in this
270 regard but we acknowledge the concerns of Wesołowski (2011) who outlined reasons why nestbox
271 studies are not directly comparable to those of birds nesting in natural cavities. Some of his
272 recommendations, such as the reporting of type and size of nestboxes, are easily adopted, but others,
273 such as comparisons with ‘reference’ natural cavities and assessment of avian breeding densities, are
274 less easily derived in an urban environment for a species that breeds in such a diversity of nesting
275 locations (Gosler and Clement, 2007). However, we accept the shortcomings of nestbox studies and
276 we support the recommendations of Wesołowski (2011) that every effort should be made to provide
277 as much accompanying information as possible in published outputs. Of course, the Blue Tit is a good
278 model species for the study of city-dwelling birds but we continue to question how findings from our
279 study can be applied to other ‘urban’ species. We believe that research over the next few years will
280 significantly improve our understanding of the breeding biology of a number of such species and we
281 encourage others in other large cities to respond to the challenge of working along their respective
282 urban gradients. A pressing concern is how we quantify urbanisation within a relevant context for a
283 breeding bird. Here, we assessed the urban matrix according to built cover and connected tree cover to
284 identify potential sites for nestboxes but this still fails to control for considerable habitat heterogeneity
285 between sites (Chamberlain *et al.*, 2008). This is especially pertinent at the urban-suburban interface
286 where dramatic changes in reproductive outputs in response to habitat type can occur (e.g. Crick *et*
287 *al.*, 2002). Recent developments using GIS by Seress *et al.* (2014) have shown some potential to
288 relate urbanisation ‘scores’ directly to aspects of avian biology (i.e. body condition scores of House
289 Sparrows [*Passer domesticus*]). Whether this approach offers similar benefits in assessing how
290 urbanisation influences the nesting biology of birds remains to be tested but we hope that this, and
291 other points of discussion in the present study, will urge researchers to investigate nest construction
292 and maintenance in much more detail in the future.

293

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301

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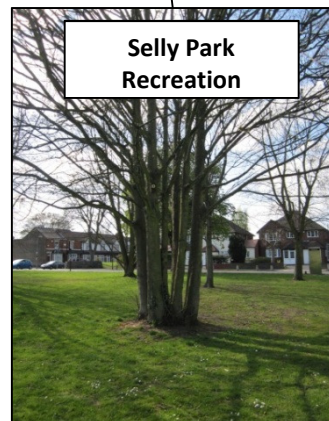
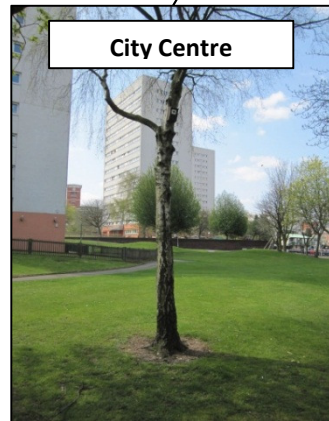
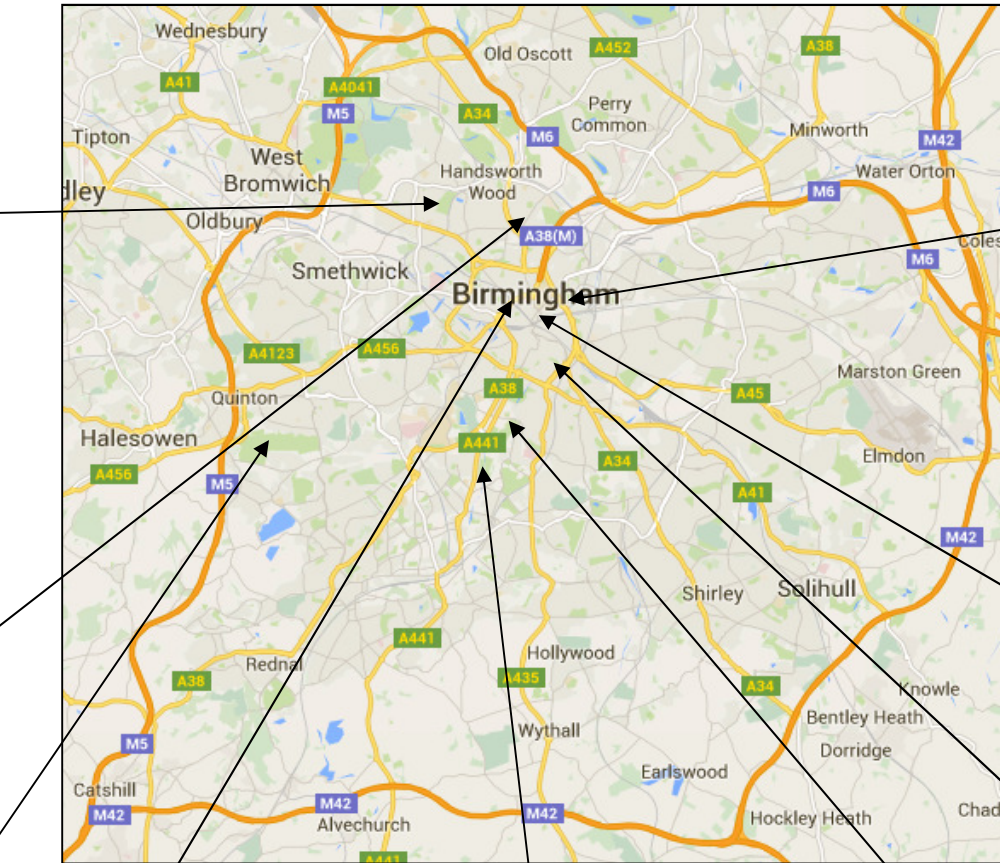
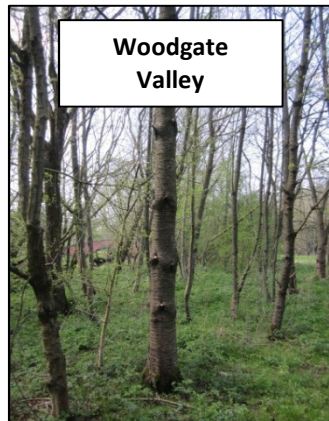
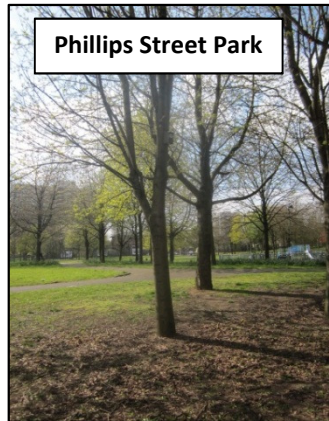
425 **Figure titles**

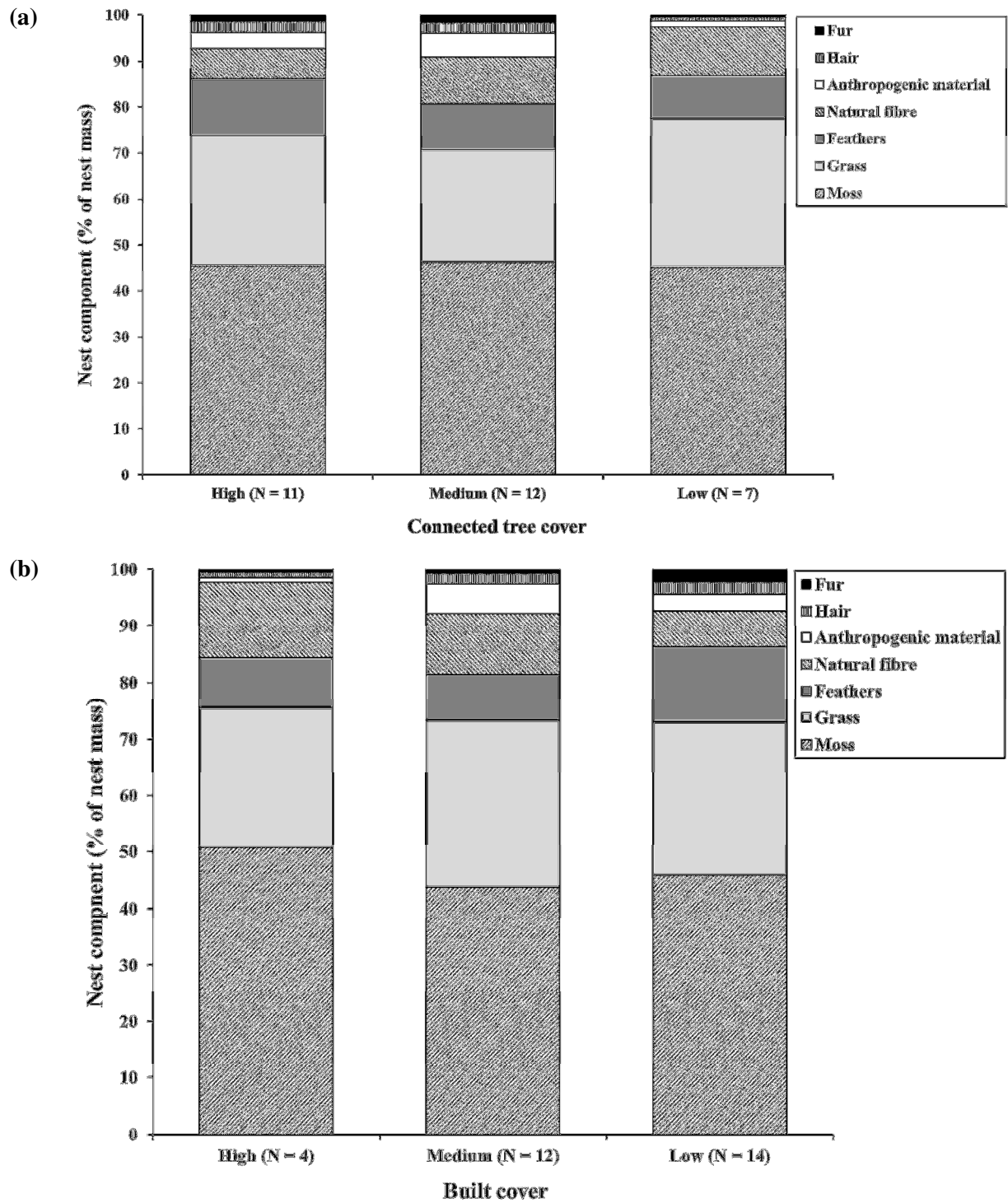
426 **Figure 1** The distribution of nine of the 31 sites in the city of Birmingham from which Blue Tit nests
427 were obtained from 10 nestboxes at each to investigate the effects of the degree of urbanisation on
428 their composition and ectoparasite load. See Appendix 1 for further details of how the urbanisation
429 measures were derived and of the 31 sites that were studied during 2014.

430 **Figure 2** The composition of Blue Tit nests collected from nestboxes at 30 sites in the city of
431 Birmingham in 2014 from various parts of the urban gradient categorised as low (0-33%), medium
432 (34-66%) and high (67-100%) according to (a) connected tree cover and (b) built cover (see Appendix
433 1 for further details of how urban measures were derived). Nest components are expressed as
434 percentages of nest mass (to control for differences in nest size) and Ns denote the number of nests
435 that were deconstructed for each category.

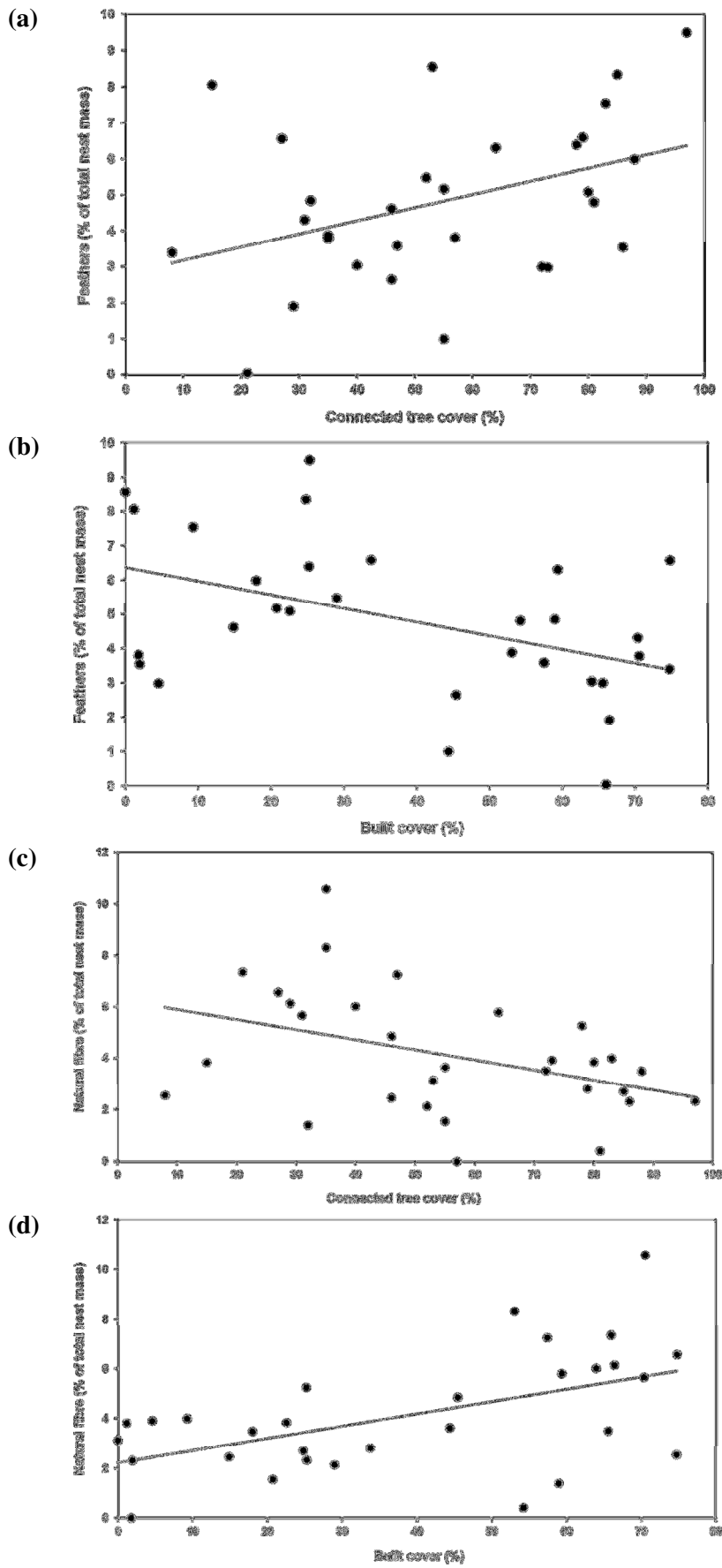
436 **Figure 3** Mean percentage mass of (a & b) feathers and (c & d) natural fibres in Blue Tit nests at 30
437 sites in the city of Birmingham in 2014 collected from nestboxes at various parts of the urban gradient
438 defined according to connected tree cover and built cover, respectively (see Appendix 1 for further
439 details of how urban measures were defined).

440 **Figure 4** The relationship between the mean ectoparasite load and the mean mass of nests of Blue Tits
441 containing chicks collected from nestboxes in the city of Birmingham in 2014 at various parts of the
442 urban gradient (see Appendix 1 for further details).

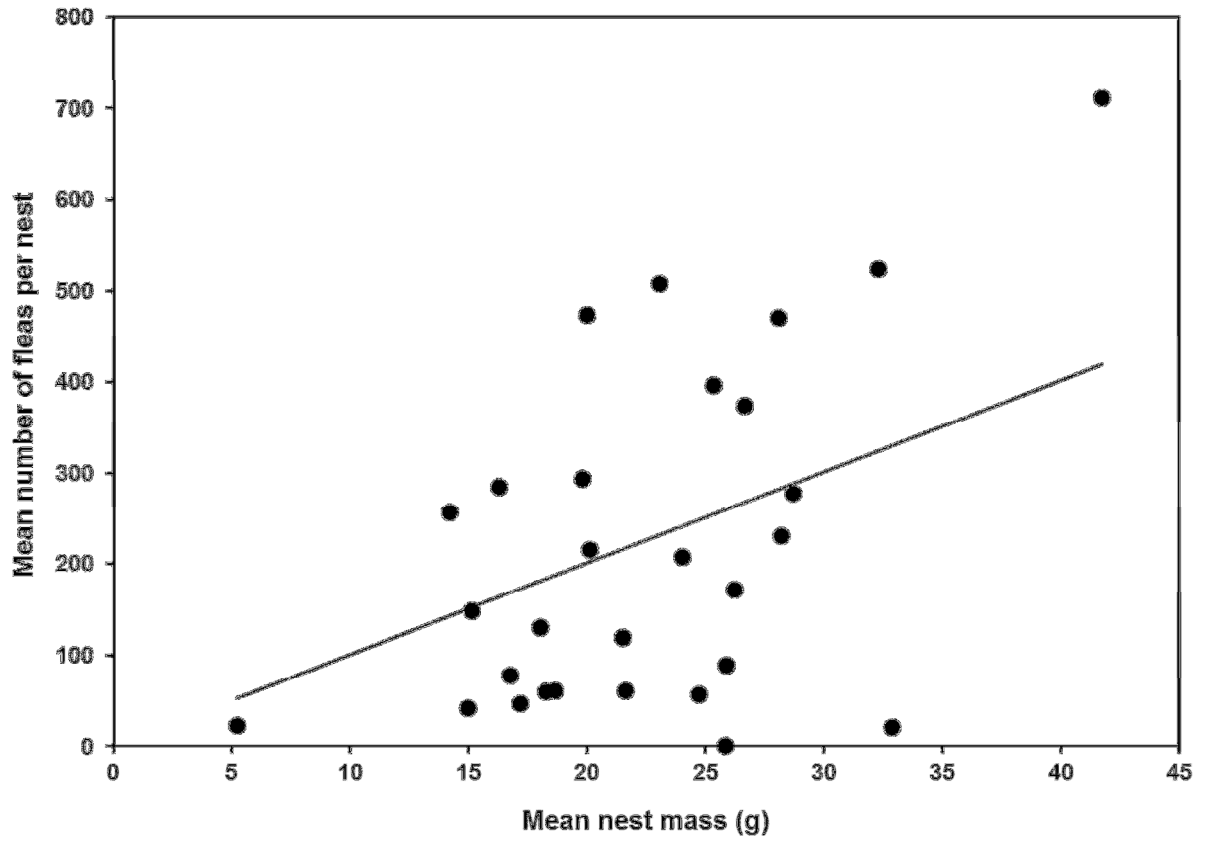




444 **Figure 2.**



445 Figure 3.



446

447 **Figure 4.**

Appendix 1. Details of each of 31 nest sites along the urban gradient of the city of Birmingham, UK, from which Blue Tit nests were removed from nestboxes for deconstruction at the end of the 2014 breeding season.

Nest site location	Longitude	Latitude	Connected tree cover* (%)	Built cover* (%)
Barrack Street Recreation Ground	52.48712	-1.87998	64	59
Batchelors Farm Park	52.48228	-1.81945	46	15
Burberry Brickworks	52.45	-1.85503	46	45
Callow Brook	52.39754	-2.00746	72	66
Chamberlain Gardens	52.4741	-1.92784	81	54
City Centre Gardens	52.48058	-1.90888	27	75
Cowley Road Recreation Ground	52.45492	-1.85157	29	66
Garrison Lane Park	52.47975	-1.87418	21	66
Grand Union Canal	52.4799	-1.88319	27	81
Handsworth Park	52.51017	-1.92668	80	23
Highgate Park	52.46958	-1.88354	40	64
Hilltop and Manwood Country Park	52.51944	-1.94563	53	0
Holders Lane Woods	52.44227	-1.90883	83	9
Moillet Street Park	52.48831	-1.94518	32	59
Oakwood Road Coppice	52.54695	-1.84722	97	25
Park Lane Pos	52.52434	-1.79095	35	53
Park Street Gardens	52.48056	-1.88966	8	75
Perry Hall Playing Fields	52.52467	-1.91674	15	1
Phillips Street Park	52.49774	-1.89448	35	71
Popes Lane	52.41084	-1.95138	85	25
Rookery Park	52.51784	-1.8368	79	34
RSPB Sandwell Valley	52.53356	-1.95051	73	5
RSPB Woodland – Cannon Hill Park	52.44854	-1.90335	88	18
Selly Park Recreation Ground	52.4385	-1.92525	52	29
Sheldon Country Park	52.45663	-1.78889	78	25
Soho Pool Wharf	52.49608	-1.92231	55	44

Sutton Park	52.55792	-1.84301	57	2
The Radleys	52.46763	-1.77304	47	57
Warstone Lane Cemetery	52.4885	-1.91525	31	70
Woodgate Valley – Country Park	52.44891	-1.99576	86	2
Woodgate Valley – The Pines	52.43688	-2.0141	55	21

*Urban land cover measures were derived using GIS layers using Lidar vector data for connected tree cover and 2 × 2 m raster pixels for built cover. For both measures we know that a circle with a 250 m radius has a total area of 196,350 m² and this was used to calculate the number of 4 m² pixels (see above) that were built/unbuilt from the raster layer, and the area of connected tree cover from the vector layer. Both cover measures are then expressed as percentages of total areas at each site. For more general information regarding how such land cover measures are derived using GIS please see Hale *et al.* (2013).

Appendix 2. Details of the composition of Blue Tit nests removed from 30 nest site locations along the urban gradient of the city of Birmingham, UK at the end of the 2014 breeding season.

Nest site location	Mean nest mass* (± 1 SE) (g)	Mean nest dry mass (± 1 SE) (g)	Mean mass (± 1 SE) (g) at each nest site location of following nest components:						
			Moss	Grass	Feathers	Hair	Fur	Natural fibres	Anthropogenic materials
Barrack Street Recreation Ground	20.26 \pm 4.07	8.90 \pm 2.27	2.78 \pm 1.20	1.90 \pm 0.45	1.13 \pm 0.39	0.18 \pm 0.06	0.01 \pm 0.004	0.99 \pm 0.34	1.92 \pm 1.80
Batchelors Farm Park	20.59 \pm 3.45	8.70 \pm 1.14	5.61 \pm 0.94	1.62 \pm 0.39	0.79 \pm 0.20	0.03 \pm 0.01	0.18 \pm 0.10	0.35 \pm 0.18	0.12 \pm 0.11
Burberry Brickworks	26.22 \pm 10.80	15.01 \pm 6.11	10.04 \pm 6.78	3.05 \pm 0.69	0.67 \pm 0.25	0.24 \pm 0.21	0.03 \pm 0.03	0.94 \pm 0.43	0.05 \pm 0.04
Callow Brook	19.68 \pm 1.76	9.63 \pm 0.88	6.03 \pm 0.70	2.09 \pm 0.22	0.58 \pm 0.16	0.02 \pm 0.007	0.01 \pm 0.008	0.74 \pm 0.30	0.15 \pm 0.12
Chamberlain Gardens	18.88 \pm 4.17	9.43 \pm 1.44	4.29 \pm 1.44	3.83 \pm 0.23	0.91 \pm 0.24	0.28 \pm 0.09	-	0.09 \pm 0.08	0.02 \pm 0.01
City Centre Gardens	15.30 \pm 3.01	8.92 \pm 2.07	3.47 \pm 1.11	3.07 \pm 0.99	0.83 \pm 0.21	0.17 \pm 0.10	0.10 \pm 0.04	1.14 \pm 0.50	0.15 \pm 0.06
Cowley Road Recreation Ground	24.02 \pm 7.58	8.41 \pm 0.82	3.90 \pm 0.78	2.87 \pm 0.30	0.41 \pm 0.15	0.03 \pm 0.01	0.02 \pm 0.02	1.02 \pm 0.57	0.18 \pm 0.10
Garrison Lane	25.85	10.99	3.60	5.29	0.01	0.08	-	1.90	0.13

Park									
Handsworth Park	24.47 ± 2.51	7.58 ± 1.26	0.92 ± 0.44	3.50 ± 0.68	1.22 ± 0.13	0.06 ± 0.04	0.07 ± 0.06	0.92 ± 0.44	0.89 ± 0.56
Highgate Park	17.19 ± 3.14	7.88 ± 1.46	4.86 ± 0.90	0.84 ± 0.36	0.47 ± 0.16	0.27 ± 0.19	0.20 ± 0.16	1.18 ± 0.65	0.06 ± 0.04
Hilltop and Manwood Country Park	20.70 ± 2.75	9.62 ± 1.57	3.18 ± 0.67	3.85 ± 0.62	1.88 ± 0.62	0.03 ± 0.01	0.01 ± 0.01	0.66 ± 0.23	0.01 ± 0.007
Holdings Lane Woods	18.26 ± 1.39	10.20 ± 0.53	5.11 ± 0.70	2.11 ± 0.61	1.37 ± 0.33	0.22 ± 0.11	0.09 ± 0.07	0.66 ± 0.21	0.64 ± 0.50
Moillet Street Park	23.00 ± 5.72	8.34 ± 1.53	4.05 ± 0.98	2.47 ± 0.13	1.22 ± 0.70	0.15 ± 0.02	0.01 ± 0.01	0.33 ± 0.13	0.11 ± 0.11
Oakwood Road Coppice	18.26	10.39	2.33	5.77	1.73	0.05	0.04	0.42	0.04
Park Lane Pos Park Street Gardens	15.78 ± 2.51	6.80 ± 1.07	2.03 ± 0.60	2.04 ± 0.48	0.64 ± 0.15	0.22 ± 0.12	0.14 ± 0.05	1.20 ± 0.31	0.54 ± 0.46
Perry Hall	19.36	8.96	4.90	2.85	0.66	0.02	0.01	0.49	0.03
Playing Fields	17.49 ± 1.47	8.71 ± 0.82	3.30 ± 0.63	3.13 ± 0.30	1.34 ± 0.45	0.06 ± 0.02	0.11 ± 0.09	0.71 ± 0.26	0.07 ± 0.05
Phillips Street Park	12.03 ± 2.95	7.10 ± 1.47	3.70 ± 0.70	1.35 ± 0.92	0.48 ± 0.23	0.08 ± 0.02	0.02 ± 0.01	1.43 ± 0.95	0.03 ± 0.03
Popes Lane	17.42 ± 1.35	7.49 ± 0.48	4.30 ± 0.65	1.25 ± 0.34	1.38 ± 0.24	0.13 ± 0.05	0.01 ± 0.003	0.43 ± 0.17	0.01 ± 0.004
Rookery Park	26.66 ± 2.08	9.39 ± 1.34	2.74 ± 0.85	3.77 ± 0.56	1.70 ± 0.41	0.20 ± 0.09	0.06 ± 0.04	0.73 ± 0.23	0.19 ± 0.12
RSPB Sandwell Valley	17.88 ± 3.81	8.24 ± 1.29	4.94 ± 0.74	1.20 ± 0.36	0.45 ± 0.19	1.08 ± 0.81	0.02 ± 0.01	0.55 ± 0.30	0.005 ± 0.004

RSPB Woodland – Cannon Hill Park	18.81 ± 2.19	11.19 ± 3.29	5.30 ± 1.47	1.93 ± 0.59	1.01 ± 0.35	0.01 ± 0.01	0.98 ± 0.98	0.51 ± 0.32	1.45 ± 1.24
Selly Park Recreation Ground	26.23 ± 7.90	10.85 ± 5.05	2.17 ± 0.38	4.77 ± 3.88	1.63 ± 0.86	0.79 ± 0.31	0.39 ± 0.11	0.89 ± 0.89	0.21 ± 0.12
Sheldon Country Park	24.09 ± 6.32	8.42 ± 1.38	3.72 ± 1.04	2.19 ± 0.30	1.30 ± 0.33	0.04 ± 0.01	0.02 ± 0.02	1.08 ± 0.54	0.07 ± 0.05
Soho Pool Wharf	15.91 ± 3.89	6.95 ± 1.65	2.29 ± 0.59	2.18 ± 1.16	0.13 ± 0.07	0.12 ± 0.05	-	0.66 ± 0.32	1.57 ± 1.51
Sutton Park	20.70	8.70	5.22	1.10	1.37	0.16	0.66	-	0.20
The Radleys	25.43 ± 4.41	10.68 ± 1.80	4.02 ± 1.33	2.96 ± 0.79	0.99 ± 0.33	0.36 ± 0.24	0.07 ± 0.07	2.07 ± 1.16	0.22 ± 0.17
Warstone Lane Cemetery	18.63 ± 4.81	7.30 ± 1.90	4.16 ± 1.27	1.03 ± 0.37	0.87 ± 0.55	0.03 ± 0.02	0.02 ± 0.02	1.12 ± 0.36	0.07 ± 0.02
Woodgate Valley – Country Park	22.20 ± 3.23	10.83 ± 1.47	7.54 ± 1.67	1.35 ± 0.38	0.77 ± 0.19	0.22 ± 0.13	0.36 ± 0.35	0.49 ± 0.20	0.10 ± 0.09
Woodgate Valley – The Pines	26.85 ± 6.98	12.54 ± 2.63	8.08 ± 2.22	2.36 ± 0.64	1.28 ± 0.24	0.10 ± 0.06	0.02 ± 0.02	0.50 ± 0.27	0.19 ± 0.18

*Nests weighed immediately after their removal from the chest freezer but before thawing and deconstruction – see Methods for further details. ‘-’ signifies an absence of a nest component.