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1 **Food availability limits avian reproduction in the city: an experimental study on great**  
2 **tits (*Parus major*)**

3

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14 ABSTRACT

15 1. The altered ecological and environmental conditions in towns and cities strongly affect demographic  
16 traits of urban animal populations, for example avian reproductive success is often reduced. Previous  
17 work suggests that this is partly driven by low insect availability during the breeding season, but robust  
18 experimental evidence that supports this food limitation hypothesis is not yet available.

19 2. We tested core predictions of the food limitation hypothesis using a controlled experiment that  
20 provided supplementary insect food (nutritionally enhanced mealworms supplied daily to meet 40-50%  
21 of each supplemented brood's food requirements) to great tit nestlings in urban and forest habitats.

22 3. We measured parental provisioning rates and estimated the amount of supplementary food consumed  
23 by control and experimental nestlings, and assessed their body size and survival rates.

24 4. Provisioning rates were similar across habitats and control and supplemented broods, but  
25 supplemented (and not control) broods consumed large quantities of supplementary food. As predicted  
26 by the food limitation hypothesis we found that nestlings in (1) urban control broods had smaller body  
27 size and nestling survival rates than those in forest control broods, (2) forest supplemented and control  
28 broods had similar body size and survival rates, (3) urban supplemented nestlings had larger body size  
29 and survival rates than those in urban control broods, and crucially (4) urban supplemented broods had  
30 similar body size and survival rates to nestlings in forest control broods.

31 5. Our results provide rare experimental support for the strong negative effects of food limitation during  
32 the nestling rearing period on urban birds' breeding success. Furthermore, the fact that supplementary  
33 food almost completely eliminated habitat differences in survival rate and nestling body size suggest  
34 that urban stressors other than food shortage contributed relatively little to the reduced avian breeding  
35 success. Finally, given the impacts of the amount of supplementary food that we provided and taking  
36 clutch size differences into account, our results suggest that urban insect populations in our study system  
37 would need to be increased by a factor of at least 2.5 for urban and forest great tits to have similar  
38 reproductive success.

39

40

41 INTRODUCTION

42 Population growth and socio-demographic factors are rapidly increasing the number and spatial extent  
43 of urban settlements across much of the globe (United Nations 2016). Urbanisation rates and associated  
44 human population densities concentrate in regions with high species richness and biodiversity hotspots  
45 (Luck 2007, Seto et al. 2012). As urban areas – especially their core regions – typically support fewer  
46 species and less diverse biotic communities than surrounding semi-natural or natural landscapes  
47 (Aronson et al. 2014, Batáry et al. 2018), urbanisation is increasingly contributing to the extinction crisis  
48 (McDonald et al. 2008, Chaudhary et al. 2018). Improved understanding of the factors that limit urban  
49 biodiversity is needed to devise urban management strategies that can enhance species' occurrence and  
50 population sizes in towns and cities, thus contributing to local, and sometimes global, conservation  
51 objectives (Ives et al. 2016, Lepczyk et al. 2017).

52 Urban biodiversity is limited by numerous factors including the spatial extent, composition and  
53 structure of vegetation, exposure to a range of pollutants (e.g. chemical, noise, heat), human disturbance  
54 and reduced availability of high quality resources including food (Williams et al. 2009, Moretto and  
55 Francis 2017, Aronson et al. 2017). Specifically, the food limitation hypothesis proposes that the  
56 reproductive performance of urban animals is limited by the reduced availability of high quality food  
57 sources, e.g. insects. Although insects' responses to urbanization are diverse and taxon-specific, several  
58 studies have found that urban areas generally support fewer insects than more natural habitats (Jones  
59 and Leather 2012, New 2015). Indeed, cities typically have reduced abundance of lepidopteran larvae  
60 (reviewed by Seress et al. 2018), that are key and preferred components of offspring diet in many  
61 insectivorous species, including most passerines, in their natural breeding habitats (Cholewa and  
62 Wesolowski 2012).

63 In contrast to the relative scarcity of natural food items, urban environments typically contain  
64 large amounts of anthropogenic food which is readily consumed by a range of species and can comprise  
65 a substantial proportion of the animals' diets (e.g. arthropods (Youngsteadt et al. 2016), birds (Robb et  
66 al. 2008), and mammalian carnivores (Bateman and Fleming 2012)). These anthropogenic food sources,  
67 however, are typically of lower nutritional quality than natural dietary components, and their  
68 consumption is often associated with adverse impacts on animals' physiology (e.g. Schulte-Hostedde et  
69 al. 2018), behaviour and disease risk (e.g. Murray et al. 2015, 2016), and reproductive success

70 (Mennechez and Clergeau 2006, Plummer et al. 2018). In combination, the abundant anthropogenic food  
71 sources and the scarcity of urban insects may drastically alter the quantity and quality of food for urban  
72 insectivorous animals, suggesting limited availability of high quality food during the brood-rearing  
73 period (Seress and Liker 2015). These impacts have been particularly well studied in birds and, as  
74 predicted by the food limitation hypothesis, may contribute to the general pattern of lower reproductive  
75 success (e.g. fewer and smaller offspring) in urban compared to non-urban avian populations  
76 (Chamberlain et al. 2009, Sepp et al. 2017). The extent to which these reductions in breeding success  
77 are ultimately driven by reduced abundance of natural dietary components in urban locations is,  
78 however, unclear.

79 Food supplementation experiments are widely used in avian ecological research, but studies  
80 manipulating nestling food quantity and/or quality in urban environments are rare and have produced  
81 inconsistent evidence for the link between food limitation and reduced breeding success. One  
82 experiment (Bańbura et al. 2011) on urban great tits (*Parus major*) reported positive effects of extra  
83 food on some traits (nestling body size and blood heterophil-to-lymphocyte ratio) but not on others  
84 (several other blood parameters) – although in this study the extent to which focal parents and their  
85 nestlings used the extra food is unclear. Other food supplementation experiments on urban birds have  
86 found negligible (Meyrier et al. 2017) or even negative (Demeyrier et al. 2017) impacts on body size  
87 and/or nestling survival. We are aware of only two studies that compared the effects of food  
88 supplementation between urban and non-urban populations of the same species. Supplementary food  
89 had similar positive effects on house sparrows' *Passer domesticus* nestling survival and number of  
90 fledglings in suburban and rural gardens, suggesting that the suburban sparrows were not more food-  
91 limited than the rural birds (Peach et al. 2014). This study, however, did not control for the confounding  
92 effects of brood size, nestling age and the amount of supplementary food obtained by different broods.  
93 A study on American crows *Corvus brachyrhynchos* found larger body size in urban supplemented  
94 nests, whilst in rural areas supplementary food reduced body size, but the study was limited by extremely  
95 small sample sizes with a total of just 7 supplemented nests (Heiss et al. 2009). These studies, with the  
96 exception of Bańbura et al. (2011), also provided no information on the amount of natural food in the  
97 urban and rural study systems and thus the potential magnitude of food shortage experienced by the

98 focal urban bird populations. There is thus a need for additional tests of the urban food limitation  
99 hypothesis that build upon earlier work by conducting food supplementation experiments across urban  
100 and rural populations using larger sample sizes, quantifying the use of supplementary food by target  
101 individuals, placing this in the context of the difference in natural food availability of urban and rural  
102 bird populations, and assessing the influence of a wider range of potentially confounding variables on  
103 metrics of avian reproductive success.

104 In a recent study, we showed that lower breeding success of urban great tits is primarily driven  
105 by increased nestling mortality, for which starvation was the most likely explanation (Seress et al. 2018).  
106 Here, we build upon this finding and experimentally test the food limitation hypothesis using a food  
107 supplementation experiment in urban and forest populations. We regularly provisioned extra insect food  
108 throughout the brood-rearing period to manipulate nestlings' diet, and compared parental provisioning  
109 behaviour, nestling body size and survival between supplemented (treatment) and non-supplemented  
110 (control) broods within and between habitat types. We predicted that (1) control broods in the urban  
111 habitat would have reduced provisioning rates, nestling body size and survival compared to control  
112 broods in forest, indicating that food availability during the nestling phase limits breeding success in  
113 urban but not in forested areas, and thus (2) control and supplementary fed broods in forested locations  
114 would exhibit negligible differences in provisioning rate, body size, and nestling survival, whilst (3)  
115 urban supplemented broods would have significantly increased provisioning rates, nestling body size  
116 and survival compared to urban control broods. Finally, if food limitation is indeed a major factor  
117 limiting breeding success and nestling development in cities, we expect to find that (4) extra insect food  
118 would eliminate or considerably mitigate the differences in reproductive success between urban  
119 supplemented and forest control groups.

120

121

## 122 METHODS

### 123 **Data collection and experimental design**

124 We studied great tits breeding in nest boxes at an urban and a forest site in Hungary in 2017. The urban  
125 study site is located in the city of Veszprém (47°05'17.29"N, 17°54'29.66"E), where the nest boxes were

126 placed in four areas of public green-space, including public parks, university campuses and a cemetery,  
127 that are surrounded by built-up areas and roads and experience frequent anthropogenic disturbance.  
128 These sites comprise one relatively large core site (23.3 ha) and three smaller sites (3.1, 7.3 and 4.4 ha)  
129 located approximately 60m, 620m, and 730m from the core site. Breeding great tits (individually marked  
130 with rings) have been observed to move between these plots during our long-term study of the  
131 population. The general habitat characteristics and dominant tree species are similar between these plots  
132 (Appendix1) thus birds breeding in each of these urban sub-sites are likely to experience very similar  
133 foraging opportunities. The forest study site, Vilma-pusztá, is located c. 3 km from the edge of Veszprém  
134 in mature deciduous woodland characterized mainly by downy oak (*Quercus cerris*) and South  
135 European flowering ash (*Fraxinus ornus*; 47°05'06.7"N, 17°51'51.4"E; the study plot covers c. 48.1 ha).  
136 This latter study location is a Natura 2000 site which is relatively free from human disturbance, e.g. it  
137 has no paved roads, has only one nearby farm and no logging activity. Ringing data indicate extremely  
138 limited dispersal between the urban and rural study sites (one recorded instance from over 1,100 re-  
139 trapping or re-sighting observations of c. 4,100 individually marked birds between 2011 and 2019).

140 To test the food limitation hypothesis, we manipulated nestlings' diet in a field experiment, in  
141 which great tit broods were allocated to a food supplementation treatment (treatment group) or received  
142 no extra food (control group). We monitored nest boxes at least twice a week from 1<sup>st</sup> March to early  
143 June to record laying and hatching dates, and the number of eggs and nestlings in active great tits nests.  
144 At each study site, we randomly assigned the first brood of the season to the supplemented or control  
145 group, and then sequentially allocated each additional brood to the supplemented or control groups to  
146 ensure similar sample sizes in each group and to avoid the potential for treatment type to be confounded  
147 with date. The experiment only included first broods (note that at these study sites most fledglings are  
148 produced by first broods (Seress et al. 2018)). During the incubation period, we equipped all nest boxes  
149 with a feeder box, which was a small (125 ml) plastic container attached to the nest box a few centimetres  
150 below the entrance (Appendix1: Fig.S1). This proximity to the nest-box helped focal birds to defend the  
151 supplementary food from non-target individuals, which was further facilitated by using opaque feeder  
152 boxes to decrease the conspicuousness of mealworms to other birds (use of mealworms by non-target  
153 individuals was very rare, see Results). The bottom of the feeder boxes had small holes (1 mm diameter)

154 that enabled rainwater drainage but did not allow supplementary food (mealworms) to escape. Control  
155 and supplemented nests were not clustered within separate parts of the study sites, and the mean distance  
156 ( $\pm$  SE) between the nearest neighbouring control and supplemented broods were  $98 \pm 12$  m (range: 37-  
157 211m) in the urban site, and  $67 \pm 8$  m (31-112m) in the forest site.

158 Treatment broods received supplementary food on a daily basis when nestlings were 3-15 days  
159 old (hatching day of the first egg = day 1). This ensured that food supplementation did not influence  
160 reproductive success by altering clutch sizes or the body condition of incubating females. We adjusted  
161 the amount of mealworms according to brood size and nestling age by providing 1.5 g/chick/day  
162 between 3-7 days of nestling age (i.e., for 5 days), and 3 g/chick/day between 8-15 days of nestling age  
163 (i.e., for 8 days). Thus, a brood with 10 nestlings received daily c. 120 and 240 larvae in the early and  
164 late nestling rearing phases, respectively. These quantities are estimated to cover 40-50% of daily food  
165 requirements of great tit nestlings (Gibb and Bets 1964, Van Balen 1973, our own unpublished data).  
166 Mealworms are widely used in avian food supplementation experiments (Bańbura et al. 2011, Peach et  
167 al. 2014, Demeyrier et al. 2017), and are suggested to be a good source of energy and digestible amino  
168 acids for birds (Finke 2002). To increase the nutritional value of mealworms we transferred the larvae  
169 from their usual wheat bran substrate to an *ad libitum* invertebrate food substrate rich in protein and  
170 vitamins (www.bugs-world.com, product code: BW-TT), at least 2-3 days before being provided to birds  
171 (for similar approach see e.g. Kaiser et al. 2014). Daily food supplementation occurred between 8:00  
172 and 13:00, and during these visits we also recorded the number of chicks (alive or dead) in the nest,  
173 which enabled us to calculate the required amount of supplementary food for each brood. To avoid  
174 inducing nest desertion, we never removed brooding parents during these checks – thus, if a parent  
175 remained on the nest during nest inspection we used the most recent data on brood size to calculate the  
176 required amount of supplementary food. Feeding boxes were cleaned daily and leftover food was  
177 weighed (to the nearest g). Control broods did not receive supplementary food but their nests were also  
178 checked daily and we spent a similar amount of time (c. 3-4 minutes) at the nest during each visit to  
179 ensure that control and supplemented broods received the same level of human disturbance.

180 When nestlings reached 15-days of age (i.e., just before fledging) we ringed and weighed them  
181 ( $\pm$  0.1 g) and also measured the length of the left tarsus ( $\pm$  0.1 mm) and right wing ( $\pm$  1 mm; from the



182 bend of the wing to the tip of the longest primary, following the ‘flattened and straightened wing’  
183 method; Svensson 1992). In the supplemented group a few hours had always passed between the most  
184 recent provision of supplementary food and the measurements ( $4.68 \pm 0.14$  h) in order to let the birds  
185 digest the supplementary food.

186 The experiment involved 52 broods initially, but due to complete breeding failure resulting from  
187 nest desertion during the incubation or early chick-rearing period (which is usually due to parental death  
188 (Santema and Kempenaers 2018)), we excluded five nests ( $n = 3$  urban control,  $n = 1$  urban  
189 supplemented,  $n = 1$  forest supplemented). Thus final sample sizes were: urban control broods 10, urban  
190 supplemented broods 14; forest control broods 12 and forest supplemented broods 11 (Appendix1: Table  
191 S1).

192 Frass sampling of the dominant tree species at each site demonstrated that, as was the case in  
193 previous years, caterpillar abundance was higher in the forest compared to the urban site in 2017  
194 (Appendix1: Fig.S2; Seress et al. 2018). Breeding success of urban and forest pairs that did not receive  
195 supplementary food was comparable to that reported between 2013-2016 from the same study sites  
196 (Seress et al. 2018; Appendix1: Table S1-S2). During the experiment there was, however, a brief unusual  
197 cold spell from 18<sup>th</sup>-21<sup>st</sup> April 2017 with occasional snowfall and low ambient temperatures (Gładalski  
198 et al. 2018; Appendix2). During this period most urban nests already contained recently hatched  
199 nestlings (Appendix2) whilst forest clutches were still being incubated (reflecting the typical trend for  
200 earlier laying in urban sites, see Seress et al. 2018). This adverse weather might have disproportionately  
201 affected the early development of urban nestlings. However, the exposure to the cold spell did not have  
202 a significant interaction with the treatment in models of any of our response variables, and control urban  
203 nestlings that experienced the cold spell did not have smaller body mass than non-manipulated broods  
204 from the same urban site from other years with normal weather conditions (Appendix2). Thus, we  
205 conclude that it is highly unlikely that the exposure of urban broods to the cold spell biased the effects  
206 of the supplementary food treatment.

207

208 **Behavioural data collection**

209 Small video cameras (HD Hero, GoPro) mounted in a non-transparent plastic box for camouflage (c. 15  
210 cm from the feeder) were used to monitor use of the feeder and parental provisioning behaviour (Seress  
211 et al. 2017). Videos (60 minutes duration) were recorded when chicks were 3-5 days old (mean  $\pm$  SE,  
212 supplemented group:  $4.1 \pm 0.3$  d, control group:  $4.3 \pm 0.1$  d) and 9-11 days old (supplemented group:  
213  $9.9 \pm 0.1$  d, control group:  $10.0 \pm 0.1$  d). Due to logistical constraints videos ( $n = 67$ ) were obtained for  
214 42 broods, of which 25 were recorded at both chick ages, and 17 broods were only recorded when chicks  
215 were 9-11 days old. Videos were only taken during favourable weather conditions (i.e. not during heavy  
216 rain or strong winds) during the morning or early afternoon (urban: 09:00-14:30, forest: 10:00-15:30).

217 From each video, we extracted data on food provisioning rates (calculated per nestling). For  
218 supplemented broods we also categorized food items into three food types: mealworm, non-  
219 supplementary food (mainly caterpillars and other arthropods), or unidentified food item (8 of the 1526  
220 feeding events). We recorded if birds (of any species) other than the focal brood's parents took  
221 supplementary food from the feeder (parents could be identified by unique colour ring combinations (66  
222 of the 84 focal parents) or unique plumage marks (e.g. width of the breast stripe and overall colouration;  
223 the remaining 18 parents). We never captured and ringed adults or measured nestlings before video  
224 recording to avoid possible disturbances to birds' behaviour (Seress et al. 2017). Finally, we also  
225 recorded if parents consumed supplementary food themselves (through either direct capture of the  
226 feeding event on the video or by assuming self-consumption if a parent took supplementary food but  
227 did not deliver it to nestlings on its subsequent visit to the nest box).

228

## 229 **Statistical analysis**

230 We conducted three analyses to further investigate how parents used the supplementary food. First, we  
231 tested if urban and forest supplemented birds utilized the same proportion of the supplementary food  
232 that was provided during the entire nestling period and compared habitats using a Mann-Whitney test  
233 (data distributions did not permit parametric tests). Second, we calculated the proportion of mealworm  
234 prey in the nestling diet to investigate how much urban and forest parents supplemented their nestlings'  
235 diet with mealworms. We fitted a linear mixed model (LME, package "nlme") in which the response  
236 variable was the ratio of mealworms across all prey items (the number of mealworms divided by the

237 number of all food items; n = 8 unidentified food items were excluded), and predictors were habitat,  
238 time of the day (number of minutes from 6:00 a.m. until the start of the video recording), nestling age  
239 and brood size. Note that as videos were recorded during the same short nestling age periods (3-5 and  
240 9-11 days post-hatch), we included nestling age as a binary variable with these two age categories. We  
241 included brood ID as random factor to control for the non-independence of two video recordings on the  
242 same broods. Third, we also calculated the proportion of mealworms consumed by parents, and  
243 compared this ratio between habitats. We built a generalized linear mixed-effects model with quasi-  
244 binomial error distribution (glmmPQL, package “MASS”), in which the response variable was the ratio  
245 of mealworms consumed by the parents (number of consumed mealworms divided by the number of all  
246 utilized mealworms), and predictors were habitat, time of the day, nestling age (two-level factor) and  
247 brood size; brood ID was a random factor. From this latter analysis we excluded one video recording  
248 (an urban brood) because the parents did not consume or provision any mealworms during the 60-min  
249 video so we could not calculate this ratio (although field observation and the usually zero amount of  
250 leftover food in the feeder confirmed that these parents usually utilized the supplementary food).

251 To test our specific predictions for the effects of food supplementation treatment on reproductive  
252 success (outlined in the Introduction) we followed the approach suggested by Ruxton & Beauchamp  
253 (2008) and applied pre-planned pairwise comparisons between specific groups of habitat and treatment  
254 combinations of interest, as this method is a powerful approach for testing a priori hypotheses. We  
255 conducted the comparisons in two steps: first, we built separate linear models for nestling body size  
256 traits, survival rate and nestling provisioning rate and used these models to identify significant  
257 confounding variables besides the effects of treatment and habitat. Second, following the specific  
258 guidance of Ruxton & Beauchamp (2008) we conduct all the pre-planned comparisons (regardless of  
259 the results of the first stage analysis) and calculated linear contrasts between specific groups of habitat  
260 and treatment combinations from linear models that also contained the confounding variables that had  
261 significant effects. These steps are described in detail below.

262 First, we fitted separate LME models for **nestling’ body mass, tarsus length and wing length**  
263 (all measured at day 15). In these three models, predictors were food supplementation treatment  
264 (supplemented or control), habitat, treatment × habitat interaction, brood size, and time of day when

265 modelling body mass. We used brood ID as a random factor in all these models. We also included date  
266 (number of days elapsed from the 1<sup>st</sup> of January until the measurement) in these models, but because  
267 forest great tits laid on average 7-8 days later than their urban conspecifics (Seress et al. 2018), we found  
268 a moderate level of collinearity between habitat type and date (variance inflation factor (VIF) > 3.26 in  
269 all cases, i.e. above the threshold above which collinearity is a concern (Zuur et al. 2010); using function  
270 ‘vif’ from package ‘car’). Thus, to reduce multicollinearity we mean-centered the date separately for  
271 urban and forest broods and used this transformed variable in the models.

272 The food limitation hypothesis predicts lower **nestling survival** due to starvation in urban areas.  
273 Thus, we calculated the proportion of nestlings surviving from day 3 to day 15 (i.e., from the start of the  
274 experiment until ringing) and built a generalized linear model (GLM) with binomial error distribution,  
275 logit link function. In this model, the response variable was the proportion of nestlings surviving (i.e.  
276 the unit of analysis was individual broods and thus we did not include brood identity as a random factor),  
277 and predictors were treatment, habitat, treatment × habitat interaction, mean-centred date and brood size.  
278 Because in the forest supplemented group survival rate was 1.00 (i.e., all nestlings survived), we applied  
279 Firth logistic regression (using package “brglm”) to handle the problem of separation.

280 We also analysed the **provisioning rates** of parents in an LME model in which the response  
281 variable was provisioning rate (transformed as  $\log_e(x + 0.5)$ ), and predictors were treatment, habitat,  
282 treatment × habitat, mean-centred date, time of the day and nestling age (two-level factor); random factor  
283 was brood ID. We were unable to include potential confounding effects of parental age, a possible proxy  
284 for experience, because this would have reduced sample sizes by between 11 and 30% for each  
285 comparison group – generating an unhelpful reduction in statistical power. Consideration of the age of  
286 parents for which data were available strongly suggests, however, that our results and inference are not  
287 biased by variation in parental age across our four groups of birds (urban control, urban supplemented,  
288 forest control and forest supplemented; Appendix1 Table S3). We report the results for all full models  
289 in the Appendix1 (Table S4).

290 In the second step, we used separate linear models to compare the means of the response variables  
291 (i.e., the three nestling body size traits, survival rate and nestling provisioning rate) between specific  
292 habitat-treatment combinations. These models always contained the habitat × treatment term, plus any

293 other confounding variable that was significant in the above described models (Appendix 1: Table S4),  
294 specifically: date in the tarsus length and survival rate models, and nestling age (as two-level factor) in  
295 the nestling provisioning rate model; the random factor was brood ID (except for the model on nestling  
296 survival). We calculated linear contrasts between groups and used function “glht” (in package  
297 “multcomp”) to test whether these contrast differed from zero after applying the false discovery rate  
298 (fdr) method for correcting *P*-values for multiple pairwise comparisons. Specifically, we compared the  
299 means of the above five response variables between the following groups: (1) forest control vs. urban  
300 control (to confirm the effect of habitat on control broods); (2) forest control vs. forest supplemented  
301 and (3) urban control vs. urban supplemented (to test for the effects of supplementary food within habitat  
302 types); and finally, (4) forest control vs. urban supplemented (to test whether the food-supplementation  
303 was sufficient to eliminate or considerably mitigate differences between habitats).

304 To aid the interpretation of nestling survival analyses, we calculated survival probabilities of  
305 nestlings in the four groups from the model’s parameter estimates. We used the same GLM as in the  
306 linear contrast analysis (see above) and transformed the habitat-treatment group mean estimates (*b*,  
307 provided on a logit scale) of the proportion of survived nestlings to survival probabilities (*p*) using the  
308 formula:  $p = \exp(b) / (1 + \exp(b))$  (Zuur et al. 2009) – this is referred to as the survival probability in the  
309 rest of the manuscript.

310 All analyses were conducted in R (v. 3.5.2, R Core Team). We checked the validity of statistical  
311 assumptions for each linear model described above (Zuur et al. 2009), and the calculated VIF values for  
312 all our models ( $VIF < 2.55$ ) were below the threshold at which results are influenced by collinearity  
313 (Zuur et al. 2010). We define the two-tailed statistical significance level at  $P < 0.05$ .

314

315

## 316 RESULTS

### 317 **Acceptance of supplementary food and provisioning behaviour of the parents**

318 Videos showed that birds in both habitats used most of the supplementary food, and we found no  
319 significant difference in the ratio of the amount of leftover food between urban (1.4%) and forest (4.2%)  
320 supplemented nests (Mann-Whitney,  $n = 25$ ,  $W = 66$ ,  $P = 0.542$ ). Videos also revealed that birds other

321 than the nest owners occasionally visited the nest boxes both in the control and in the supplemented  
322 groups. Species that visited the nest boxes (in control and supplemented groups combined) included  
323 great tits (7 cases), great spotted woodpeckers *Dendrocopos major* (3), collared flycatchers *Ficedula*  
324 *albicollis* (2), tree sparrows *Passer montanus* (2) and a blue tit *Cyanestes caeruleus*. Visitor birds  
325 appeared on 16.7% (5 out of the 30) of the control videos, and on 24.3% (9 out of 37) of the  
326 supplemented videos, stealing mealworms from the feeders in 6 out of the 9 videos. However, on these  
327 6 videos (5 urban, 1 forest), the amount of food stolen (57 mealworms in total, mean  $\pm$  SE:  $8.14 \pm 3.12$   
328 per video) was small compared to the amounts utilized by the focal parents (390 mealworms,  $55.71 \pm$   
329  $11.14$ ; paired-test,  $t_6=3.72$ ,  $P = 0.009$ ). Visiting great tits (all in the urban habitat) may have largely  
330 comprised of floaters and were either not ringed, or were ringed but not included in the experiment,  
331 except one urban male that was the parent of a neighbouring supplemented brood. We did not record  
332 any great tits from the control group stealing supplementary food from the feeders on supplemented nest  
333 boxes.

334 In supplemented nests we found that parents readily fed their chicks with the supplementary  
335 food, as the proportion of mealworms in nestlings' diet was 81.1% in urban and 75.3% in forest broods,  
336 but neither habitat type (LME,  $b \pm$  SE:  $0.02 \pm 0.09$ ,  $t_{21} = 0.192$ ,  $P = 0.849$ ), nor any other predictor had  
337 significant influence on the proportion of mealworm in the diet of supplemented nestlings ( $P > 0.351$  in  
338 all cases). Investigating the proportion of mealworms that parents consumed, we found a marginally  
339 non-significant habitat effect (GLM,  $b \pm$  SE:  $0.55 \pm 0.31$ ,  $t_{20} = 1.77$ ,  $P = 0.093$ ), with urban parents  
340 tending to consume more mealworms (24.7%) than forest parents (18.1%). We also found a significant  
341 effect of nestling age, as parents consumed more extra food themselves when they were raising younger  
342 nestlings (3-5 days old) compared to when they were provisioning older chicks (9-11 days) (GLM,  $b \pm$   
343 SE:  $-0.80 \pm 0.28$ ,  $t_{13} = -2.83$ ,  $P = 0.014$ ).

344 Nestling provisioning rate was similar between treatment groups and habitats, and none of the  
345 four pre-planned pairwise comparisons revealed significant differences between groups (Table 1a).  
346 Provisioning rate was significantly higher in the 9-11 day compared to the 3-5 day old age category  
347 (Appendix1: Table S4).

348

349 **Nestling body size**

350 The results of the pre-planned pairwise comparisons for body mass, wing and tarsus lengths confirmed  
351 that (1) forest control nestlings were significantly larger than urban control nestlings for all three body  
352 size metrics (Fig.1a-c, Table 1b-d). In line with our expectations, we found that (2) forest control and  
353 forest supplemented groups did not differ significantly in any variables, whereas (3) supplementary  
354 feeding significantly increased body mass, wing and tarsus lengths in urban supplemented nestlings  
355 compared to the control group (Fig.1a-c, Table 1b-d). Finally, (4) supplementary feeding effectively  
356 mitigated the differences in body mass, wing and tarsus lengths that occurred between control forest and  
357 urban broods (Fig.1a-c, Table 1b-d). Although the difference between forest control and urban  
358 supplemented groups was close to statistical significance in body mass (Table 1b) and was statistically  
359 significant in wing length (Table 1c), the magnitude of these differences were small (body mass (g):  
360  $0.90 \pm 0.46$ , wing length (mm):  $3.58 \pm 1.58$ ).

361

362 **Nestling survival**

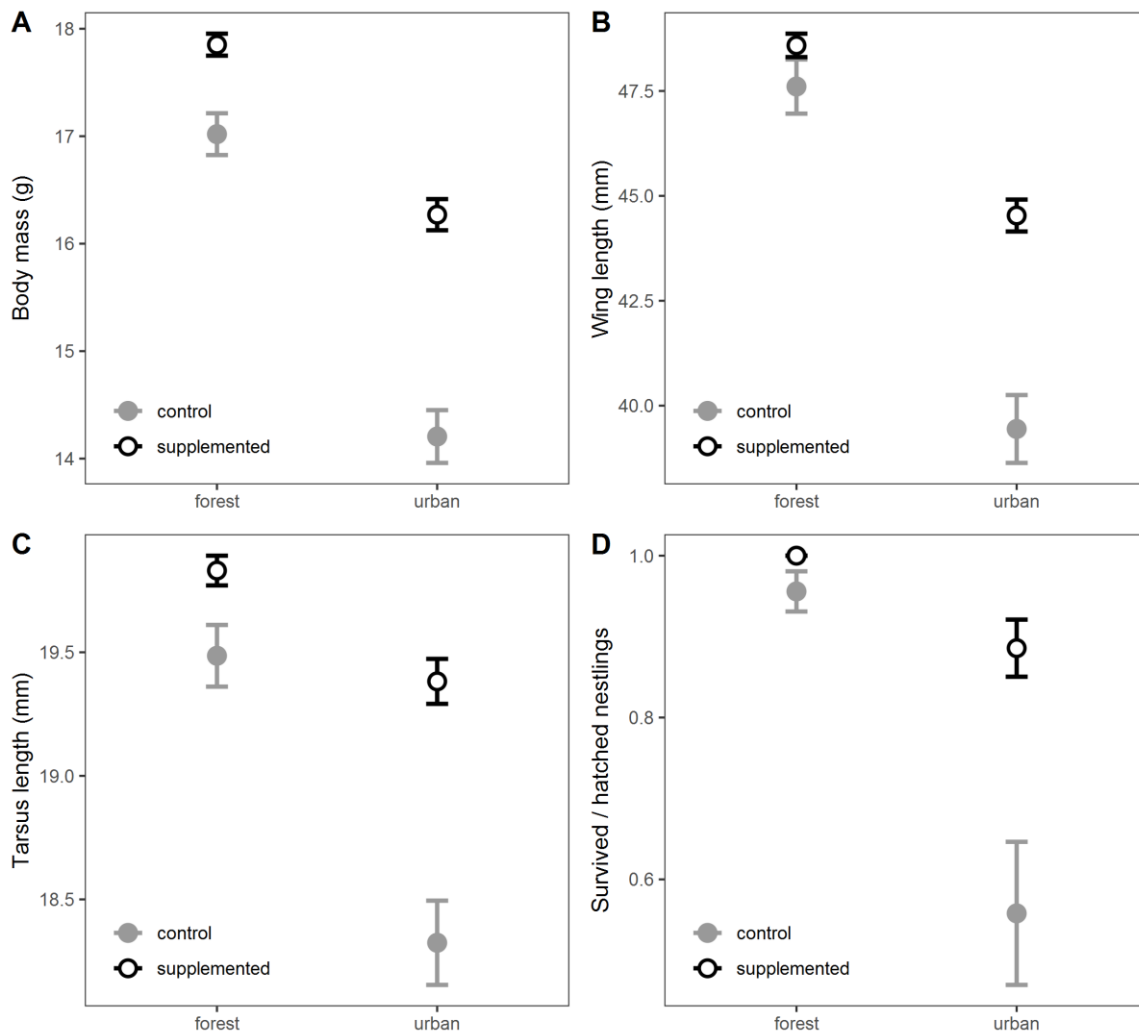
363 Nestling survival probabilities (p), estimated from the GLM model, were 1.00 and 0.95 in forest  
364 supplemented and control broods, respectively, while this was 0.88 in the urban supplemented and only  
365 0.58 in urban control broods. The pre-planned pairwise comparisons indicated significant differences in  
366 nestling survival probabilities between (1) forest control and urban control groups (Table 1e; Fig.1d).  
367 The difference in survival probability between (2) forest supplemented and forest control groups was  
368 close to statistical significance but remained slight, whereas (3) survival was significantly and  
369 considerably higher in the urban supplemented compared to the urban control groups (Table 1e; Fig.1d).  
370 Finally, whilst we found that the difference in survival probability (4) between the forest control and  
371 urban supplemented groups was close to statistical difference its magnitude was small; Table 1e; Fig.1d).

372

373

374 **Fig. 1.** Differences (means  $\pm$  SE) in 15-days old great tit nestlings' (a) body mass, (b) wing length, (c)  
375 tarsus length and (d) nestling survival in the groups of different habitat  $\times$  treatment combinations.

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## 381 DISCUSSION

382 Urbanisation can be associated with adverse impacts on demographic traits (Sepp et al. 2017), and these  
 383 impacts probably contribute to the reduced biodiversity of towns and cities (Aronson et al. 2014). The  
 384 mechanisms driving reduced demographic success in urban environments are, however, poorly  
 385 understood (Rodewald and Gehrt 2014). In this study we used a food supplementation experiment, using  
 386 mealworms fed on an enriched diet, to test if the reduced abundance of insect food sources in urban  
 387 environments (e.g. Seress et al. 2018) explains reduced reproductive success and smaller nestling size  
 388 in an insectivorous bird.



389           As predicted by the food limitation hypothesis, control broods that did not receive supplementary  
390 food were smaller and had lower survival rates in the urban site than the forest site – matching previous  
391 studies of reproductive success in unmanipulated great tit populations (Bailly et al. 2016, de Satgé et al.  
392 2019) including our focal study populations (Seress et al. 2018). Crucially, urban supplemented broods  
393 had considerably higher fledging success and produced larger nestlings than urban control pairs, whereas  
394 supplementary feeding of forest broods had only small and statistically non-significant effects on these  
395 traits. Furthermore, supplementary fed urban broods had similar body sizes and survival rates to those  
396 of control broods in the forest environment. Collectively, these results provide rare and strong  
397 experimental evidence that the negative impacts of urbanization on avian nestling size and survival is  
398 caused by the reduced availability of high-quality invertebrate food sources, and these effects can be  
399 mitigated by providing arthropod-based supplementary food. Our experiment suggests that food  
400 limitation can strongly influence even successful urban adapter species such as the great tit, which across  
401 its range is one of the commonest birds in towns and cities (Gosler and Clement 2007). The very small  
402 differences in nestling size and survival between urban supplemented and forest control chicks suggest  
403 that food availability alone can explain much of the reduction in reproductive success in insectivorous  
404 woodland bird species occupying temperate urban environments. Other urban stressors, such as habitat  
405 modification and light pollution, thus seem likely to play only a limited direct role in lowering the  
406 productivity of insectivorous passerines in these situations – although their indirect effects on birds *via*  
407 reducing urban populations of moths and other insects might be still substantial.

408           The positive effects of supplementary food on urban nestlings' body size and survival were clearly  
409 detectable and strong compared to previous studies in urban great tit populations (Bañbura et al. 2011,  
410 Demeyrier et al. 2017). Although these earlier studies differ in several methodological details from our  
411 experiment (measured traits, length of food supplementation, type of food, etc.) the much stronger effect  
412 we found may arise primarily due to the enhanced quality of mealworms and the higher amounts of extra  
413 food per nestling we provided throughout most of the brood-rearing period. Alternatively or  
414 additionally, the natural availability of arthropods may be lower in our urban site than in the habitats  
415 involved in the above studies, making supplementary food more valuable and effective in our  
416 experiment (Ruffino et al. 2014). The estimated biomass of arboreal caterpillars (the optimal nestling

417 food for many passerines; Cholewa and Wesołowski 2012) during the brood-rearing period in our urban  
418 site was extremely low (approximately 8-times higher in the forest site; and similar even more dramatic  
419 differences in caterpillar biomass occur in other years (2013-2016, Appendix1: Fig.S2; Seress et al.  
420 2018)), but we consider such differences to be a common feature of urban environments (Shawkey et  
421 al. 2004, Marciniak et al. 2007, Pollock et al. 2017, Hajdasz et al. 2019).

422         The strong treatment effect that we found on urban but not forest birds' breeding success is  
423 unlikely to be driven by the more extensive use of supplementary food by urban parents than those in  
424 the forest habitat for three reasons. First, the amounts of leftover food was very low in both habitats, and  
425 consecutive nest checks on day 15 (i.e. food supplementation and later that day, nestling measurements)  
426 also indicated that birds usually consumed all the provided food within a few hours. Second, the video  
427 recordings confirmed that the supplemented mealworms were utilized predominantly by supplemented  
428 parents in both habitats. Finally, the videos confirmed that the proportion of mealworms in the nestling  
429 diet was high in both urban (81%) and forest (75%) supplemented broods. It thus appears clear that  
430 forest birds are not food limited, and importantly that supplementary feeding with nutritionally enhanced  
431 mealworms provided forest supplemented pairs with a food source that was of broadly similar nutritional  
432 quality to the food sources utilised by forest control pairs – otherwise one would expect supplemented  
433 pairs to have lower nestling body size and survival rates than the controls.

434         Besides the presumable direct (calorific and nutritional) benefits of the extra arthropod food on  
435 urban broods, indirect mechanisms might also have played a role in improving brood performance. The  
436 parents of supplemented broods consumed significant proportions of the mealworms themselves, and  
437 this tended to be higher in urban pairs. The resultant reduction in the time parents needed to invest in  
438 foraging for themselves, and the potentially higher body condition, may have enabled females to invest  
439 more in brooding and feeding young nestlings. Additionally, food supplementation can also enhance  
440 breeding success by increasing parents' nest defence behaviour, for example because parents can spend  
441 more time in the proximity of their nest and thus defend it against predators (see Vafidis et al. 2018 and  
442 references). We did not record brood losses attributable to nest predation in any of our experimental  
443 groups, thus it is unlikely that this latter mechanism played an important role in our case – although it  
444 may be important in other regions or species with higher rates of nest predation.

445 Finally, our data can provide a broad indication of the magnitude of urban food limitation in this  
446 study system. Supplying 40-50% of urban nestlings' food requirements enabled them to more or less  
447 match the performance of forest broods. This implies that, at current densities and brood sizes, urban  
448 caterpillar populations need to be doubled if urban and rural chicks are to have similar performance  
449 without supplementary food. Urban great tit brood sizes are, however, typically c. 75% of those of forest  
450 broods in our study areas (Seress et al. 2018). Assuming that such reductions are driven by food  
451 limitation and that clutch size linearly increases with food availability it seems likely that urban  
452 caterpillar populations need to be increased by at least a factor of 2.5 to equalise urban and forest great  
453 tit brood size and performance. However, much higher increases are likely to be required given that  
454 other urban passerine species, including other tit species or woodpeckers (Smith and Smith 2019), also  
455 depend on caterpillars for provisioning their young and will thus compete to some extent with great tits.  
456 Achieving such large increases will be challenging – although there is substantial capacity to increase  
457 the volume of urban tree canopy through tree planting (Kroeger et al. 2018), the benefits of this would  
458 take time to accumulate and many urban trees fail to come close to their mature size due to high mortality  
459 rates (Widney et al. 2016).

460 This study provides rare experimental evidence for the strong effects of food limitation in urban  
461 areas on avian nestling size and survival rates. Provision of mealworms that are fed on an enriched diet  
462 largely mitigated the marked differences in nestling size and survival rates between non-supplemented  
463 urban and forest broods. Our focal species specialises on provisioning nestlings with caterpillars, which  
464 is a common strategy in many groups of birds occurring in urban areas across the temperate zone  
465 including tits, chickadees, finches, and woodpeckers. Thus, food limitation may be a similarly major  
466 factor limiting reproductive success in several other urbanized bird species. The provision of higher  
467 quality supplementary food to such species during the breeding season may increase the body size and  
468 nestling survival rates in their urban populations. The increased growth might have also yielded  
469 additional fitness advantages for urban supplemented broods given that effects of early nutritional  
470 conditions can be carried to adulthood, affecting adult body size (e.g. Cleasby et al. 2011) or even  
471 cognitive abilities such as song learning (Nowicki et al. 2002). Urban nestlings' benefit from the  
472 arthropod-rich food was especially prominent in their pre-fledging body mass (ca. 2 grams), which might

473 have also increased their recruitment rate (Schwagmeyer and Mock 2008) given that pre-fledging body  
474 mass correlates positively with post-fledging survival in many passerine species, including great tits  
475 (Magrath 1991). To what extent could the increased nestling survival and development contribute to  
476 urban populations' size and stability, is still an unanswered question though. For example, whilst  
477 supplementary feeding improved breeding success in sub-urban house sparrows (Peach et al. 2014) this  
478 did not generate an increase in population size (Peach et al. 2018). Whilst further work on the impacts  
479 of supplementary feeding on population dynamics is certainly needed, it is clear that the decreased  
480 abundance of key arthropod food sources in urban areas can limit avian reproductive success. Thus,  
481 management methods that overcome this limitation are likely to be beneficial in supporting and  
482 enhancing urban biodiversity, especially considering the marked and ongoing decline of global insect  
483 populations (see Owens et al. 2019 and references in it).

484

485

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487

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#### 498 AUTHOR CONTRIBUTIONS

499

500 GS and AL conceived the ideas; GS and KS designed methodology, collected and prepared the data; GS  
501 analysed the data with advice from KLE; GS, KLE and AL interpreted the data and wrote the  
502 manuscript; and all authors worked on the manuscript's revision. All authors gave final approval for  
503 publication.

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#### 506 DATA AVAILIBILITY STATEMENT

507 Data available from the Dryad Digital Repository: <https://doi:10.5061/dryad.qbzkh18dj> (Seress et al.  
508 2020).

509 **Table 1.** The results of the pre-planned pairwise comparisons showing the differences in (a) great tit  
510 parents' provisioning rates (log-transformed using the formula  $\log_e(x+0.5)$ , and in their nestlings' (b-d)  
511 body size and (e) proportion of survived nestlings (on a logit scale) between groups of treatment  $\times$   
512 habitat combinations. The linear contrasts between groups were calculated from linear models (LME  
513 for a-d, and GLM for e), containing the habitat  $\times$  treatment interaction, plus any confounding variable  
514 that was proven to be significant in the full model (Appendix1: Table S4). Statistically significant ( $P <$   
515 0.05) differences are highlighted in bold and marginally non-significant ( $0.05 < P < 0.10$ ) differences  
516 are shown in italic.

517

Pairwise comparisons	contrast $\pm$ SE	z	adj. P
<i>(a) Provisioning rate (feeding/nestling/hour)<sup>1</sup></i>			
forest control – urban control	0.20 $\pm$ 0.21	0.94	0.654
forest control – forest supplemented	-0.09 $\pm$ 0.20	-0.45	0.654
urban control – urban supplemented	-0.31 $\pm$ 0.20	-1.53	0.502
forest control – urban supplemented	-0.12 $\pm$ 0.17	-0.66	0.654
<i>(b) Nestling body mass (g; day 15)<sup>2</sup></i>			
forest control – urban control	2.90 $\pm$ 0.52	5.54	<b>&lt; 0.001</b>
forest control – forest supplemented	-0.78 $\pm$ 0.48	-1.61	0.107
urban control – urban supplemented	-2.00 $\pm$ 0.51	-3.92	<b>&lt; 0.001</b>
forest control – urban supplemented	0.90 $\pm$ 0.46	1.97	<i>0.066</i>
<i>(c) Nestling wing length (mm; day 15)<sup>2</sup></i>			
forest control – urban control	9.13 $\pm$ 1.79	5.10	<b>&lt; 0.001</b>
forest control – forest supplemented	-0.73 $\pm$ 1.66	-0.44	0.662
urban control – urban supplemented	-5.55 $\pm$ 1.74	-3.19	<b>0.003</b>
forest control – urban supplemented	3.58 $\pm$ 1.58	2.27	<b>0.031</b>
<i>(d) Nestling tarsus length (mm; day 15)<sup>2</sup></i>			
forest control – urban control	1.25 $\pm$ 0.35	3.59	<b>0.001</b>
forest control – forest supplemented	-0.34 $\pm$ 0.31	-1.12	0.348
urban control – urban supplemented	-1.06 $\pm$ 0.34	-3.09	<b>0.004</b>
forest control – urban supplemented	0.19 $\pm$ 0.29	0.66	0.512
<i>(e) Nestling survival (between day 3-15)<sup>3</sup></i>			
forest control – urban control	2.67 $\pm$ 0.50	5.33	<b>&lt; 0.001</b>
forest control – forest supplemented	-2.48 $\pm$ 1.49	-1.67	<i>0.096</i>
urban control – urban supplemented	-1.68 $\pm$ 0.37	-4.49	<b>&lt; 0.001</b>
forest control – urban supplemented	0.99 $\pm$ 0.53	1.86	<i>0.084</i>

518

519 <sup>1</sup> Number of broods (control/supplemented): urban: 8/13, forest: 11/10

520 <sup>2</sup> Number of nestlings (nr. of broods; control/supplemented): urban: 45 (9)/96 (14), forest: 99 (12)/104  
521 (11)

522 <sup>3</sup> Number of broods (control/supplemented): urban: 10/14, forest: 12/11

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