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2 **Foraging on human-derived foods by urban bird species**

3

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Short title: Urban birds prefer peanuts

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Key words: Avian foraging, food preferences, supplementary feeding

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18 **Summary**

19 **Capsule:** Providing peanuts on bird feeders was shown to attract more individuals and more
20 species than providing cheese or bread.

21 **Aims:** To investigate how the provision of different human-derived foods affects visitation rates
22 of urban birds at bird feeders.

23 **Methods:** A fully replicated study design was set up in parkland, offering a binary choice from
24 three food types (peanuts, bread and cheese), on bird tables. Birds were observed using a scan-
25 sample method.

26 **Results:** Peanuts attracted more visits and a greater diversity of species than cheese or bread.
27 This preference was strongest for Blue Tits and Great Tits, whereas Robins visited all food types
28 equally, and Blackbirds preferred cheese. Bread was the most consumed food type when
29 measured in mass, but this could be linked to varying bite sizes.

30 **Conclusion:** Our results indicate that most birds preferred to visit the most protein- and energy-
31 rich food, but that some birds still choose the carbohydrate-rich bread. The findings indicate that
32 peanuts, rather than household scraps like bread and cheese, attract the highest number of bird
33 species as well as individuals to bird tables. The findings are of interest to the public and to
34 organisations providing information on bird feeding for recreational purposes.

35

36 Introduction

37 With increasing urbanisation comes habitat destruction and alteration, resulting in the loss
38 of natural nesting and foraging habitats for wildlife, including birds (Evans et al. 2009). An
39 estimated 48% of the UK population feed birds in their gardens (Davies *et al.* 2009),
40 potentially impacting the birds' ecology and diet. Householders provide supplementary food
41 to birds to nurture interest in the natural world or because feeding provides a connection to
42 nature, or to assist birds through the winter (Jones & Reynolds 2008; Cox & Gaston 2016).
43 Supplementary feeding is also a standard conservation intervention (e.g. Castro *et al.* 2003;
44 Phipps *et al.* 2013; Mallord *et al.* 2010). Fuller *et al.* (2008) found that avian abundance
45 increased with greater densities of feeders in an area. However, it is difficult to separate the
46 effect of feeders on population abundance as opposed to feeders attracting birds, and
47 another study in the same area found no effect of the presence of supplementary feeders on
48 bird assemblages, leaving the actual effect uncertain. In fact, supplementary feeding can
49 increase the risk of pathogen transmission or malnutrition (Murray *et al.* 2016; Galbraith *et*
50 *al.* 2016), and so it is essential to take due care when feeding wild animals. Conservation
51 organisations such as the Royal Society for the Protection of Birds (RSPB) and British Trust for
52 Ornithology (BTO) strongly recommend bird feeding, and also suggest different food types to
53 attract specific bird species, for example feeding mealworms to attract Robins *Erithacus*
54 *rubecula* and Blue Tits *Cyanistes caeruleus* (RSPB 2009). However, there is little evidence to
55 back up these suggestions. Although there are numerous studies on the foraging behaviour
56 of individual species in laboratory environments (e.g. Diaz *et al.* 1990; Murray *et al.* 1993),
57 there is very little *in situ* research into the supplementary food choices of garden birds (Jones
58 & Reynolds 2008; but see Mckenzie *et al.* 2007).

59 The British Trust for Ornithology (2006) estimates that the total annual expenditure
60 on outdoor bird feeding in the UK is £200 million. Despite the impressive scale of this
61 industry, households maintain the provision of scrap foods to urban bird populations but
62 minimal research has taken place to assess the food types and quantity provided, in addition
63 to the ecological effects of providing such subsidies. A broad range of food types are
64 suggested for garden feeders including seeds, nuts and grated cheese, yet bread appears to
65 be a contentious subject. RSPB (2012), BTO (2012) and Allison (2007) suggest the main
66 negative attached to bread is that it is filling but has a low nutritional content (low fat, low
67 protein), with suggestions that if bread makes up the vast majority of their diet then the bird
68 will be subjected to critical vitamin deficiency or starvation (although the scientific evidence
69 for this appears lacking).

70 Optimal foraging theory predicts that birds should prefer to eat high-energy food,
71 especially in winter when food is scarce and thermoregulatory demands are high (MacArthur
72 and Pianka 1966). As such, where a choice is available birds should select the food with the
73 most energy yield for the energy expended in finding or processing it. However, energy is not
74 the only requirement for bird survival. Nutrients, such as vitamins and minerals, are also
75 necessary to reach a balanced, healthy diet (e.g. Klasing 1998; Ramsay & Houston 1998;
76 Larcombe *et al.* 2008). If high-energy food is eaten in large amounts, this may lead to
77 nutrient deficiencies, impacting on fitness related traits, such as immune function (Blount *et al.*
78 *al.* 2003), locomotary performance (Larcombe *et al.* 2008) or offspring quality (Arnold *et al.*
79 2007). For example, Plummer *et al.* (2013a) reported that winter feeding with fat resulted in
80 smaller egg yolks compared to feeding with fat plus Vitamin E. Their follow-up study
81 documented lower productivity in Blue Tits after supplementary feeding compared with
82 controls (Plummer *et al.* 2013b). Depending on the remainder of their diet, birds may need

83 to choose the supplementary feeds which complement their existing food sources, which
84 will differ among species. Several studies have analysed which types of food birds prefer to
85 eat under laboratory conditions and compared these to the predicted optimal choices (e.g.
86 Diaz *et al.* 1990; Murray *et al.* 1993; Glück 1985; Krebs *et al.* 1977; Willson 1971). However,
87 these have been natural or semi-natural foods, such as mealworms or seeds. Human-derived
88 food, on the other hand, is provided to wild birds throughout the world, but it is unknown
89 whether urban birds exhibit optimal foraging behaviour with human-derived foods such as
90 cheese and bread.

91 A number of environmental and social factors are predicted to affect the foraging
92 behaviour and diet selection of birds. In winter, when food is scarce and thermoregulatory
93 costs high, birds utilise supplementary feeders more often (Chamberlain *et al.* 2005;
94 Herborn *et al.* 2014) and accrue body mass earlier in the day (Macleod *et al.* 2005) than
95 under less harsh conditions. Moreover, when temperatures drop, food preferences may
96 change to incorporate human-derived foods, higher-energy foods or larger food items to
97 build up energy reserves (Diaz, 1990; Myton and Ficken 1967). Thus, birds may use air
98 temperature as a cue to predict starvation risk, and hence optimise foraging rate (Fitzpatrick
99 1997), or food-type preferences. High wind speeds have been shown to lead to lower bird
100 activity due to the high cost of movement, with impacts on foraging rates (Grubb 1978;
101 reviewed in Wingfield & Ramenofsky 2011).

102 Clearly, the implementation of supplementary feeding as a management approach
103 requires detailed knowledge on both food preferences and the effects of certain food types
104 on individual species. The majority of this data has been collected by the wild bird food
105 industry itself, consisting of preferences for food types, feeder design and location, time of

106 day and season, food colour, taste and nutritional composition (Jones & Reynolds 2008).
107 However, a negligible amount of information is available on the selection of one food type
108 over another when offered simultaneously, in addition to the significance of such preference
109 information and its role in conservation management. The three food types used in this
110 experiment, bread, cheese and peanuts, were selected based on two surveys that we carried
111 out in Hull (see Supplementary Online Material) and advice provided by avian conservation
112 organisations (RSPB 2012; BTO 2012). The overall aim for this study was to investigate
113 whether different human-derived foods can affect avian food choices at urban bird feeders.
114 Specifically we addressed: 1) Do different food types attract different numbers of avian
115 species? 2) Do urban birds show interspecific differences in their food preferences? 3) How
116 do visit rates vary depending on weather conditions?

117

118 **Methods**

119 Seven observation sites were set up in similar habitats around the campus grounds of the
120 University of York, UK and in adjacent green spaces. All sites were in a park-like, managed
121 landscape, with lawns, hedges and a selection of native and non-native trees and shrubs
122 similar to garden areas (see Fig. A1 in Supporting Information). Sites were positioned at least
123 200m apart, i.e. one minimum robin territory, with approximately half the sites at least
124 500m apart thus minimising the likelihood of individuals moving between sites on the same
125 day. Two Gardman bird feeding tables with a brush roof were used at each site, placed at a
126 reasonable distance apart from each other ($420\text{ cm} \pm 30\text{ cm}$) and from surrounding
127 vegetation ($120\text{ cm} \pm 90\text{ cm}$) to control for distance to cover and perceived predation risk at
128 the sites. The observation period ran from January to March in 2014. Observation periods

129 did not take place when there was any precipitation. It was important that the birds were
130 aware of the food before measurements begun. Therefore, tables were pre-baited with a
131 mixed seed bird feed, ensuring that food was available for two consecutive days prior to an
132 observation session.

133 Three different food types were used: grated cheese (Heritage Mild Cheddar),
134 chopped peanuts (Gardman Peanut Bites for Wild Birds), and crumbled pieces of white
135 bread (Warburton's Medium White). Peanuts and bread were found to be commonly
136 provided by households to garden birds in a preliminary survey (Supplementary Online
137 Material). Cheese, although not included in the survey, was chosen because it has been
138 recommended for bird feeding (RSPB, 2009) without there being much evidence that this is a
139 preferred feed for birds. The food types also differ in their nutritional content (Molokwu *et*
140 *al.* 2011; SELF Nutrition Data 2013; Table 1). For each observation period, 50 grams of one
141 food type was put on each of the two tables, allowing us to record bird choice between
142 these two food types. All combinations of the three foods were observed across all sites and
143 both tables to control for spatial preferences, leading to 42 observation sessions. There were
144 no observations where the same food was provided on both tables. Birds tend to be most
145 active in the morning (Farine and Lang 2013; Rollfinke and Yahner 1990), so a maximum of
146 two observation sessions were carried out within three hours of sunrise (sunrise times from
147 Timeanddate.com, as recommended by The Royal Observatory Edinburgh). The sampling
148 was based on a strategic sampling schedule so that food types and sites were not repeatedly
149 observed at the same time of day. The observer was positioned approximately 15 m from
150 the nearest table, and a timer was started when the observer was in the correct position
151 after leaving the food on the tables. The observer then applied a scan-sample method for

152 one hour, with a bird count every 60 seconds (i.e. 60 counts per one hour observation period
153 and 42 observation sessions in total). The number of individuals on the feeders was recorded
154 at every count as well as which species they were. One “visit” was defined as one individual
155 being present on one feeder at the point of a 60-second scan. This sampling method was
156 used as this was considered the best way of collecting data on what could be a highly
157 dynamic situation involving birds that were not individually marked. It should be noted that
158 there is no way of knowing how many individuals visited the feeders, and it is also possible
159 (although in our opinion unlikely) that the same individuals were observed at several sites,
160 so these data should be treated with some caution. After each observation session, the
161 remaining food was removed and weighed to calculate the amount of eaten food.

162 Data on weather conditions for each observation day were collected from the
163 University of York campus weather station, using a Vaisala WXT520. This included average air
164 temperature, average wind speed and total rainfall from the previous day. Data from the day
165 prior to the observation period were used, because the same-day weather data would
166 largely measure weather that occurred after the morning observations, and the weather in
167 the previous 24 hours determines the energetic status of a bird in the morning. Ground
168 conditions at the observation site were also recorded (snow/frost/wet/dry), because
169 changes in conditions such as snow cover can impact foraging behaviour and access to food
170 (Brotons 1997).

171 **Ethical Note**

172 Care was taken to ensure that hard or stale bread and whole peanuts were not used during
173 observations, as these may cause birds to choke. Tables were also wiped after the
174 observation period with a bird safe disinfectant (Chapelwood wildlife care, Droitwich, UK), as

175 the congregation of birds at feeders has been implicated in disease transmission particularly
176 with platform feeders (Brittingham & Temple 1986). After completion of the experiment, the
177 tables were allowed to empty naturally for five days so that individuals could make a gradual
178 transition to alternative food sources. All experiments were carried out in accordance with
179 ASAB/ABS's Guidelines for the Treatment of Animals in Research:
180 <http://asab.nottingham.ac.uk/ethics/guidelines.php>.

181 **Statistical analysis**

182 All analyses were conducted using R statistical software (R Core Development Team 2011),
183 using the packages 'Stats', 'lme4' and 'nlme'. The visit count data were transformed into
184 presence/absence data for each minute. This was done to avoid the statistical problem of
185 zero inflation which would occur with count data, and it had minimal impact on the dataset
186 which largely consisted of 0s and 1s. This data is thus the probability of presence of a bird of
187 any species on the bird table at any given minute. This variable was then the response
188 variable of a Generalised Linear Mixed Model (GLMM), with food type as a fixed factor, table
189 (A or B) nested within observation session (1-42) within site (1-7) as random effects, and a
190 binomial distribution. In addition, it was necessary to control for the temporal
191 autocorrelation in the data. We created a variable that consisted of the presence/absence of
192 birds in the previous minute, and added this to the model. Although not a perfect statistical
193 method, this improved the model fit and worked better than any of the more complex
194 methods to control for temporal autocorrelation (most of which are made for normally
195 distributed data). It is useful to note that the conclusions from the model remained the
196 same regardless of which correction was used, and so we consider the results to be fairly
197 robust despite the challenging structure of the dataset. The same procedure was run for

198 each of the five most common species, with the response variable being presence/absence
199 of the species of interest.

200 Weather conditions were assessed with the same model structure as above, using
201 presence/absence of birds as the response variable and weather conditions (rainfall,
202 temperature and wind speed from the previous day and ground conditions from the same
203 day) as fixed effects, with each weather variable analysed in a separate model.

204 Species richness was defined as the total number of species recorded during an
205 observation session. A GLMM used species richness as the response variable, food type as
206 the fixed factor and table nested within site as a random effect, with a Poisson error
207 structure.

208 The amount of food eaten in each observation session was analysed with a linear
209 mixed effects model, where the response variable was the amount of food eaten from each
210 table in grams, log-transformed after adding 1. Food type was the fixed effect and table was
211 nested within site as a random effect.

212

213 **Results**

214 **Impact of food type on bird presence**

215 There was a significantly higher probability of presence of birds of any species at tables
216 providing peanuts than those providing bread (GLMM, $Z = 5.46$, $p < 0.001$; Fig. 1), and no
217 significant difference between those with cheese and bread (GLMM, $Z = 1.81$, $p = 0.07$).

218 **Impact of weather on visit rates**

219 None of the weather variables (rain, wind, temperature or ground conditions) had any effect
220 on the probability of the presence of birds (GLMM, all $p > 0.2$). However, the relatively
221 steady weather might mean we did not see sufficient variation to conclude in this respect.

222 **Species-specific food preferences**

223 There was a higher probability of seeing Great Tits *Parus major* (Fig. 2a) and Blue Tits (Fig.
224 2b) at tables with peanuts than those with bread (GLMM, $Z = 4.35$, $p < 0.001$ and $Z = 4.40$, p
225 < 0.001 respectively). Robins (Fig. 2c) and Dunnocks *Prunella modularis* (Fig. 2d) did not
226 show a particular preference (GLMM, all $p > 0.05$), whereas Blackbirds *Turdus merula* (Fig.
227 2e) were more likely to be seen on tables with cheese (GLMM, $Z = 2.22$, $p = 0.03$).

228 **Species richness**

229 We observed a total of nine species (Eurasian Robin *Erithacus rubecula*, Great Tit *Parus*
230 *major*, Blue Tit *Cyanistes caeruleus*, Blackbird *Turdus merula*, Common Moorhen *Gallinula*
231 *chloropus*, Dunnock *Prunella modularis*, Coal Tit *Periparus ater*, Long-tailed Tit *Aegithalos*
232 *caudatus* and House Sparrow *Passer domesticus*). Species richness was significantly higher
233 on bird tables with peanuts than tables with bread (GLMM, $Z = 3.11$, $p < 0.01$; Fig. 3), and
234 there was no difference between tables with bread and cheese (GLMM, $Z = 1.37$, $p = 0.17$).

235 **Weight of eaten food**

236 There was no difference between the food types when measured in total weight eaten per
237 observation session (GLMM, all $p > 0.20$, Fig. 4). In total across the entire study period,
238 bread was consumed the most (104 g), followed by peanuts (79 g) and cheese (75 g).

240 Discussion

241 Urban birds showed a preference for feeding on peanuts instead of cheese or bread. Peanuts
242 also attracted the highest number of bird species. This could be useful information when
243 planning supplementary feeding for increased urban biodiversity and human engagement
244 with biodiversity (Cox & Gaston 2016). Goddard *et al.* (2010) emphasise the importance of
245 urban green spaces for biodiversity, encouraging wildlife-friendly management which
246 enhances the potential of gardens and parks (see also Evans *et al.* 2009). However, only nine
247 species were observed, and a number of species were observed only rarely. From our
248 experimental design we cannot determine whether this was due to the low abundance of
249 some species in urban areas, aversion to the food types provided or a neophobic response to
250 the food delivery method (Echeverría & Vassallo 2008; Herborn *et al.* 2010). Thus, there is a
251 possibility that supplementary feeding for urban birds only benefits certain types of species
252 (e.g. granivores and/or generalists) (Chamberlain *et al.* 2009).

253 Peanuts attracted more visits in total to the feeders as well as attracting higher
254 numbers of species. Considering the high energy content of peanuts, it is economical for the
255 birds to forage on this food type, so this supports the optimal foraging theory (MacArthur
256 and Pianka 1966). Birds have been shown to selectively choose higher-energy foods in
257 earlier studies with natural food types (Glück 1985; Krebs *et al.* 1977; Willson 1971). This
258 aspect of our results indicates that this preferential selection for high quality foods also
259 occurs for urban birds feeding on human-derived foods.

260 Great Tits had a particularly strong preference for peanuts, which has been observed
261 in an earlier study (Cowie and Hinsley 1988). Blue Tits showed the same preference. On the
262 other hand, Robins and Dunnocks appeared to have no preference for any particular food
263 type, and Blackbirds selected cheese more often than any other species. Due to the variation
264 in energy content between the foods, choosing cheese appears to not support the optimal
265 foraging theory. There might be a hidden cost to selecting peanuts for these species, for
266 example due to differences in beak morphology between insectivores and seed/nut eaters
267 (Lederer 1975), they might be limited in some nutrient found mostly in cheese (such as
268 calcium or phosphorous; Reynolds & Perrins 2010), or they may be foraging sub-optimally
269 (Matsumura *et al.* 2010). Further study is needed to find the reasons behind this choice,
270 possibly looking into taste preferences in these species. Note that there were only observed
271 eleven Dunnock visits throughout the study period, so the data is less robust for this species,
272 and the trend was for them to prefer peanuts. This trend might have been significant with
273 more data.

274 It is interesting to note that a different pattern emerged when considering how much
275 food was eaten in grams. In fact, when looking at the total amount of food eaten by the
276 birds, there was more bread consumed in weight than cheese or peanuts. Considering the
277 calorie content of the food types, the total amount of food eaten across the observation
278 period equates to 448 kcal for peanuts, 276 kcal for bread, and 301 kcal for cheese. Thus, in
279 total, the birds visited the peanut feeder more often, but ate less in weight, yet ultimately
280 gained more calories from it. This means peanuts should be the optimal choice if choosing
281 only based on calories. It appears that some birds did, in fact, not forage optimally, as they
282 chose bread over peanuts. It is possible that they required more carbohydrates in their diet,

283 as white bread is high in carbohydrates, that they found it easier to digest, or that it had
284 higher palatability.

285 Our data, however, is likely confounded by the size of the bites of food provided to
286 the birds. Despite our attempts to provide equally sized bites for all food types, this was not
287 possible to completely standardise, and in practice the size of each bite of food varied, both
288 between and within each food type. Bread bites tended to be more variable in size, and it
289 could be hypothesised that the birds, when they did choose bread, chose the bigger pieces
290 so they could minimise the number of flights required, and therefore were able to visit the
291 bread feeders less often. If so, it is possible that birds received, in total, a similar amount of
292 calories from the food types – either from few trips to fetch big chunks of calorie-poor
293 bread, or many trips to fetch small bits of calorie-rich peanuts. Indeed, there are a number
294 of factors that can influence the choice of prey size, for example handling time, difficulty in
295 discriminating between sizes, and availability of prey items (see for example Krebs *et al.*
296 1977, Naef-Daenzer 2000, Turner 1982). Unfortunately, it is impossible to draw any firm
297 conclusions with our data, as we would need data on both the bite sizes and the flight
298 distances for this analysis. The implication, however, remains – providing small bites of
299 peanuts means the birds have to visit more often, and so will be more desirable if the
300 preferred outcome is to observe as many birds as possible (i.e. for recreational bird feeding
301 in gardens).

302 **Conclusions and implications**

303 In our study, birds mostly chose to forage most frequently on peanuts, the most energy-rich
304 food type. This indicates that the optimal foraging theory not only applies to captive birds

305 foraging on natural foods, but might also apply to urban birds feeding on human-derived
306 foods. This applied especially for Great Tits and Blue Tits, whereas the Blackbird appeared to
307 prefer cheese. However, overall birds consumed a higher mass of bread than other food
308 types, which could be explained by the variable bite sizes of the food provided. The most
309 robust and important conclusion from our results is that providing small bites of peanuts as
310 supplementary feeding to urban birds will attract higher numbers of individuals, as well as
311 higher numbers of species, than providing bread or cheese. Feeding peanuts will tend to
312 attract Tit species in particular, whereas cheese can be fed if the Blackbird is a desired visitor.
313 This information can be useful for the enjoyment of individual garden owners, but also be
314 useful for conservation when using supplementary feeding to increase biodiversity in urban
315 areas.

316

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324

325 **References**

- 326 Allison, S. 2007. *Backyard Birds & Bird Feeding: 100 things to know*. Mechanicsburg: Stackpole Books.
- 327 Arnold, K. E., Blount, J. D., Metcalfe, N. B., Orr, K. J., Adam, A., Houston, D. and Monaghan, P. 2007. Sex-specific
328 differences in compensation for poor neonatal nutrition in the zebra finch *Taeniopygia guttata*. *Journal*
329 *of Avian Biology* - **38**: 356-366.
- 330 Blount, J. D., Metcalfe, N. B., Birkhead, T. R. and Surai, P. F. 2003. Carotenoid modulation of immune function
331 and sexual attractiveness in zebra finches. *Science* - **300**: 125-127.
- 332 British Trust for Ornithology, BTO. 2012. *Food for thought: Feed the birds* [Online]. Norfolk: British Trust for
333 Ornithology, BTO. <http://www.bto.org/news-events/press-releases/food-thought-feed-birds>.
334 Accessed: 24/09/2014.
- 335 Brittingham, M. C., & Temple, S. A. 1986. A survey of avian mortality at winter feeders. *Wildlife Society Bulletin*
336 - **14**: 445-450.
- 337 Brotons, L. 1997. Changes in foraging behaviour of the Coal Tit *Parus ater* due to snow cover. *Ardea* - **85**: 249-
338 257.
- 339 Castro, I., Brunton, D. H., Mason, K. M., Ebert, B. and Griffiths, R. 2003. Life history traits and food
340 supplementation affect productivity in a translocated population of hihi (*Stitchbird*, *Notiomystis*
341 *cincta*). *Biological Conservation* – **114**: 271–280.
- 342 Chamberlain, D. E., Vickery, J. A., Glue, D. E., Robinson, R. A., Conway, G. J., Woodburn, R. J., & Cannon, A. R.
343 2005. Annual and seasonal trends in the use of garden feeders by birds in winter. *Ibis* - **147**: 563-575.
- 344 Chamberlain, D.E., Cannon, A.R. & Toms, M.P. Leech, D. I., Hatchwell, B. J. and Gaston, K. J. 2009. Avian
345 productivity in urban landscapes: a review and meta-analysis. *Ibis* - **151**: 1-18.
- 346 Cowie, R. J., & Hinsley, S. A. 1988. Feeding ecology of great tits (*Parus major*) and blue tits (*Parus caeruleus*),
347 breeding in suburban gardens. *Journal of Animal Ecology* - **57**: 611-626.
- 348 Cox D. T. C. & Gaston K. J. 2016. Urban Bird Feeding: Connecting People with Nature. PLoS ONE – **11**: e0158717.
349 doi:10.1371/journal.pone.0158717

350 Davies, Z. G., Fuller, R. A., Loram, A., Irvine, K. N., Sims, V., Gaston, K. J. 2009. A national scale inventory of
351 resource provision for biodiversity within domestic gardens. *Biological Conservation* - **142**: 761-771.

352 Diaz, M. 1990. Interspecific patterns of seed selection among granivorous passerines: effects of seed size, seed
353 nutritive value and bird morphology. *Ibis* - **132**: 467-476.

354 Echeverría, A.I., Vassallo, A.I., 2008. Novelty Responses in a Bird Assemblage Inhabiting an Urban
355 Area. *Ethology* - **114**: 616–624.

356 Evans, K. L., Newson, S. E. and Gaston, K. J. 2009. Habitat influences on urban avian assemblages. *Ibis*, **151**: 19-
357 39.

358 Farine, D. R., Lang, S. D. 2013. The early bird gets the worm: foraging strategies of wild songbirds lead to the
359 early discovery of food sources. *Biology letters* – **9**: 20130578.

360 Fitzpatrick, S. 1997. The timing of early morning feeding by tits. *Bird Study* – **44**: 88-96.

361 Fuller, R. A., Warren, P. H., Armsworth, P. R., Barbosa, O., & Gaston, K. J. 2008. Garden bird feeding predicts the
362 structure of urban avian assemblages. *Diversity and Distributions* – **14**: 131-137.

363 Galbraith, J. A., Stanley, M. C., Jones, D. N. & Beggs, J. R. 2016. Experimental feeding regime influences urban
364 bird disease dynamics. *Journal of Avian Biology*. Accepted Author Manuscript. doi:10.1111/jav.01076

365 Glück, E. E. 1985. Seed preference and energy intake of Goldfinches *Carduelis carduelis* in the breeding season.
366 *Ibis* – **127**: 421-429.

367 Goddard, M. A., Dougill, A. J., & Benton, T. G. 2010. Scaling up from gardens: biodiversity conservation in urban
368 environments. *Trends in Ecology & Evolution* - **25**: 90-98.

369 Grubb Jr, T. C. 1978. Weather-dependent foraging rates of wintering woodland birds. *The Auk* – **95**: 370-376.

370 Herborn, K.A., McLeod, R., Miles, W.T.S., Schofield, A.N.B., Alexander, L. & Arnold, 2010. Personality in captivity
371 reflects personality in the wild. *Animal Behaviour* - **79**: 835-843.

372 Herborn, K. A., Heidinger, B. J., Alexander, L., & Arnold, K. E. 2014. Personality predicts behavioral flexibility in a
373 fluctuating, natural environment. *Behavioral Ecology* - **25**: 1374-1379.

- 374 Jones, D. N. and Reynolds, S. J. 2008. Feeding birds in our towns and cities: a global research opportunity.
375 *Journal of Avian Biology* – **39**: 265-271.
- 376 Klasing, K. 1998. Comparative Avian Nutrition. *Cab International*: Wallingford, Oxon & New York.
- 377 Krebs, J. R., Erichsen, J. T., Webber, M. I., & Charnov, E. L. 1977. Optimal prey selection in the great tit (*Parus*
378 *major*). *Animal Behaviour* - **25**: 30-38.
- 379 Larcombe, S.D., Tregaskes, C.S., Coffey, J., Stevenson, A.E., Alexander, L., Arnold, K.E. 2008. The effects of short-
380 term antioxidant supplementation on oxidative stress and flight performance in adult budgerigars
381 *Melopsittacus undulatus*. *Journal of Experimental Biology* - **211**: 2859-2864.
- 382 Lederer, R. J. 1975. Bill size, food size, and jaw forces of insectivorous birds. *The Auk* – **92**: 385-387.
- 383 MacArthur, R. H., & Pianka, E. R. 1966. On optimal use of a patchy environment. *American Naturalist* - **100**:
384 603-609.
- 385 Mckenzie, A.J., Petty, S.J., Toms, M.P. & Furness. R.J. 2007. Importance of Sitka Spruce *Picea sitchensis* seed and
386 garden bird-feeders for Siskins *Carduelis spinus* and Coal Tits *Periparus ater*. *Bird Study* – **54**: 236-247.
- 387 Macleod, R., Gosler, A.G., Cresswell, W., 2005. Diurnal mass gain strategies and perceived predation risk in the
388 great tit *Parus major*. *Journal of Animal Ecology* - **74**: 956–964.
- 389 Mallord, J., Orsman, C., Ockendon, N., Haines, W. and Peach, W. 2010. The effects of supplementary feeding on
390 productivity and population size of urban house sparrows *Passer domesticus* - evidence from a
391 replicated field experiment across London. Wild bird care in the garden: A scientific look at large scale,
392 do-it-yourself, wildlife management, UFAW International Animal Welfare Symposium, London.
- 393 Matsumura, S., Arlinghaus, R., & Dieckmann, U. 2010. Foraging on spatially distributed resources with
394 sub-optimal movement, imperfect information, and travelling costs: departures from the ideal free
395 distribution. *Oikos* - **119**: 1469-1483.
- 396 Molokwu, M. N., Nilsson, J. Å., Olsson, O. 2011. Diet selection in birds: trade-off between energetic content
397 and digestibility of seeds. *Behavioral Ecology* – **22**: 639-647.

398 Murray, M. H., Becker, D. J., Hall, R. J., & Hernandez, S. M. 2016. Wildlife health and supplemental feeding: A
399 review and management recommendations. *Biological Conservation* – **204**: 163-174.

400 Murray, K. G., Winnett-Murray, K., Cromie, E. A., Minor, M., Meyers, E. 1993. The influence of seed packaging
401 and fruit color on feeding preferences of American robins. In *Frugivory and seed dispersal: ecological
402 and evolutionary aspects* (pp. 217-226). Springer Netherlands.

403 Myton, B. A., & Ficken, R. W. 1967. Seed-size preference in chickadees and titmice in relation to ambient
404 temperature. *The Wilson Bulletin* - **79**: 319-321.

405 Naef-Daenzer, L., Naef-Daenzer B., and Nager, R.G. 2000. Prey selection and foraging performance of breeding
406 Great Tits *Parus major* in relation to food availability. *Journal of Avian Biology* - **31**: 206-214.

407 Phipps, W. L., Willis, S. G., Wolter, K. and Naidoo, V. 2013. Foraging Ranges of Immature African White-Backed
408 Vultures (*Gyps africanus*) and Their Use of Protected Areas in Southern Africa. *Plos One* – **8**: e52813

409 Plummer, K.E., Bearhop, S., Leech, D.I., Chamberlain, D.E., Blount, J.D. 2013a. Fat provisioning in winter impairs
410 egg production during the following spring: a landscape-scale study of blue tits. *Journal of Animal
411 Ecology* – **82**: 673–682.

412 Plummer, K.E., Bearhop, S., Leech, D.I., Chamberlain, D.E., Blount, J.D. 2013b. Winter food provisioning reduces
413 future breeding performance in a wild bird. *Scientific Reports*, **3**. DOI: 10.1038/srep02002

414 R Core Development Team 2012. R: A language and environment for statistical computing. R Foundation
415 for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-375 0, URL <http://www.R-project.org/>.

416 Ramsay S. L., Houston, D.C. 1998. The effect of dietary amino acid composition on egg production in blue tits.
417 *Proc. R. Soc. Lond. B* - **265**: 1401-1405.

418 Reynolds, S. J., & Perrins, C. M. 2010. Dietary calcium availability and reproduction in birds. In *Current
419 Ornithology Volume 17* (pp. 31-74). Springer New York.

420 Rollfinke, B.F. & Yahner, R.H. 1990. Effect of time of day and season on winter bird counts. *The Condor* - **92**: 215-
421 219.

422 RSPB (Royal Society for Protection of Birds). 2009. *What food to provide*. Available at:
423 <http://www.rspb.org.uk/advice/helpingbirds/feeding/whatfood/>. Accessed 03.12.13.

424 RSPB. (Royal Society for Protection of Birds). 2012. *Household Scraps* [Online]. England: Royal Society for the
425 Protection of Birds, RSPB. Available at:
426 <http://www.rspb.org.uk/advice/helpingbirds/feeding/whatfood/scraps.aspx> . Accessed 24/09/2014.

427 SELF Nutrition Data. 2013. *Nutrition Facts: "Bread, white, commercially prepared (includes soft bread crumbs)"*.
428 Available at: <http://nutritiondata.self.com/facts/baked-products/4872/2>. Accessed 08.12.13.

429 Turner, Angela K. 1982. Optimal foraging by the swallow (*Hirundo rustica, L*): prey size selection. *Animal*
430 *Behaviour* – **30**: 862-872.

431 Willson, M. F. 1971. Seed selection in some North American finches. *The Condor* – **73**: 415-429.

432 Wingfield, J. C. and M. Ramenofsky. 2011. Hormone-Behavior Interrelationships of Birds in Response to
433 Weather - *Advances in the Study of Behavior* **43**:93-188.

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438 Table 1. Nutritional content for 100 g of unsalted peanuts, mild cheddar and white bread, used for
439 bird feeding. Nutritional data from SELF Nutrition Data; <http://nutritiondata.self.com>.

440

	Peanuts (unsalted)	Mild cheddar	White bread
Energy, kcal	567	403	266
Protein, g	25.8	24.9	7.6
Fat, total lipid, g	49.2	33.1	3.3
Carbohydrate, g	16.1	1.3	50.6
Fibre, total dietary, g	8.5	0	2.4
Sugars, total, g	4	0.5	4.3
Calcium, mg	92	721	151
Magnesium, mg	168	28	23
Phosphorous, mg	376	512	99

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444 **Figure legends**

445 Figure 1. Probability estimates for observing a bird of any species at a table with each of the food
446 types. Back-transformed estimates from the output of the GLMM model, presented with +/- 1
447 standard error.

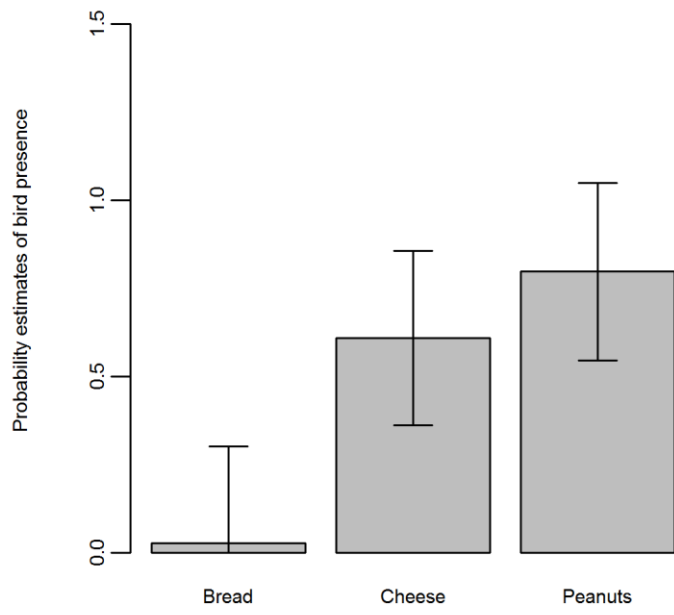
448 Figure 2. Probability estimates for observing a a) Great Tit, b) Blue Tit, c) Robin, d) Dunnock and e)
449 Blackbird at a table with each of the food types. Back-transformed estimates from the output of the
450 GLMM models, presented with +/- 1 standard error.

451 Figure 3.

452 Estimates of species richness for each of the food types. Back-transformed estimates from the GLMM
453 model, presented with +/- 1 standard error.

454 Figure 4. Mass of food consumed in grams during each observation session, for each of the three
455 food types. The bold line shows the median value, the boxes show first and third quartile, and
456 whiskers show the extreme data still within 1.5 IQR of the lower/upper quartile.

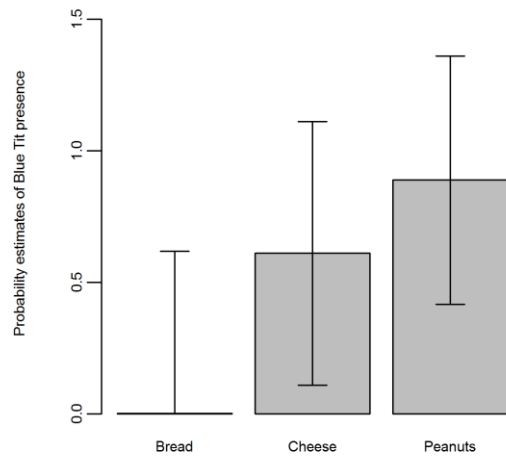
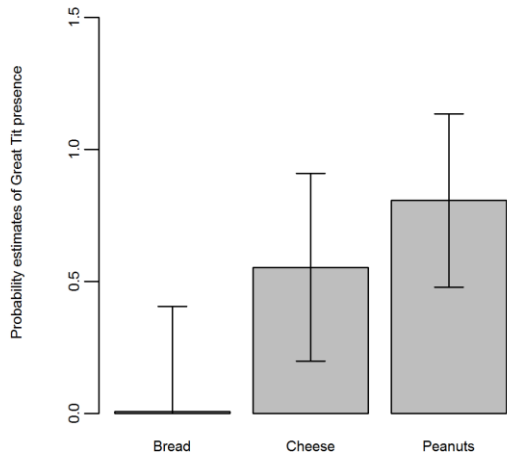
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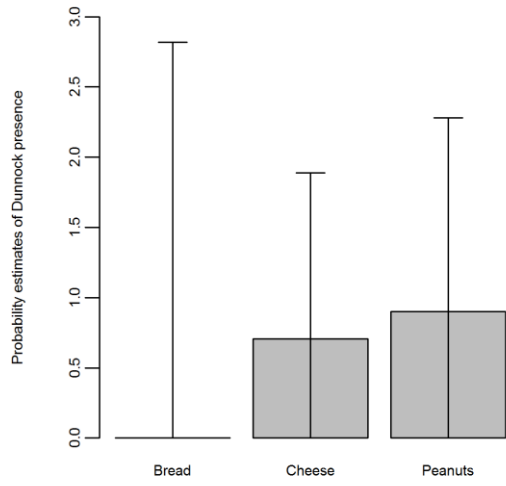
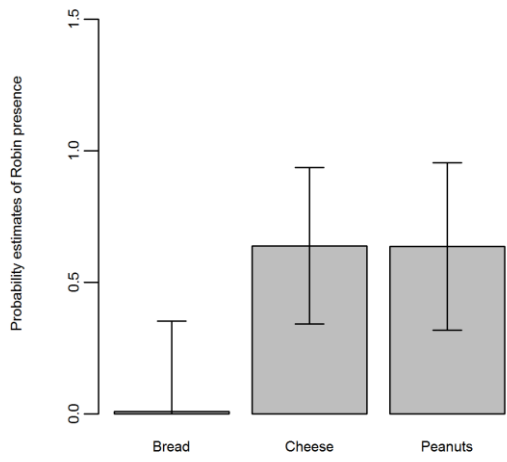
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459 Figure 1

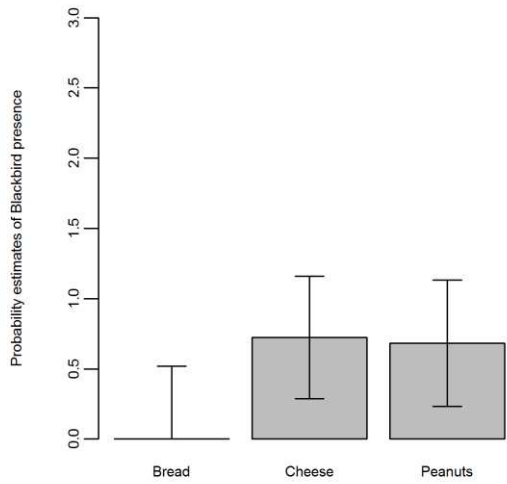
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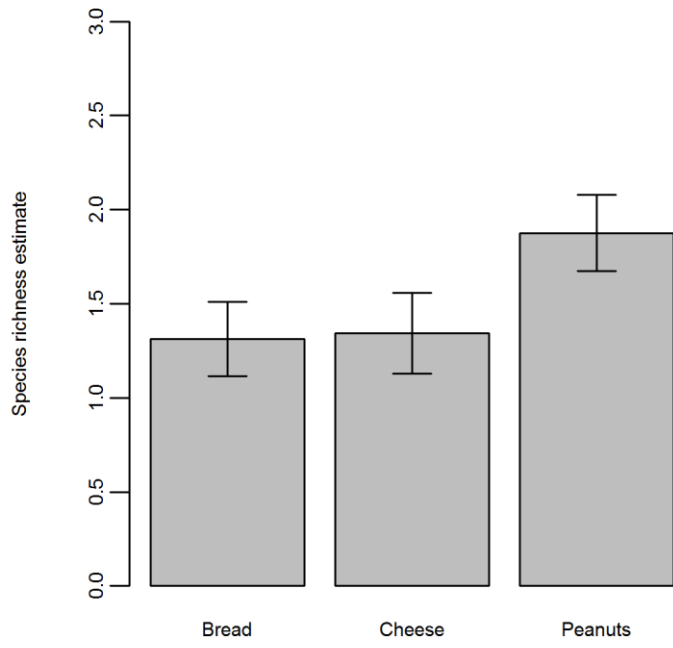
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Figure 2

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466 Figure 3