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**Article:**

Støstad, Hanna N., Aldwinckle, Phil, Allan, Andrew et al. (1 more author) (2017) Foraging on human-derived foods by urban bird species. *Bird study*. pp. 1-9. ISSN 0006-3657

<https://doi.org/10.1080/00063657.2017.1311836>

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

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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

## 317 **Acknowledgements**

318 We would like to thank G. Eastham and the Grounds Maintenance Team at the University of  
319 York. Many thanks to Sarah Hobbs for providing access to survey data on foods provided by  
320 households to wildlife. We are also very grateful to several anonymous reviewers and Dan  
321 Chamberlain for valuable help with statistics and other feedback. This research was funded  
322 by the University of York. Kathryn Arnold was funded by a Royal Society University Research  
323 Fellowship.

324

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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.

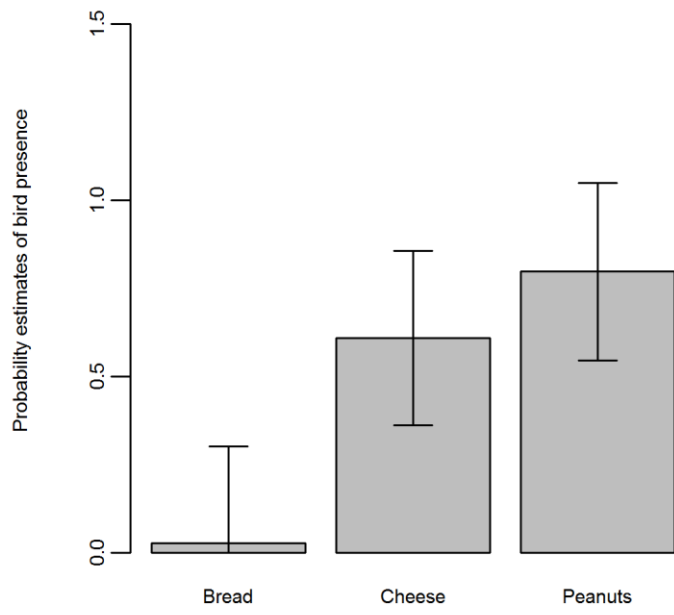
448 Figure 2. Probability estimates for observing a a) Great Tit, b) Blue Tit, c) Robin, d) Dunnock and e)  
449 Blackbird at a table with each of the food types. Back-transformed estimates from the output of the  
450 GLMM models, presented with +/- 1 standard error.

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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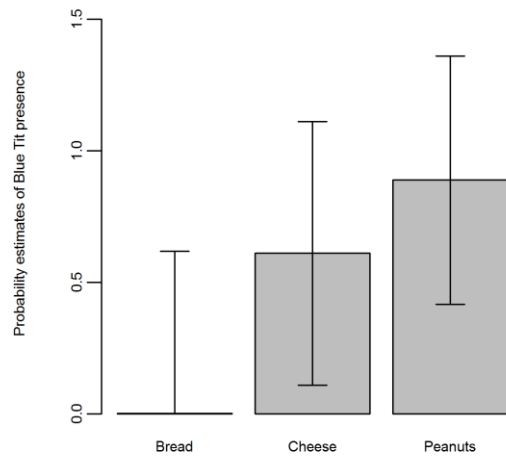
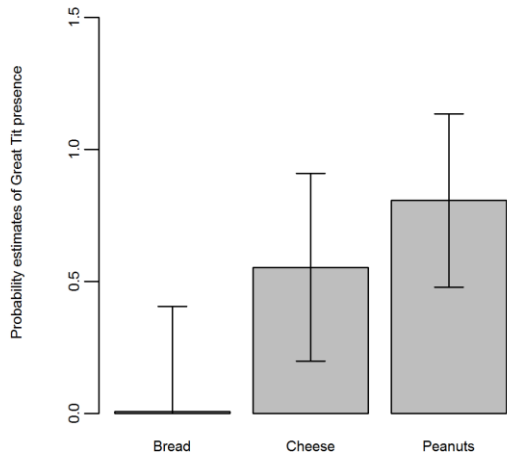


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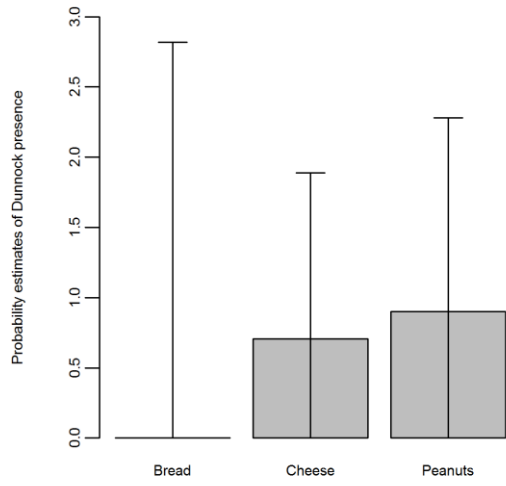
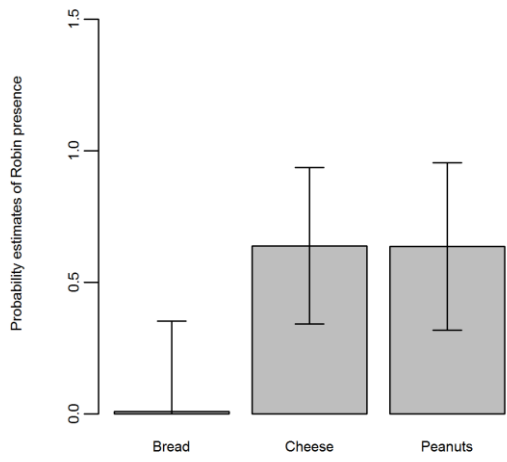
459 Figure 1

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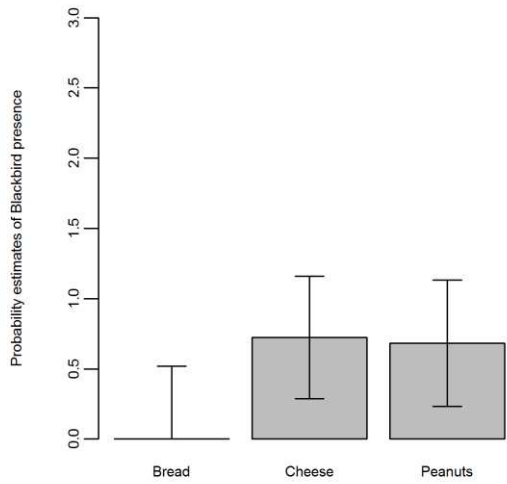




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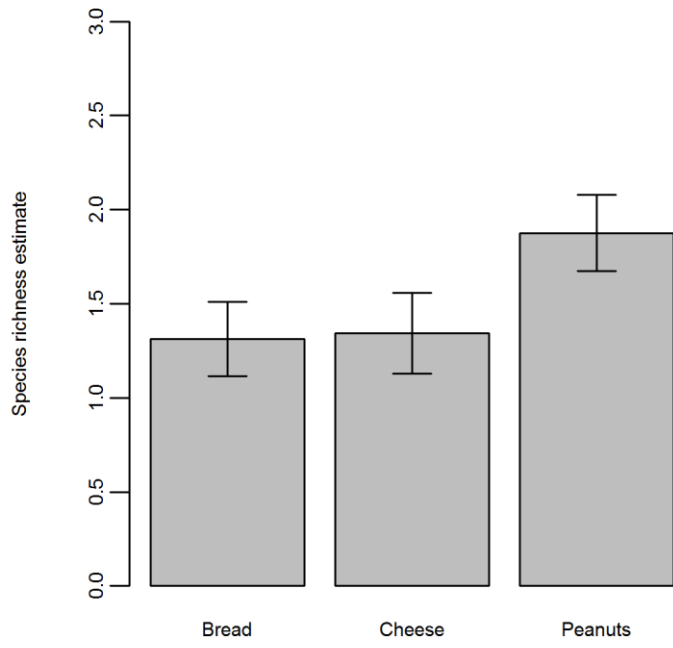
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Figure 2

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466 Figure 3