

# *Introduced grey squirrels subvert supplementary feeding of suburban wild birds*

Article

Accepted Version

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Hanmer, H. J., Thomas, R. L. and Fellowes, M. D. E. (2018) Introduced grey squirrels subvert supplementary feeding of suburban wild birds. *Landscape and Urban Planning*, 177. pp. 10-18. ISSN 0169-2046 doi: <https://doi.org/10.1016/j.landurbplan.2018.04.004> Available at <https://centaur.reading.ac.uk/76790/>

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To link to this article DOI: <http://dx.doi.org/10.1016/j.landurbplan.2018.04.004>

Publisher: Elsevier

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1            **Been caught stealing: Introduced Grey**  
2            **Squirrels subvert supplementary feeding of**  
3            **suburban wild birds**

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26           **Short running title:** Grey Squirrels and supplementary bird feeders

27           **Key words:** Garden birds, Grey Squirrel, human-wildlife interactions, supplementary feeding, urban  
28           ecology

29

30 **Abstract**

31 Providing food for wild birds is perhaps the most widespread intentional interaction between people  
32 and wildlife. In the UK, almost half of households feed wild birds, often as peanuts and seed supplied  
33 in hanging feeders. Such food is also taken by the introduced, invasive Grey Squirrel *Sciurus*  
34 *carolinensis*. Little is known of how Grey Squirrels utilise this resource and how they affect feeder  
35 use by wild birds. To assess this we recorded the numbers and time spent by animals visiting  
36 experimental feeding stations in suburban gardens, and also asked if exclusionary guards (to prevent  
37 Grey Squirrel access), food type (peanut, mixed seed), habitat and weather conditions influenced  
38 visits. Using automated cameras, we recorded 24825 bird and 8577 Grey Squirrel visits. On average  
39 >44% of the time feeders were utilised, they were being visited by Grey Squirrels. Grey Squirrel  
40 presence prevented birds from feeding at the same time (>99.99%). Feeders where Grey Squirrels  
41 were dominant were less likely to be visited by birds, even in their absence. Guards reduced Grey  
42 Squirrel use to a minimum on seed feeders, and by approximately half on peanut feeders. Squirrels,  
43 food type, guard status, habitat and rainfall all influenced bird activity and timing of feeder visits.  
44 Our work suggests that Grey Squirrels reduce the availability of supplementary food to wild birds,  
45 while gaining large volumes of food resources with corresponding benefits. Given the ubiquity of  
46 supplementary feeding, it is likely that this is an important resource for urban Grey Squirrels; feeder  
47 guards mitigate this effect.

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## 62 Introduction

63 Globally, over half of people live in urban areas (UN, 2011), rising to over 80% of national  
64 populations in countries such as the UK and USA (UNPFA, 2007). Urban areas are extremely altered,  
65 novel ecosystems, where native species face challenges and opportunities unlike any other. For birds  
66 urban ecosystems can be a place to exploit for urban adapters (Kark et al., 2007; Evans et al., 2011),  
67 in part due to the very high volumes of supplementary food (Davies et al., 2009; Orros and Fellowes,  
68 2015) provided by human residents. Conversely, urban ecosystems can be challenging, as urban  
69 areas have exceptionally high densities of predators, such as the domestic cat (*Felis catus*) (Thomas  
70 et al., 2012), and introduced competitor/predator species such as the Eastern Grey Squirrel (*Sciurus*  
71 *carolinensis*; hereafter the Grey Squirrel) (Bonnington et al., 2014b, c). Understanding the interplay  
72 between such factors and bird abundance and diversity must be an important link in our efforts to  
73 build opportunities for bird conservation in our towns and cities.

74 Urban areas generally, and in particular the surrounding suburban areas, hold large populations of  
75 many bird species (Bland et al., 2004; Cannon et al., 2005), and for some species suburbia provides a  
76 refuge for declining populations (e.g. the UK Red listed Song Thrush (*Turdus philomelos*); Gregory  
77 and Baillie 1998). Garden bird feeding is perhaps the most important way for people to engage with  
78 wildlife in many parts of the world (Cox and Gaston, 2016). Some 48% of households in Britain  
79 (Davies et al., 2009) and 53 million households in the USA feed wild birds (US Fish and Wildlife  
80 Service, 2014), providing an enormous and highly localized additional food resource (Orros and  
81 Fellowes, 2015).

82 Suburban feeding stations typically provide supplementary food for seed-eating and omnivorous  
83 passerines (Lepczyk et al., 2004; Cannon et al., 2005; Chamberlain et al., 2005). In the UK, the most  
84 common supplementary food types provided (i.e. non-table scraps) are peanuts and mixed seed,  
85 each typically provided in specialist feeders (Orros and Fellowes, 2015). Positive associations  
86 between supplementary feeding, breeding population size and reproductive success have been  
87 documented (Fuller et al., 2008; Robb et al., 2008), although this is not always so (Harrison et al.,  
88 2010; Plummer et al., 2013). Indeed, recent work in both the UK and North America suggests that  
89 supplementary feeding during the breeding season may increase local nest predation (Hanmer et al.,  
90 2017a; Malpass et al., 2017). Some species may also benefit more than others due to the suitability  
91 of food provided and relative competitive ability and adaptability of some species (Evans et al., 2009;  
92 Evans et al., 2011). Therefore, supplementary feeding may be directly and indirectly affecting the  
93 structure of urban bird communities (Galbraith et al., 2015).

94 Despite the enormous influence of supplementary food on the ecology of urban birds, we have little  
95 understanding of how this resource may be utilised by non-target species, and the consequential  
96 effects on the species the resource is intended to support. In the UK, the most visible mammal at  
97 supplementary feeding stations is the Grey Squirrel. Grey Squirrels were deliberately introduced into  
98 Great Britain on several occasions between 1876 and 1929 and elsewhere in Europe during the 20<sup>th</sup>  
99 century (Bertolino et al., 2008). In Britain, the Grey Squirrel is common in urban areas (Baker and  
100 Harris, 2007; Bonnington et al., 2014c), and is spreading rapidly from introductions in other parts of  
101 Europe (Bertolino et al., 2008). Grey Squirrels are considered to be a significant conservation threat,  
102 particularly to the native Red Squirrel (*Sciurus vulgaris*) (Bertolino et al., 2014). Grey Squirrels carry  
103 disease (squirrelpox, Bruemmer et al. 2010; *Borrelia burgdorferi*, the agent of Lyme disease, Millins  
104 et al., 2015, Millins et al., 2016), and cause economic losses in forestry (Mayle and Broome, 2013). In  
105 the context of this work, evidence suggests that urban Grey Squirrel population size and density is  
106 associated with the provision of supplementary food in gardens (Bowers and Breland, 1996; Parker  
107 and Nilon, 2008) and there is some evidence that they can competitively exclude birds at

108 supplementary feeders (Hewson et al., 2004; Bonnington et al., 2014a). Bonnington et al. (2014a)  
109 used taxidermied Grey Squirrels on feeders, and showed that resource use by birds was reduced by  
110 98% in the presence of a mounted animal. However, we have no quantitative data on how the  
111 presence of live Grey Squirrels affects feeder usage by garden birds, nor how much of the food  
112 provided is taken by the squirrels. This is crucial, as the Grey Squirrel is both a competitor for  
113 supplementary resources and a nest predator, and so may locally directly and indirectly affect the  
114 breeding success of some native bird populations (Newson et al., 2010; Bonnington et al., 2014b;  
115 Hanmer et al., 2017a).

116 Furthermore, a highly conservative estimate suggests that enough supplementary food is provided  
117 in the UK (Orros and Fellowes, 2015) to support a Grey Squirrel population around four times the  
118 estimated 2.5 million individuals found in the country (Battersby, 2005). What is not understood is  
119 how much supplementary food is actually taken by Grey Squirrels. It is thought that Grey Squirrels  
120 typically spend considerable periods of time using supplementary feeders (Pratt, 1987), but no  
121 published study to our knowledge has attempted to quantify this experimentally using live wild  
122 animals over a prolonged period or considered how this affects feeder use by different urban bird  
123 species.

124 Nevertheless, while data are lacking, both purchasers and manufacturers of feeding stations have  
125 recognised that Grey Squirrels may be consuming food intended for birds, so specialised feeders and  
126 feeder guards are produced to counter this. Typically, standard feeders are surrounded by guards to  
127 prevent access by squirrels and other large species such as corvids and invasive parakeets (Antonov  
128 and Atanasova, 2003; Sorace and Gustin, 2009). Such guards should decrease the food taken by Grey  
129 Squirrels and thus their negative impact on supplementary feeder usage by target birds (Bonnington  
130 et al., 2014a; Hanmer et al., 2017a). Furthermore, if the presence of Grey Squirrels reduces resource  
131 intake rates by birds (Bonnington et al., 2014a), we may expect to see a behavioural response to  
132 their presence. We speculate that excluded species may respond to high levels of Grey Squirrel  
133 presence by altering the timing of their visits to established supplementary feeding stations, thus  
134 extending foraging opportunities or utilising alternative food sources.

135 We have little understanding of how providing food may be unintentionally affecting the very  
136 species people wish to support due to the use of feeding stations by non-target species, such the  
137 invasive Grey Squirrel. Here, we report the results of a manipulative field experiment in suburban  
138 gardens using live birds and Grey Squirrels for the first time. The objectives were to investigate a)  
139 how Grey Squirrel presence affected the rate and timing of feeder use by garden birds, and whether  
140 this interaction was altered b) by the type of food resource provided (peanuts or mixed seed) or c)  
141 the presence of a feeder guard. Furthermore, we examine how these overall patterns of feeder  
142 utilisation were influenced by d) local (urban) habitat or e) weather conditions.

143

## 144 **Methods**

### 145 **Study Area**

146 This study was conducted in the suburbs of the large urban district centred on Reading, South East  
147 England. Greater Reading covers approximately 72 km<sup>2</sup> and has a population of ~290 000 people  
148 (Office for National Statistics 2013). The eastern suburbs of Lower Earley and Woodley where  
149 fieldwork was carried out have human populations of 32,000 and 35,470 individuals respectively.

### 150 **Individual Site Selection**

151 To represent typical suburban residential areas in the southern UK, twenty study areas of  
152 predominately detached/semi-detached houses at least 500 m apart and >100 m away from any  
153 patches of natural or public urban green space (such as parks and playing fields) were selected. One  
154 volunteer participant who already fed birds regularly using bird feeders was recruited in each of the  
155 20 areas. Areas selected were broadly similar in terms of local habitat availability, with housing  
156 densities of ~10 households/ha and 30-50 % constructed surfaces, with garden sizes of 100-200 m<sup>2</sup>.

### 157 **Study Design**

158 Experimental work was carried out between 4 September and 30 November 2014. A paired peanut  
159 and two port seed feeder (CJ Wildlife small defender feeders, Shrewsbury, UK) on the same feeder  
160 stand was placed in each of the 20 volunteer back gardens. Food supplied was the Hi-Energy No  
161 Mess Seed Mix (c.550 calories per 100g) and Premium Whole Peanuts (c.560 calories per 100 g) from  
162 CJ Wildlife (Shrewsbury UK). Feeding stations were placed ca. 2 m clear from garden boundaries and  
163 vegetation cover, and the feeders were within 0.5m of each other at least 10 days before the start of  
164 data recording to allow animals to discover them. Ten gardens received a wire cage guarded (using  
165 individual CJ Wildlife small feeder guardian cages) pair of feeders to exclude Grey Squirrels and other  
166 large animals (locally these are primarily Eurasian Magpies (*Pica pica*), Western Jackdaws (*Corvus*  
167 *monedula*) and Great Spotted Woodpeckers (*Dendrocopus major*)) and ten received a pair of  
168 identical but unguarded feeders. No other feeders or artificial food sources were present in the  
169 study gardens during this period. Feeders may have been present in adjacent gardens, but all were  
170 at least 20 m distant and were believed to be similar across the sites. Feeder visitors were recorded  
171 using an infra-red motion triggered camera trap (Ltl Acorn 5310; Ltl Acorn Inc, Wisconsin, USA)  
172 which could record visits to both feeders at the same time. The camera was set to record 10 second  
173 video clips with a one minute gap between each recording to maximise memory and battery life. The  
174 lag time between triggering movement and the camera recording was 0.6 s. Feeders were refilled up  
175 to twice a week depending on need, to ensure that feeders were never empty.

### 176 **Video processing**

177 The presence of all individuals was recorded to species for every video featuring an animal on a  
178 feeder. Feeding visits were recorded to feeders rather than to individuals as individual identification  
179 was not possible. The time spent on the feeders by every individual videoed animal was recorded to  
180 the nearest full second. Visits to each food type (peanut or seed) were recorded separately. Days  
181 where part of the data were missing, such as through the temporary loss of a feeder, view  
182 obstruction or with gaps where food was clearly missing were not included in the analyses.

### 183 **Metrological and habitat data**

184 Meteorological data for each study day was sourced from the metrological station on the University  
185 of Reading's Whiteknights campus (51°27'0N, 0°58'0W) on the edge of Lower Earley, positioned  
186 within 4.4 km of all the study gardens. Weather data for amount of rain (mm), proportion of time  
187 spent raining, maximum wind speed (m/s) and minimum and average temperature (°C) was  
188 recorded for the 24 hour period beginning 0900 GMT but for simplicity was attributed to the  
189 calendar date. Habitat data for the proportion of gardens (mixed surfaces), buildings and trees for a  
190 200m buffer around each study garden was calculated in ArcGIS 10 (ESRI 2011) as defined by land  
191 use data from the Ordnance Survey Mastermap collection (EDINA, University of Edinburgh) and  
192 distance to the closest woodland fragment (defined as a wooded area of over 400 m<sup>2</sup> in area)  
193 measured.

### 194 **Analysis**

195 All analyses were carried out within the program R version 3.4 (R Core Team, 2017). Species identity,  
196 length of time (in seconds) and time of visit was noted for every recorded feeder visit by an animal.  
197 Daily total numbers and recorded time on feeders were calculated for each individual feeder and  
198 garden for every full recording day. Individual records were pooled to create a summary for the  
199 feeder usage for each day, for every individual bird feeder, as well as an overall summary daily for  
200 each feeding station.

201 Collinearity in explanatory weather and habitat variables was assessed using variance inflation  
202 factors (VIF) with a threshold of  $VIF = 3$ , above which variables were excluded from analyses (Zuur et  
203 al., 2007). This resulted in the removal of the proportion of buildings and trees within 200m, amount  
204 of rain, maximum wind speed, and minimum and average temperature as explanatory variables. This  
205 left the proportion of habitat made up of gardens within 200m, distance to closest woodland patch  
206 (km) and the proportion of the day spent raining as factors in further analyses.

207 To examine effectors on daily visits and time spent on different types of bird feeders by birds and  
208 squirrels, Poisson distribution general linear mixed effect models (GLMMs) were performed in R  
209 package lme4 (version 1.1-12; Bates et al. 2015) with an observation-level random effect added to  
210 account for high levels of over-dispersion (Harrison, 2014). Global models were constructed a priori  
211 for each individual animal usage variable. Feeding station (i.e. study garden) and observation day  
212 were included as random effects to account for repeated measures. Independent factors included in  
213 these global GLMMs were whether the feeders were guarded, food type, total proportion of  
214 recorded animal visit time made up by Grey Squirrels that day for that feeding station, the  
215 proportion of garden habitat within 200 m, the distance in kilometres to the closest patch of  
216 woodland and the proportion of the 24 hour period spent raining. To account for the various  
217 potential influences of feeder guards and food type on Grey Squirrel and bird feeder usage a three-  
218 way interaction between guard presence, food type and proportion time taken by squirrels was  
219 included. Separate models were run for both visit and time data with individual models for all birds  
220 and individual species of birds as well as the squirrels. For GLMMs considering factors affecting  
221 squirrel feeder usage this variable with the proportion of squirrel time on feeder was not included,  
222 making a two-way interaction between food type and guard status instead.

223 Following Grueber et al. (2011) each global model was then standardised prior to model selection  
224 and averaging using R package arm (version 1.9-3; Gelman et al. 2009). Relative model fit of all  
225 possible models within the relevant global models was then evaluated for each set of candidate  
226 models using  $\Delta AICc$  and Akaike weights for global models against a null model (Burnham and  
227 Anderson, 2002) using the “dredge” function in R package MuMin (version 1.15.6; Barton, 2016). As  
228 multiple models were found within two  $\Delta AICc$  of all  $AICc$  selected models, model averaging was used  
229 to produce a conditional average model with adjusted standard errors in the R package MuMin  
230 (Barton, 2016). For these average models the relative importance of each term (including  
231 interactions) was automatically calculated as a sum of the Akaike weights over all of the models in  
232 which the term appears (Barton, 2016).

233 Examination of the data showed that due to variation between gardens in animal visiting rates, it  
234 was not possible to directly test if there was also reduction in bird visits in the *absence* of Grey  
235 Squirrels. Therefore we grouped feeders into low ( $\leq 50\%$ ) and high ( $> 50\%$ ) Grey Squirrel use. Mann-  
236 Whitney U tests were carried out to compare the mean daily number of overall birds visiting and the  
237 mean daily total time spent on feeders by birds between feeders with high and low Grey Squirrel  
238 use.



239 To explore the effect of guarding feeding stations on the timing of the first feeding first in a day  
240 Mann-Whitney U tests were carried out within species and for birds overall. To account for changes  
241 in day length, time of first visit was converted to hours from sunrise. Spearman's rank correlation  
242 was then used to test for any significant correlations between Grey Squirrel feeder usage and bird  
243 visit timing. To account for multiple comparisons made between species, p was automatically  
244 adjusted to account for the false discovery rate.

245

## 246 **Results**

247 A total of 24825 individual bird (of 16 species) and 8577 individual squirrel visits were recorded,  
248 totalling 128473 and 77178 recorded seconds respectively across 881 recording days. Accounting for  
249 camera errors and other data loses, 19 gardens and 38 bird feeders were each monitored for a mean  
250 of 48 days (median = 45, range = 17 – 80). Blue Tits (*Cyanistes caeruleus*), Great Tits (*Parus major*)  
251 and Grey Squirrels combined accounted for the majority of feeder usage across all feeder types  
252 (Figure 1).

### 253 **Determinants of feeder usage**

254 In addition to bird visits overall, and Grey Squirrel visits, Blue Tit, Coal Tit (*Periparus ater*), Dunnock  
255 (*Prunella modularis*), Great Tit, Eurasian Nuthatch (*Sitta europaea*) and European Robin (*Erithacus*  
256 *rubecula*) produced converging models for recorded visits allowing model averaging to take place.  
257 Models using daily time on feeders are included in STable 1 and STable 2.

#### 258 *Food type*

259 Seed feeders received more overall daily bird visits than peanut feeders (Table 1). All individual bird  
260 species examined were also more likely to visit seed feeders (Table 2), though the difference varied  
261 with Blue Tits showing little difference compared to the other species and unlike all other bird  
262 species they spent more time on peanut feeders (STable 2). In comparison, Grey Squirrels favoured  
263 peanut feeders (Table 1).

#### 264 *Guard status*

265 Unguarded feeders received considerably more overall bird visits than guarded feeders (15663 and  
266 9162 visits respectively) and were associated in the models overall with an increased number of  
267 birds visiting feeders (Table 1), and increased numbers of Blue Tit, Dunnock and Robin visits (Table  
268 2). Coal Tit, Great Tit and Nuthatch showed increased visits rates at guarded feeders, although in the  
269 case of Great Tit the effect was negligible (Table 2). Guarding did reduce the number of Grey Squirrel  
270 visits (Table 1). This suggests that it was an effective exclusionary method against Grey Squirrels, but  
271 also some species of birds were discouraged from visiting by the use of feeder guards (Table 1; Table  
272 2).

#### 273 *Feeder usage by Grey Squirrels*

274 Increased Grey Squirrel usage of feeders was associated with reduced visits by birds overall (Table 1,  
275 Figure 2). Similarly, this was associated with a decrease in Blue Tit, Coal Tit, Great Tit and Robin  
276 feeder visits (Table 2), indicating an exclusionary effect. However, Grey Squirrel usage was positively  
277 associated with Dunnock visits and showed no influence on Nuthatches (Table 3) suggesting that  
278 Grey Squirrels had no or little direct effect on their use of feeders or that other factors such as food  
279 and habitat are more important in driving their use of feeders.

280 *Interactions between food type, guard status and Grey Squirrel use of feeders*

281 The interactions between Grey Squirrel feeder usage and food type for Blue Tit, Coal Tit and  
282 Dunnock were positive, which may reflect an increased preference for seed feeders with increased  
283 Grey Squirrel presence (Table 2). Great Tit and Nuthatch showed the opposite pattern (Table 2),  
284 which may be a negative response to the increased presence of Grey Squirrels. There were negative  
285 interactions between Grey Squirrel feeder usage and guard type with Dunnock and Nuthatch (Table  
286 2), suggesting displacement by Grey Squirrels from unguarded feeders. For Grey Squirrel visits, the  
287 interaction between seed feeders and unguarded feeders was also positive (Table 1), suggesting that  
288 Grey Squirrels were associated with unguarded rather than guarded seed feeders. Likewise, Robin  
289 showed a similar positive significant association with a preference for unguarded seed feeders (Table  
290 2) whereas Dunnock, Great Tit and Nuthatch showed the opposite relationship indicating a  
291 preference for unguarded seed feeders over guarded seed feeders (Table 2), although for Dunnock  
292 the effect was small. Between food type, guard status and Grey Squirrel usage there was a negative  
293 three-way interaction for Dunnock (Table 2) indicating unguarded feeders discourage them, possibly  
294 due to the presence of Grey Squirrels. This three-way interaction was positive with Nuthatch,  
295 suggesting a preference for seed and guarded feeders regardless of the presence of Grey Squirrels  
296 (Table 2).

297 *Habitat*

298 The proportion of gardens within 200m was negatively associated with overall bird visits (Table 1),  
299 and specifically for Blue Tit, Dunnock, Great Tit, Nuthatch and Robin visits (Table 2) suggesting the  
300 increased availability of alternative food sources in the local area leads to a smaller concentration of  
301 these species at feeders. Grey Squirrel and Coal Tit were positively associated with garden habitat  
302 availability, suggesting they preferred garden habitats (Table 1 and 2). Increased distance from  
303 woodland was associated with increased bird visits overall (Table 1) and for species, increased Blue  
304 Tit, Great Tit and Nuthatch visits (Table 2). However, increased distance from woodland was  
305 associated with reduced Grey Squirrel ( $F = -3.46$ ; Table 1) as well as Coal Tit, Dunnock and Robin  
306 visits (Table 2). This suggests that some species are more reliant than others on woodland patches  
307 and may suggest that birds moving further away may be seeking to avoid competition by Grey  
308 Squirrels, with the pattern found in birds overall driven by Blue and Great Tit as the commonest bird  
309 species recorded.

310 *Rainfall*

311 Rain was a minor negative predictor of overall bird visits (Table 1) and specifically for Blue Tits, Great  
312 Tit, Nuthatch and Grey Squirrel visits (Table 1 and Table 2) while it had a small positive effect on  
313 Robin visits (Table 2), suggesting that while rain could affect feeder usage, this was relatively  
314 unimportant compared to the other variables considered.

315

316 **Influence of Grey Squirrel feeder dominance on bird usage**

317 Grey Squirrels were dominant (present >50% of the recorded overall usage time) on five of the 19  
318 feeding stations. Significantly fewer birds visited feeders daily on average where Grey Squirrels were  
319 dominant, indicating that even when they were absent the numbers of birds using feeders heavily  
320 frequented by them was depressed ( $W = 13$ ,  $p = 0.044$ ). Birds also spent significantly less daily time  
321 on average on Grey Squirrel dominated feeders ( $W = 12$ ,  $p = 0.034$ ).

322

### 323 **Squirrel presence and timing of first visit to feeders**

324 Blue Tits and Robins arrived first to feeders earlier in the day with increasing time present on feeders  
325 by Grey Squirrels ( $r_s = -0.09$ ,  $p = 0.036$  and  $r_s = -0.10$ ,  $p = 0.044$  respectively), while Great Tits,  
326 European Greenfinches (*Chloris chloris*) and House Sparrows (*Passer domesticus*) arrived later ( $r_s =$   
327  $0.14$ ,  $p = 0.002$ ;  $r_s = 0.27$ ,  $p = 0.018$ ;  $r_s = 0.32$ ,  $p = 0.004$ ; respectively). Birds overall, Grey Squirrel and  
328 Blue Tit were found to make their first visit in a day significantly earlier to unguarded feeding  
329 stations than guarded whereas Coal Tit, Greenfinch (albeit non-significant), House Sparrow and  
330 Long-tailed Tit (*Aegithalos caudatus*) showed the opposite pattern (Figure 3). Only 147 visits (0.044%  
331 of all visits) by all animal types were recorded before sunrise.

332

### 333 **Discussion**

334 The presence of Grey Squirrels on bird feeders in our study system reduced both absolute numbers  
335 and length of time birds spent accessing supplementary food, confirming anecdotal and past indirect  
336 experimental evidence (Bonnington et al., 2014a). The presence of a Grey Squirrel effectively  
337 excluded all birds from a feeding station, and at our study sites they were present on average for  
338 44.3% of the recorded total feeding time on unguarded feeding stations during a day. This is a  
339 minimum value, as video clips were limited to 10 seconds per minute, and in contrast to Grey  
340 Squirrels, most bird species spent much less than this time per visit (Figure 4). Grey Squirrels and  
341 most bird species were more often associated with unguarded feeders. More birds were recorded  
342 using seed feeders, but Grey Squirrels preferred peanut feeders. Grey Squirrels and most bird  
343 species were less likely to use feeders on days with increased rainfall. The response to habitat was  
344 mixed with Grey Squirrels and several bird species less likely to use feeders that were further away  
345 from woodland patches while the commonest bird species (Blue Tit and Great Tit) were more likely  
346 to use them when closer to woodland patches. Intriguingly, increased feeder use by Grey Squirrels  
347 was associated with changes in the start of feeding for several bird species, suggesting that they  
348 were altering their foraging behaviour in response to these species. Together, we show that Grey  
349 Squirrels are dominant at bird feeders, reduce food availability to target bird species, and that  
350 visiting birds may alter their patterns of feeder use to compensate for reduced feeding  
351 opportunities.

352 Grey Squirrels effectively prevent small birds from accessing feeders while present, and overall most  
353 species studied showed a reduction in numbers using feeders associated with an increase in feeder  
354 use by Grey Squirrels. Only 10 cases were recorded (<99.99% of records) of a bird (all either Blue Tit  
355 or Great Tit) taking food while a squirrel was present at a feeding station and never when two  
356 squirrels were present. Furthermore, the reduction in overall bird activity on feeders dominated by  
357 Grey Squirrels in addition to increasing Grey Squirrel usage suggests that not only is the time  
358 available for birds to feed reduced, but also that the effect lasts longer than individual squirrel visits  
359 to feeders. It is worth speculating on what this means in terms of Grey Squirrel energy consumption  
360 at feeding stations. Taking the estimated energy supplied per garden per day for UK from Orros and  
361 Fellowes (2015) which was a median of 628 kcal/day and a minimum provisioning of 101 kcal/day  
362 (assuming all food was consumed and ignoring food type differences), and making the highly  
363 conservative assumption that all species feed at the same rate, then a median of 278 kcal/day (45  
364 kcal/day minimum) of food intended for wild birds is being taken by Grey Squirrels at unguarded  
365 feeders in this experimental system. While by necessity this is simply an estimate, this suggests that  
366 such feeder use alone could support the average daily energy requirements (137 kcal/day) of two  
367 adult Grey Squirrels (Harris and Yalden, 2008; Orros and Fellowes, 2015). At guarded feeding stations

368 Grey Squirrels were largely but not entirely excluded, as they were sometimes able to access food  
369 though the top of the guarded bird feeders. This shows that feeder guards are an effective means of  
370 reducing the volume of food taken by unintended beneficiaries (Orros and Fellowes, 2015).

371 Nevertheless, while the use of guards did reduce competition with small birds by Grey Squirrels. In  
372 absolute numbers small birds preferentially visited unguarded feeders, suggesting that guards may  
373 also discourage them to an extent. Only Dunnock showed a preference for guarded feeders, with all  
374 other species showing no preference. This suggests that while garden owners can reduce the volume  
375 of food taken by species such as Grey Squirrels, this may come at a cost in terms of reduced use of  
376 guarded feeders by small birds. We speculate that this may be a result of the feeder guards  
377 presenting a barrier to escape or delaying predator detection (Devereux et al., 2006; Cresswell et al.,  
378 2009), increasing the risks associated with using the feeders.

379 The use of baffles designed to stop Grey Squirrels from being able to access feeders may offer an  
380 alternative means of reducing access of squirrels to food, while not restricting or discouraging bird  
381 access. However, such feeding equipment will still allow other potential competitors and nest  
382 predators such as corvids (Hanmer et al., 2017a) to access food. Feeders which are capable of  
383 excluding animal access to food based on weight avoid this problem, but the increased costs  
384 involved in purchasing such exclusionary feeders may greatly discourage members of the public from  
385 using them, although the greater cost may be offset by the reduced volumes of food taken by larger  
386 feeder users with higher energy requirements (Orros and Fellowes, 2015).

387 We have some evidence that birds may alter their daily first visiting times in response to local rates  
388 of feeder use by Grey Squirrels, showing similar patterns to those seen with increased activity of  
389 hawks (Roth and Lima, 2007). Blue Tits and Robins arrived to feeders earlier and Great Tits,  
390 Greenfinches and House Sparrows arrived later with increasing use of feeders by Grey Squirrels. The  
391 two species arriving earlier may be showing a behavioural response where they attempt to feed  
392 before the arrival of Grey Squirrels to feeders and so avoid exclusion from the resource by extending  
393 their potential feeding time. The three species arriving later may be unable to adapt in this way or  
394 are utilising other resources first instead to account for this exclusion. Guarded feeding stations also  
395 significantly altered the timing of first visit for several species. Blue Tits and Greenfinches as well as  
396 birds overall arrived significantly earlier to feed on unguarded feeders. Conversely, Coal Tits, House  
397 Sparrows and Long-tailed Tits arrived earlier on guarded feeders. When feeders are guarded and  
398 therefore larger animals excluded, there may therefore be less need to adjust feeding behaviour to  
399 avoid exclusion by these larger competitors.

400 Sites were purposefully selected to be broadly similar in local habitat and garden size. However, local  
401 habitat did influence both bird and Grey Squirrel supplementary feeder usage. For Grey Squirrel,  
402 birds overall and most bird species examined (with the exception of Coal Tit), an increasing  
403 proportion of garden habitat within 200m of a feeding station was negatively associated with feeder  
404 usage, suggesting that where alternative food sources were available, these were increasingly used.  
405 Feeder usage by Grey Squirrels and several bird species declined with increasing distance from  
406 nearest woodland patch. These woodland patches are likely to provide resting sites and enemy free  
407 space given domestic cat roaming behaviour (Thomas et al., 2014; Hanmer et al., 2017b). This  
408 suggests that feeding stations in urban areas further away from woodland patches may be more  
409 available to small birds due to fewer Grey Squirrels being present, as suggested by the increased  
410 feeder visits by Blue Tit and Great Tit in gardens further away from woodland patches, although bird  
411 numbers may still be depressed at supplementary feeding stations in more highly urbanised areas  
412 even in the absence of this competition (Chace and Walsh, 2006; Tratalos et al., 2007; Bonnington et  
413 al., 2014b).

414 The autumn of 2014 was relatively mild with no frosts, snow or extreme weather events recorded  
415 during the monitoring period so it was unsurprising that no influence of temperature or wind speed  
416 was found on bird visits or length of time on feeders. However, increased rain duration depressed  
417 both bird and Grey Squirrel feeding activity to some extent. These results conflict with Cowie and  
418 Simons (1991) who found wind but not rain to be related to feeding activity and Zuckerberg et al.  
419 (2011) who found precipitation (including snowfall) to be associated with increased winter feeder  
420 usage in some North American passerines.

421 Perhaps it is worth thinking of the relationship between the garden owners who provide  
422 supplementary food and the garden birds who feed on that food as a mutualism, where in exchange  
423 for food resources, birds provide pleasure and perhaps even health benefits to the many millions of  
424 people who feed them (Cox and Gaston, 2015, 2016; Cox et al., 2017). In this context, Grey Squirrels  
425 take food from the intended beneficiaries, with the longer term consequence of benefitting Grey  
426 Squirrel population growth. However, it should also be noted that many people in the UK have  
427 positive attitudes towards Grey Squirrels, purposefully allowing them to benefit from supplementary  
428 food (Rotherham and Boardman, 2006). Irrespective of motivation, we suggest that the use of bird  
429 supplementary feeding stations by Grey Squirrels leads to both reduced availability of food for  
430 garden birds, and potentially increases the rate of local nest predation in the breeding season  
431 (Hanmer et al., 2017a). Furthermore, this may contribute to the success of Grey Squirrels as their  
432 range expands and further comes into conflict with forestry and Red Squirrel conservation efforts in  
433 the UK. People can use guarded feeders as a counter-measure, but at the cost of possibly reducing  
434 feeder use by most garden birds. Despite this, we suggest that given the potential direct and indirect  
435 consequences of unintentionally providing very large volumes of supplementary food to Grey  
436 Squirrels, it would be wise to provide supplementary food in a manner which limits access to this  
437 invasive species.

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587 **List of tables**

588 Table 1. Standardised average Poisson generalized mixed effect models of effectors on recorded  
589 visits on peanut and seed feeders at unguarded and guarded feeding stations for total birds and  
590 Grey Squirrels with all models converging within delta 2 AICc of their respective minimal models.  
591 Where: Feeding station identity and study day were random effects, Food = food type (peanut set to  
592 intercept), Guard = guard status (guarded set to the intercept), Distance = distance to closest  
593 woodland patch, Garden% = the proportion of habitat made up by gardens within 200 m, Rain% =  
594 the proportion of the day spent raining and ‘:’ indicates an interaction term between covariates.  
595 Both Null models had  $\Delta AICc > 50$  and model weights  $\leq 0.001$ . Relative importance indicates the  
596 relative importance of the covariate across the models within  $\Delta 2 AICc$  of the AICc selected model, as  
597 a sum of the Akaike weights over all of the models in which the term appears and N indicates the  
598 number of models the covariate featured in.

599 Table 2. Standardised average Poisson generalized linear mixed effect models for daily recorded  
600 visits on peanut and seed feeders at unguarded and guarded feeding stations for all bird species with  
601 all models converging within delta 2 AICc of their respective minimal models. All Null and Global  
602 models had delta AICcs  $> 4$  to their respective minimal models. Where: Feeding station identity and  
603 study day were random effects, Food = food type (peanut set to intercept), Guard = guard status  
604 (Guarded set to intercept), Squirrel% = daily proportion of total feeder usage by squirrels, Garden% =  
605 proportion of garden within 200 m, Rain% = Proportion of day spent raining, Distance = distance  
606 (km) to closest patch of woodland and ‘:’ indicates an interaction term between covariates. Relative  
607 importance indicates the relative importance of the covariate across the models selected for  
608 averaging, as a sum of the Akaike weights over all of the models in which the term appears and N  
609 indicates the number of models the covariate featured in.

610 **Figure legends**

611 Figure 1. Proportion of animal visits and time as metrics of bird feeder usage for the different types  
612 over the course of the study. N = 426 and 454 total observation days for guarded and unguarded  
613 supplementary feeding stations respectively.

614 Figure 2. Effect of Grey Squirrel feeder usage (proportion of total daily time on feeders) on a) total  
615 daily visits and b) total daily time spent on feeding stations (both feeders together). Fitted with a  
616 smoothed line of best fit with 95% confidence intervals based on locally weighted regression for  
617 illustrative purposes.

618 Figure 3. Summary of the median ( $\pm IQR$ ) time of first visit after sunrise for Grey Squirrels, all birds  
619 and all common bird species for guarded and unguarded feeding stations. Mann-Whitney test  
620 statistics are between the first visit by that species/grouping in a day to a guarded and unguarded  
621 feeding station. For P value significance: •  $p = 0.1 - 0.05$ , \*  $p < 0.01$ , \*\*  $p < 0.001$ , \*\*\*  $p < 0.0001$   
622 (adjusted using the false discovery rate).

623 Figure 4. Median ( $\pm IQR$ ) recorded individual visit time (up to 10 second videos) spent on all different  
624 types of bird feeders in the study by species with interquartile ranges.

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| Tested Model   | Variables        | Estimate | SE     | P       | Relative Importance | N   |
|----------------|------------------|----------|--------|---------|---------------------|-----|
| Birds          | Intercept        | 1.201    | 0.4416 | 0.0065  | N/A                 | N/A |
|                | Distance         | 0.5655   | 0.8891 | 0.5247  | 0.15                | 2   |
|                | Food             | 0.9682   | 0.055  | <0.0001 | 1                   | 10  |
|                | Food : Squirrel% | -0.2059  | 0.1344 | 0.1253  | 0.53                | 5   |
|                | Garden%          | -1.514   | 0.8553 | 0.0768  | 0.79                | 8   |
|                | Guard            | -0.5966  | 1.0099 | 0.5547  | 0.14                | 2   |
|                | Rain%            | -0.1102  | 0.0592 | 0.0625  | 0.83                | 8   |
|                | Squirrel%        | -0.4989  | 0.0887 | <0.0001 | 1                   | 10  |
| Grey Squirrels | Intercept        | -2.542   | 0.5031 | <0.0001 | N/A                 | N/A |
|                | Distance         | -3.462   | 1.025  | 0.0007  | 1                   | 2   |
|                | Food             | -0.8339  | 0.1603 | <0.0001 | 1                   | 2   |
|                | Food : Guard     | 2.008    | 0.326  | <0.0001 | 1                   | 2   |
|                | Garden%          | 0.2667   | 1.091  | 0.8069  | 0.27                | 1   |
|                | Guard            | 3.280    | 1.040  | 0.0016  | 1                   | 2   |
|                | Rain%            | -0.2929  | 0.1417 | 0.0388  | 1                   | 2   |

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632 Table 1

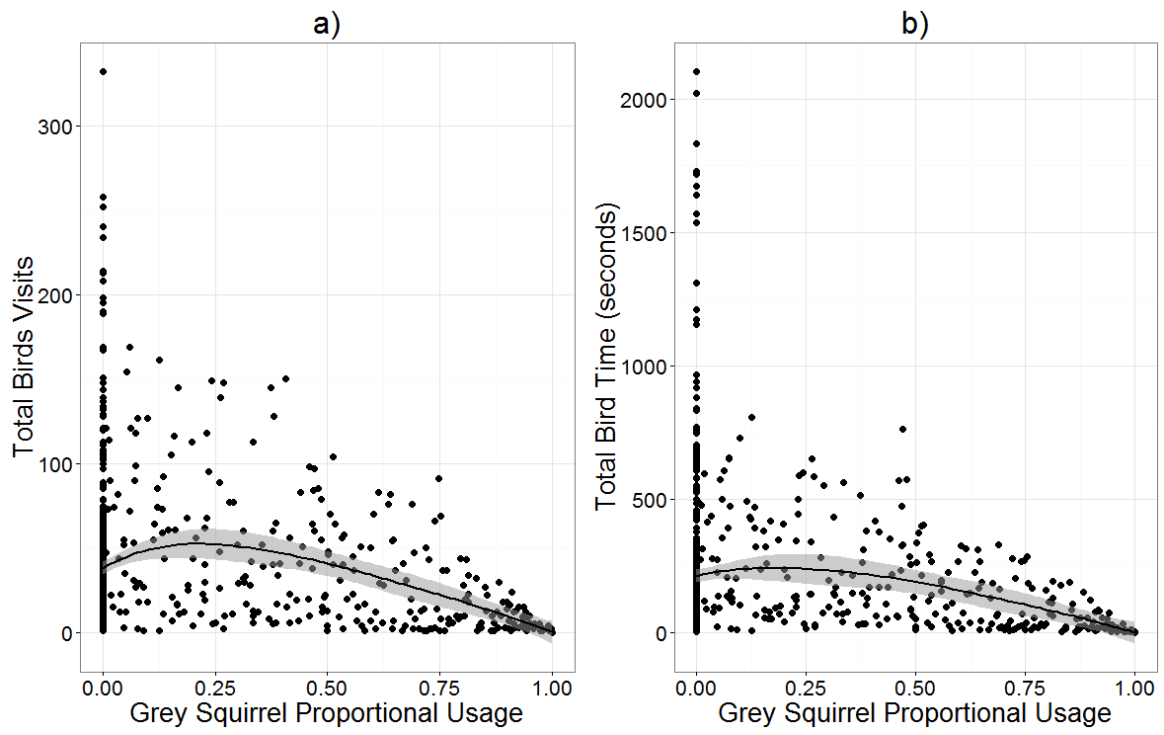
633

| Tested Model | Variables                | Estimate | Adjusted SE | P       | Relative Importance | N   |
|--------------|--------------------------|----------|-------------|---------|---------------------|-----|
| Blue Tit     | Intercept                | 0.1437   | 0.4264      | 0.7361  | N/A                 | N/A |
|              | Distance                 | 0.2533   | 0.8606      | 0.7685  | 0.15                | 1   |
|              | Food                     | 0.1393   | 0.0638      | 0.0291  | 1                   | 4   |
|              | Food : Squirrel%         | 0.3306   | 0.1584      | 0.0369  | 1                   | 4   |
|              | Garden%                  | -1.390   | 0.8320      | 0.0949  | 0.71                | 3   |
|              | Guard                    | -0.5986  | 0.9715      | 0.5378  | 0.17                | 1   |
|              | Rain%                    | -0.1568  | 0.0693      | 0.0237  | 1                   | 4   |
|              | Squirrel%                | -0.6641  | 0.1082      | <0.0001 | 1                   | 4   |
| Coal Tit     | Intercept                | -6.500   | 1.419       | <0.0001 | N/A                 | N/A |
|              | Distance                 | -1.003   | 1.958       | 0.6083  | 0.1                 | 2   |
|              | Food                     | 1.815    | 0.2103      | <0.0001 | 1                   | 14  |
|              | Food : Squirrel%         | 0.9048   | 0.6843      | 0.1861  | 0.43                | 6   |
|              | Garden%                  | 2.391    | 2.461       | 0.3312  | 0.31                | 5   |
|              | Guard                    | 3.255    | 2.430       | 0.1804  | 0.45                | 6   |
|              | Rain%                    | -0.1798  | 0.2152      | 0.4034  | 0.22                | 4   |
|              | Squirrel%                | -0.9086  | 0.3506      | 0.0096  | 1                   | 14  |
| Dunnock      | Intercept                | -8.988   | 2.267       | <0.0001 | N/A                 | N/A |
|              | Distance                 | -7.993   | 5.135       | 0.1196  | 0.73                | 2   |
|              | Food                     | 3.156    | 0.4355      | <0.0001 | 1                   | 3   |
|              | Food : Guard             | -0.0440  | 0.8551      | 0.9590  | 1                   | 3   |
|              | Food : Guard : Squirrel% | -6.214   | 1.917       | 0.0012  | 1                   | 3   |
|              | Food : Squirrel%         | 0.9480   | 0.9613      | 0.3241  | 1                   | 3   |
|              | Garden%                  | -1.087   | 2.875       | 0.7055  | 0.2                 | 1   |
|              | Guard                    | -6.874   | 4.068       | 0.0911  | 1                   | 3   |
|              | Guard : Squirrel%        | -1.915   | 1.014       | 0.0590  | 1                   | 3   |
|              | Squirrel%                | 1.587    | 0.5091      | 0.0018  | 1                   | 3   |
| Great Tit    | Intercept                | -0.3893  | 0.4776      | 0.4150  | N/A                 | N/A |
|              | Distance                 | 1.175    | 0.9455      | 0.2139  | 0.23                | 1   |
|              | Food                     | 1.806    | 0.0858      | <0.0001 | 1                   | 5   |
|              | Food : Guard             | -1.018   | 0.1723      | <0.0001 | 1                   | 5   |
|              | Food : Squirrel%         | -0.1527  | 0.2216      | 0.4907  | 0.14                | 1   |
|              | Garden%                  | -1.887   | 1.049       | 0.0721  | 0.81                | 4   |
|              | Guard                    | 0.0521   | 1.154       | 0.9640  | 1                   | 5   |
|              | Rain%                    | -0.1576  | 0.0843      | 0.0615  | 0.86                | 4   |
|              | Squirrel%                | -0.3974  | 0.1327      | 0.0027  | 1                   | 5   |
| Nuthatch     | Intercept                | -9.982   | 2.022       | <0.0001 | N/A                 | N/A |
|              | Distance                 | 0.4619   | 2.705       | 0.8644  | 0.06                | 1   |
|              | Food                     | 1.820    | 0.5892      | 0.0020  | 1                   | 11  |
|              | Food : Guard             | -0.1693  | 1.548       | 0.9129  | 0.47                | 5   |
|              | Food : Guard : Squirrel% | 9.104    | 6.035       | 0.1314  | 0.16                | 2   |
|              | Food : Squirrel%         | -2.569   | 2.912       | 0.3777  | 0.21                | 3   |
|              | Garden%                  | -2.411   | 2.804       | 0.3898  | 0.21                | 3   |
|              | Guard                    | 0.3488   | 2.658       | 0.8956  | 1                   | 11  |
|              | Guard : Squirrel%        | -3.895   | 2.155       | 0.0708  | 1                   | 11  |

|       |              |         |        |         |      |     |
|-------|--------------|---------|--------|---------|------|-----|
|       | Rain%        | -0.3605 | 0.3044 | 0.2363  | 0.34 | 4   |
|       | Squirrel%    | 0.0047  | 1.068  | 0.9965  | 1    | 11  |
| Robin | Intercept    | -2.038  | 0.4290 | <0.0001 | N/A  | N/A |
|       | Distance     | -1.062  | 0.8411 | 0.2067  | 0.4  | 3   |
|       | Food         | 3.405   | 0.1558 | <0.0001 | 1    | 7   |
|       | Food : Guard | 2.016   | 0.3018 | <0.0001 | 1    | 7   |
|       | Garden%      | -0.9463 | 0.9242 | 0.3059  | 0.26 | 2   |
|       | Guard        | -0.8267 | 0.9157 | 0.3666  | 1    | 7   |
|       | Rain%        | 0.0769  | 0.0917 | 0.4016  | 0.22 | 2   |
|       | Squirrel%    | -0.3041 | 0.1533 | 0.0474  | 0.91 | 6   |

634 Table 2

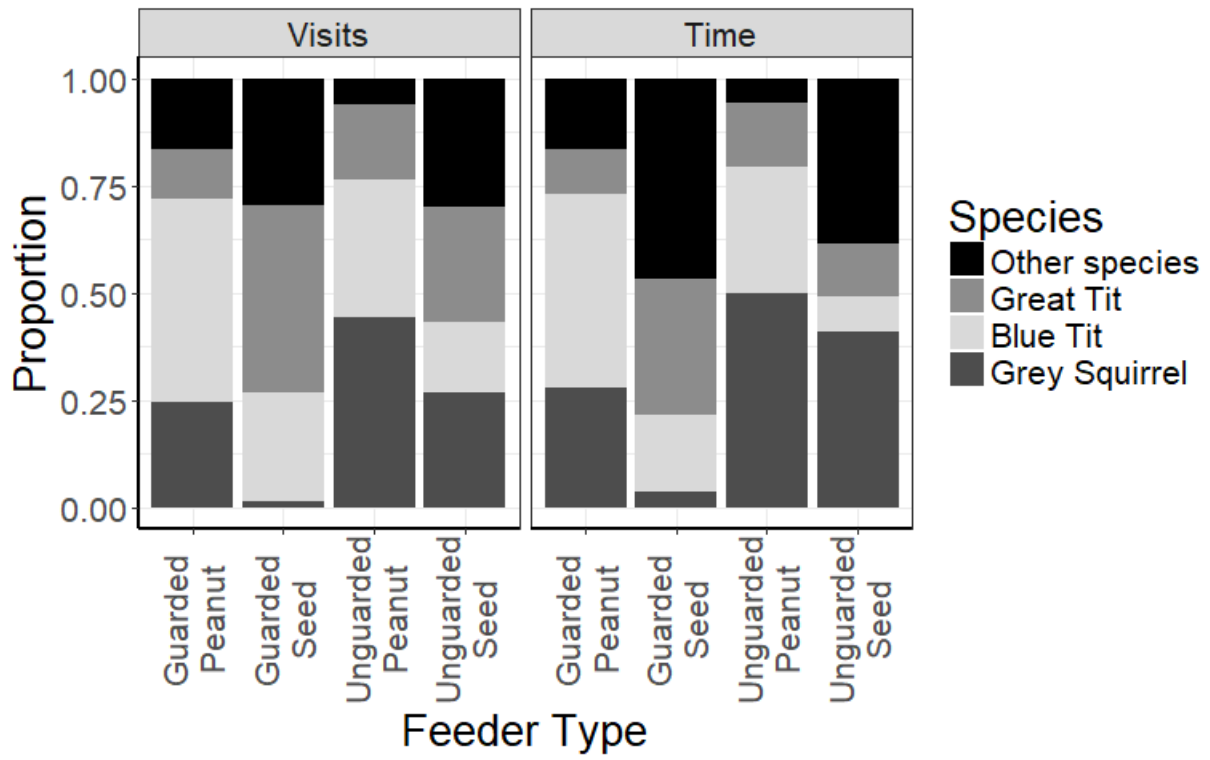
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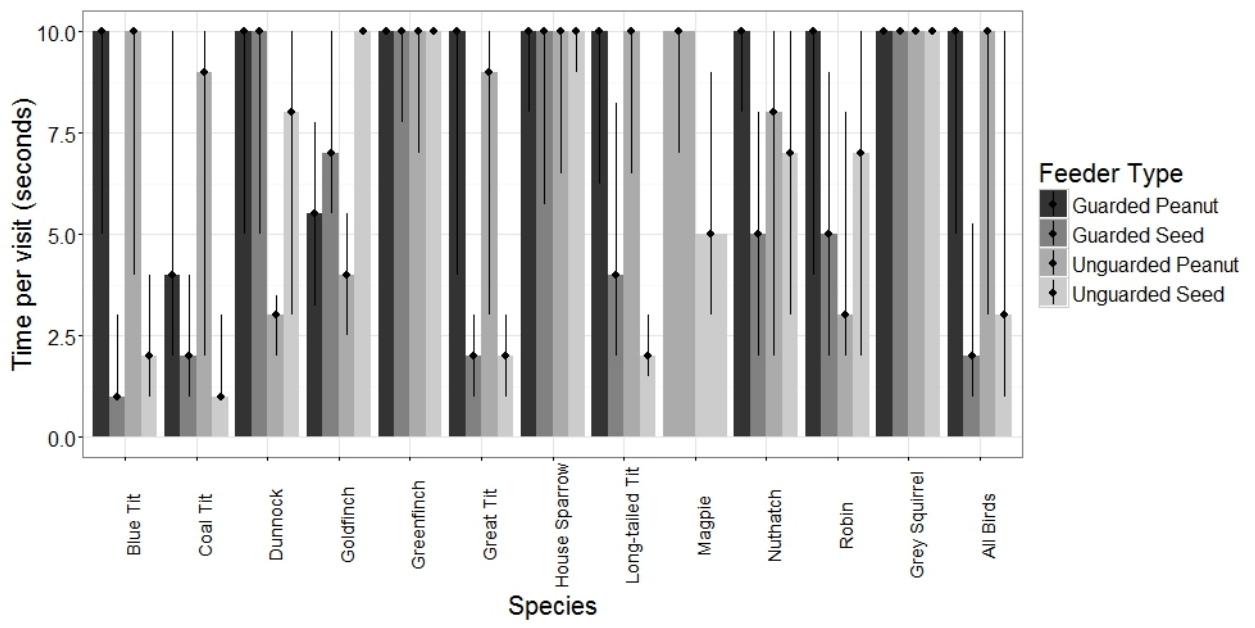
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637 Figure 1

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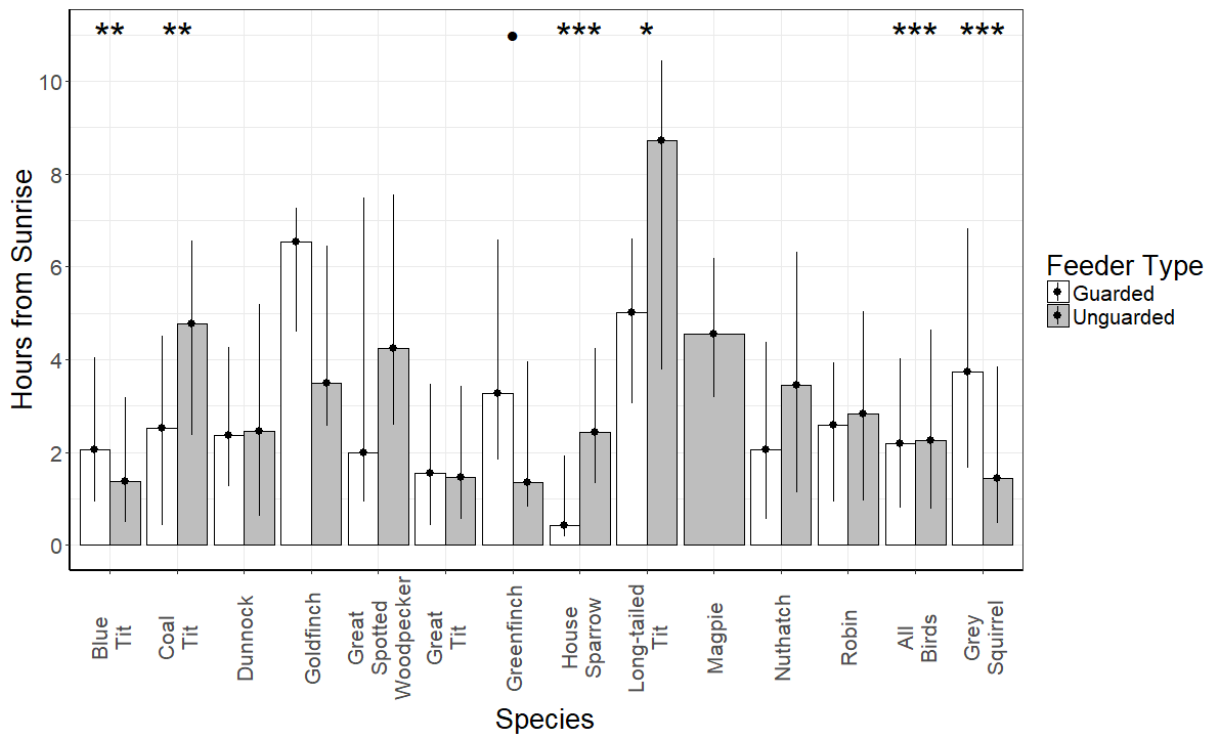


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644 Figure 3

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648 Figure 4