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Provision of supplementary food for wild birds may increase the risk of local nest predation

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17 In countries such as the UK, USA and Australia, approximately half of households provide
18 supplementary food for wild birds, making this the public's most common form of active engagement
19 with nature. Year round supplementary feeding is currently encouraged by major conservation
20 charities in the UK as it is thought to be of benefit to bird conservation. However, little is understood
21 of how the provision of supplementary food affects the behaviour and ecology of target and non-target
22 species. Given the scale of supplementary feeding, any negative effects may have important
23 implications for conservation. Potential nest predators are abundant in urban areas and some species
24 frequently visit supplementary feeding stations. We asked if providing supplementary food affected
25 the likelihood of nest predation in the vicinity of the feeder, by acting as a point attractant for potential
26 nest predators. We provided feeding stations (empty, peanut feeder, peanut feeder with guard to
27 exclude potential nest predators) in an area of suburban parkland in the UK and monitored the
28 predation rate experienced by eggs placed in artificial nests located at distances which replicate the
29 size of typical suburban gardens. Nest predators (Magpies *Pica pica*, Grey Squirrels *Sciurus
30 carolinensis*) were frequent visitors to filled feeders, and predation caused by Magpies, European Jays
31 *Garrulus glandarius* and Grey Squirrels was significantly higher when nests were adjacent to filled
32 feeders. The presence of a feeder guard did not significantly reduce nest predation. As supplementary
33 feeding is becoming increasingly common during the breeding season in suburban habitats, we
34 suggest that providing point attractants to nest predators at this time may have previously
35 unconsidered consequences for the breeding success of urban birds.

36

39

Introduction

Garden bird feeding engages more people with wildlife than any other activity. Some 48% of households in Britain (Davies *et al.* 2009) and 53 million households in the USA feed wild birds (U.S. Fish and Wildlife Service 2011), providing an enormous and highly localised additional food resource. For example, in suburban Reading, UK, over 55% of householders provide supplementary food for wild birds, two-thirds of whom feed year round (Orros & Fellowes 2015a). The majority of individuals provide peanuts, a range of seed types (e.g. sunflower, nyger, wheat) and fat to birds visiting their gardens. A conservative estimate suggests that enough food is annually provided in the UK to support over 30 million garden birds (Orros & Fellowes 2015a). This is reflected by the size of the bird feeding industry, which ten years ago was estimated to be worth £200 million *per annum* (British Trust for Ornithology 2006). This figure is likely to be considerably higher today.

Supplementary feeding in urban areas affects the abundance and distribution of species as diverse as the Red Kite *Milvus milvus* (Orros & Fellowes 2014, 2015b), hummingbirds (Hill *et al.* 1998, Courter *et al.* 2013) and the Blackcap *Sylvia atricapilla* (Chamberlain *et al.* 2005, Rolshausen *et al.* 2009, Plummer *et al.* 2015). While feeding has been shown to increase adult overwinter survival (Jansson *et al.* 1981, Brittingham & Temple 1988), effects on bird productivity are variable, and overwinter supplementary feeding has been found to both increase (Robb *et al.* 2008) and decrease (Plummer *et al.* 2013a, b) breeding success in subsequent seasons. Similarly, supplementary feeding experiments during the breeding period have found mixed results, with evidence for both decreases (Harrison *et al.* 2010) and increases (Peach *et al.* 2013, Smith & Smith 2013) in productivity. Furthermore, feeding stations may facilitate the transmission of disease (Bradley & Altizer 2007), which can lead to rapid population declines (e.g. trichomonosis in greenfinch; Robinson et al. 2010).

Urban birds tend to lay eggs earlier, have smaller clutch sizes, lower nestling weight and lower productivity per nesting attempt (Chamberlain *et al.* 2009). Open-cup nesters decline with increasing urbanisation but remain part of the avifauna (Máthé & Batáry 2015) and UK gardens hold significant populations of several such species (Bland *et al.* 2004). While food availability and habitat suitability are important limiting factors for urban bird populations (Shochat 2004, Máthé & Batáry 2015), nest

67 predation is a key cause of nest failure for open-cup nesters (Ricklefs 1969, Martin & Li 1992),

68 possibly also limiting their populations (Jokimaki & Huhta 2000). Predator densities in urban areas

69 may be higher than in rural areas for some nest predators, such as corvids (Jokimaki & Huhta 2000,

70 Antonov & Atanasova 2003, Jokimäki et al., 2005, Sorace & Gustin 2009), although it is unclear if

71 this apparent increase in potential predator density depresses prey populations (Shochat 2004, Madden

72 *et al.* 2015). Eurasian Magpies *Pica pica* and introduced Grey Squirrels *Sciurus carolinensis* are

73 common in UK urban areas and are frequent nest predators (Eaton *et al.* 2013, Bonnington *et al.*

74 2014a). Increased nest predation in an urban area is associated with increased corvid density, although

75 no association was found with grey squirrel population size (Bonnington *et al.* 2015).

76 Nest predators, such as Eurasian Magpies and Grey Squirrels, can be attracted by garden feeding

77 stations (Chamberlain *et al.* 2005, Väisänen 2008, Bonnington *et al.* 2014b). As a result, those

78 providing supplementary food can also purchase caged feeders, which aim to exclude larger species,

79 including squirrels and corvids. At a domestic garden scale the provision of bird feeders reduces the

80 local abundance of insects (Orros & Fellowes 2012, Orros *et al.* 2015), and the provision of

81 supplementary food for ungulates (Cooper & Ginnett 2000, Selva *et al.* 2014) and woodland predators

82 (Borgmann *et al.* 2013) increased local nest predation. In each case the supplementary food appears to

83 attract predators to a point source, which in turn foraged locally on other prey. The most parsimonious

84 explanation is that the presence of a reliable or high quality food resource both increases the numbers

85 of potential nest predators and the time they spend foraging near the food source.

86 It is not known if supplementary feeding of the type practised by tens of millions of garden owners

87 increases the risk of local nest predation in urban and suburban habitats. These habitats support

88 significant populations of native bird species in the UK including a number of open-cup nesting

89 species that have undergone national declines in recent decades, such as the Blackbird (*Turdus*

90 *merula*), the Dunnock (*Prunella modularis*), and the UK red-listed Song Thrush (*Turdus philomelos*)

91 (Gregory & Baillie 1998, Bland *et al*. 2004). Given the near ubiquity of supplementary feeding in

92 urban areas, and the recommendation from bird conservation NGOs (e.g. RSPB 2009) to feed birds

93 throughout the year, it is possible that individuals providing supplementary food in their gardens are

94   inadvertently increasing nest predation rates suffered by their garden birds. To investigate this further

95   it is first necessary to establish if nest predation is elevated near bird feeding stations. By using both

96   guarded (food inaccessible to nest predators) and unguarded feeders (food accessible), we can test if it

97   is the presence of food (both accessible and inaccessible) or the availability (food accessible in

98   unguarded feeders) of food which affects predation rates.

99   Studying nest predation using real nests would result in considerable practical and ethical challenges.

100   As a result, artificial nests provide an important tool for studying bird nest predation (Major & Kendal

101   1996, Miller & Hobbs 2000). Typically nests are baited with quail and/or model eggs and monitored

102   over a set period. Artificial nests are undefended by adults and lack the activity of real nests;

103   nevertheless, they provide experimental nest predation data at scales which would be difficult to

104   achieve in natural studies, while avoiding the ethical issues of experimenting with natural nests

105   (Major & Kendal 1996, Moore & Robinson 2004). Using camera monitored artificial nests we

106   investigated nest survival around caged, uncaged and empty bird feeders. Our objectives were to

107   determine if a) potential nest predators were attracted to bird feeding stations providing

108   supplementary food, b) if so, if this was associated with differences in rates of nest predation, c) if

109   increased nest predation was associated with access to food (unguarded feeders) or the presence of

110   food (guarded and unguarded feeders) and d) if nest predation rates were affected by distance from

111   the supplementary food source.

112   **Materials and methods**

113   *Study area*

114   The study was conducted at the University of Reading's Whiteknights Campus (UK; 51°27'N,

115   0°58'W), in an area of open parkland and woodland comprising approximately 68% natural surfaces

116   overall, embedded in a typical UK suburban landscape broadly conforming to Marzluff *et al.* (2001).

117   The town of Reading covers approximately 40 km^2 with a population of 230 000 people (Office for

118   National Statistics 2013).

119   *Experimental design*

120 Experimental work was carried out between the 5th of May and the 17th of June 2014, which is during

121 the peak bird breeding season for the UK (Robinson 2005). Fifty-four locations were selected on the

122 edge of grassy clearings and open spaces with adjacent areas of shrubs and bushes, 50-100m apart,

123 replicating typical suburban feeder distribution (Fuller *et al*. 2008). The experiment consisted of six

124 two-week sample cycles. During each cycle, nine peanut feeders (CJ Wildlife small defender feeder,

125 Shrewsbury, UK) were positioned (three each of empty, filled and unguarded, filled and fitted with a

126 cage guard). Feeders were randomly placed in each of the study locations, one week before the nests,

127 to allow habituation. Sites were not reused and all were at least 20 m away from the closest building.

128 Experimental cycles were staggered at one week intervals to reduce the sampling time required for the

129 whole experiment.

130 Two artificial nests were placed diametrically opposed ca. 5m ('near') and 10m ('far') from each

131 feeder (±1 m), replicating typical distances between feeders and suburban garden boundaries (Gaston

132 *et al.* 2007). In total 108 nests were placed (one 'near', one 'far', at each of the 54 feeder locations).

133 Nests were constructed of 15x15cm squares of small-gauge wire mesh lined with dried grass and

134 attached to branches to imitate a Blackbird nest (Kurucz *et al*. 2010, Kurucz *et al*. 2012). Nest height

135 was at 1.5 ± 0.5m and were placed to mimic natural blackbird nest-sites and attempted to provide

136 similar visual accessibility to potential predators following Swanson *et al*. (2012). Two fresh Quail

137 *Coturnix japonica* eggs were placed in each nest (Buler & Hamilton 2000). Blackbirds are a common

138 breeding species in UK gardens along with the less common but similarly sized Song Thrush (Bland

139 *et al*. 2004), making them an appropriate species to simulate. Nests were monitored for seven days

140 (168 hours) as 90% of predation events occur within 6 days of placement (Burke *et al*. 2004).

141 Each nest was continually monitored by a concealed motion-triggered camera trap (Ltl Acorn 5310;

142 Ltl Acorn Inc, USA), set to the highest sensitivity setting, taking three photographs with a three

143 second interval when triggered.

144 Feeders were checked every 3.5 days and refilled where necessary. Feeder usage was sampled using

145 camera traps, but each was monitored for 3.5 days either at the beginning or end of the week to ensure

146   coverage with limited traps. At any one time one of each feeder type was monitored and two thirds of

147   all feeders were sampled for usage.

148   Nest fate was recorded and for predated nests, predation time and predator identity determined. Any

149   damage to or removal of eggs was considered a predation event. Visitation rates per species were

150   recorded at the feeders; as visitors could not be individually identified, a visitor was considered an

151   individual when either separated by a photograph without the animal or when four or more minutes

152   had elapsed without a feeding event.

153   *Data Analysis*

154   All analyses were carried out within the program R (R Core Team 2016), with nest survival tested

155   using Cox's proportional hazard model in base R survival package (version 2.39-4, Therneau 2015).

156   This approach was used over a logistic exposure or regression approach (Shaffer 2004) because exact

157   survival time and fate was known for each nest and exposure period did not vary. Covariates were

158   feeder type (empty, guarded, unguarded), distance from feeder (near, far) and study week block (as a

159   random effect) with time until predation (hours) and predation status as response variables. No

160   interaction terms were used. We evaluated the relative fit of each candidate model using Akaike's

161   Information Criterion with a small-sample bias adjustment, comparing models using Akaike weights

162   and delta AICc (Burnham & Anderson 2002).

163   Mean daily feeder visitation (as a proxy for usage) was first compared using Kruskal-Wallis tests

164   between treatment, by individual species, all potential 'predator' species, all small birds and all

165   animals. Binomial logistic mixed model regression was then used to test for specific relationships

166   between animal feeder usage and predation overall. Two separate global models were constructed

167   both with study week block as a random effect factor and whether a nest was predated as the binomial

168   response variable in the R lme4 package (version 1.1-12, Bates et al 2015). First, a model that

169   considered overall predator visits and small bird visits to feeders as variables effecting nest predation.

170   Second, a model considering feeder visits by Squirrels, Magpies and small birds as variables effecting

171   nest predation. Because Magpie and squirrel visits are subsets of overall predator visits it is not

172 possible to utilise species and overall visits in the same model. Jays were not included in the

173 individual models due to their infrequent visits. Relative model fit was then separately evaluated using

174 delta AICc and Akaike weights for both global models as above against a null model containing only

175 the intercept and study week as a random factor. There was insufficient data to effectively compare

176 effectors on predation for individual predator species or at specific feeder types.

177 **Results**

178 *Feeder visitation*

179 Thirty-three of the 54 feeders were monitored (10 empty, 11 guarded, 12 unguarded). Eleven species

180 were recorded making 5251 individual feeder visits (empty feeders: 17; guarded: 3522; unguarded:

181 1712 visits).

182 Grey Squirrels contributed 43.9% of visits to unguarded and 9.3% of visits to guarded feeders while

183 smaller birds were more likely to visit guarded feeders (Table 1). Magpies were a regular visitor to

184 unguarded feeders but rare at empty and guarded feeders. One exception was an individual guarded

185 feeder, which did receive frequent visits (Figure 1). Despite predating 27.5% of all recorded nests,

186 Jays only visited feeders eight times. All species visiting more than two individual feeders (excluding

187 unknowns) show a significant difference between their feeder usages (Table 1; Figure 1).

188 *Nest survival*

189 Of the 108 experimental nests, 102 were successfully monitored, with 74 recorded predation events

190 (magpie: 37; jay: 28; grey squirrel: 8; one unknown). Six nest predation events were missed due to

191 camera errors or human interference and so were omitted from the analysis (3 empty, 2 guarded and 1

192 unguarded). From the different feeder types 51.5% of empty feeder nests, 76.5% of guarded feeder

193 nests and 88.6% of unguarded feeder nests were predated during the course of the experiment. No

194 predation events were recorded between 20:10 and 05.32.

195 When AICc selection was carried out on the global hazard model, the AICc selected model with

196 distance from feeder removed had a delta AICc of less than 2 from the global model so for

197　completeness we present both the global (Wald = 23.05, d.f. = 6.42, p < 0.001, AICc = 600.4, model

198　weight = 0.210; Table 2) and AICc selected model (Wald = 22.93, d.f. = 5.43, p < 0.001, AICc =

199　598.5, model weight = 0.672; Table 2). Separate post hoc ANOVAs of both models (following

200　Therneau 2015) found feeder type and week were significant effectors of nest survival overall (χ^2 =

201　11.8, d.f. = 2, p = 0.003 and χ^2 = 17.6, d.f. = 3.4, p < 0.001 for feeder type and study week

202　respectively in both models). In both models nests near filled feeders were significantly more likely to

203　be predated than those near empty feeders and week was a significant covariate with identical hazard

204　ratios after rounding (Table 2; Figure 2). Nest distance from feeder did not significantly affect

205　predation rates in the global model (p = 0.67) and was eliminated in the AICc selected model (Table

206　2). No significant difference in survival was found between nests adjacent to guarded and unguarded

207　feeders (post-hoc Tukey test p = 0.82; Figure 2).

208　*Nest predation and feeder usage*

209　Overall feeder activity by predators (Grey Squirrels, Jays and Magpies) was significantly associated

210　with increased nest predation (Wald Z = 2.518, p = 0.019) in the AICc selected mixed effect model

211　(Table 3). In the model considering individual predator usage, Grey Squirrel usage was significantly

212　associated with increased overall nest predation (Wald Z = 2.305, p = 0.021) in the AICc selected

213　model (Table 3). However, support for this model is weak with little separation between all possible

214　model AICcs and similar Akaike weights in several models (Table 3). Usage by small birds was not a

215　significant factor in any model (Table 3).

216

217　**Discussion**

218　We that the provision of supplementary food during the breeding season for wild birds in a form

219　common in urban and suburban habitats may increase the likelihood of local nest predation. The

220　survivorship of nests adjacent to unguarded feeders was less than 20% of that seen when artificial

221　nests were placed near empty feeders. There was no difference in nest survival near guarded feeders

222　when compared with those placed adjacent to unguarded feeders. Increased predation was associated

8

223   with Magpies, Jays and Grey Squirrels. Magpies and Grey Squirrels were significantly more likely to

224   visit unguarded feeders, while Jays were largely absent. Overall, nest predation was associated with

225   increased predator visits, particularly by Grey Squirrels, to feeders. There was no effect on nest

226   predation rates of distance to feeder at the scales we considered. Species assemblages differed

227   between treatments; empty feeders received few visits or no visits, guarded feeders were mostly

228   visited by small passerines and unguarded feeders attracted a higher proportion of corvids and

229   Squirrels. Despite being unable to feed at guarded feeders, predators still made up 9.4% of total visits

230   to them. No mammalian nest predators other than Grey Squirrels were recorded despite being present

231   at the study site and in UK urban areas generally (e.g. Brown Rat *Rattus norvegicus*, mice *Apodemus*

232   spp., Red Fox *Vulpes vulpes*, Domestic Cats *Felis catus*: Baker & Harris 2007, Thomas *et al*. 2012).

233   Two nests recorded mouse visits but no predation attempts were observed.

234   Nests adjacent to filled feeders suffered greatly increased predation rates, with the majority of nest

235   predation events caused by corvids (Magpies and Jays) and Grey Squirrels. Nest predation by corvids

236   is a frequent occurrence in urban habitats (Jokimaki & Huhta 2000, Thorington & Bowman 2003,

237   Jokimäki et al., 2005, Bonnington *et al.* 2015), where densities are high due to their omnivorous diet

238   and adaptability, as well as reduced numbers of larger predators and/or competitors (Soh *et al.* 2002,

239   Marzluff *et al.* 2007).

240   Despite our record of animal usage and clear evidence for an effect of the presence of supplementary

241   food, the exact nature of the link between feeder usage and local nest predation remains unclear.

242   There is a significant positive relationship overall between feeder usage by predators, in particular

243   Grey Squirrels, and increased nest predation. Predation by Grey Squirrels themselves was lower than

244   the two corvid species, suggesting there was not a direct link between Squirrel feeder usage and nest

245   predation by Squirrels. We lack sufficient samples and model support to investigate this further, but

246   we speculate that their presence at bird feeders may influence predation rates by Jays and Magpies.

247   We propose two non-mutually exclusive mechanisms that may lead to this.

248   First, Jays and Magpies may be responding to the increased density of other omnivores which have

249   been attracted by the presence of supplementary food. They in turn may be more likely to enter the

250 feeder area, associating it with increased feeding potential, even if they themselves are not primary

251 users of the bird feeders. In particular the frequency of Jay predation was unexpected due to their

252 infrequent attendance at feeders, while Magpies did utilise feeders, but in low numbers. Second, the

253 presence of Squirrels on feeders may exclude other omnivorous predators as well as small birds,

254 resulting in increased foraging in the vicinity of the feeders, hence increasing local nest predation.

255 Taken together, these results suggest that feeder usage by nest predators is associated with increased

256 predation on our experimental nests, but this effect is not simply a result of nest predators being

257 attracted to a point source, but instead perhaps also by being attracted by other feeder users to the

258 vicinity of the food source.

259 We tested to see if nest predation changed with distance from the feeder, but there was no effect. The

260 distances chosen for the study (5 and 10 metres) were relatively small and are consistent with the

261 layout of a typical UK suburban garden (Smith *et al.* 2006, Loram *et al.* 2007). However, we suggest

262 that there could still be a distance effect. While not explicitly recorded, we observed no evidence of

263 increased predation suffered by nests placed close to an empty feeder when the closest replicate was a

264 filled feeder. Therefore we suggest that while the increased risk of nest predation is present when

265 nests are within 10 metres of a feeder, this effect may be lost at a distance up to 40 metres away (the

266 minimum distance between a feeder and the next closest nest associated with another feeder under our

267 experimental design). Further testing over a larger range of distances with independent nests would be

268 required to effectively test this theory.

269 The use of artificial nests does present some interpretive challenges (Buler & Hamilton 2000, Burke

270 *et al.* 2004, Moore & Robinson 2004). They lack the odours, activity and defending adults of natural

271 nests (Swanson *et al.* 2012). Concerns have also been raised over the use of Quail eggs in artificial

272 nests, with suggestions that they may be too large for some small predators (Burke *et al.* 2004). This

273 also means that artificial nests may not be representative of smaller common UK open cup nesting

274 birds, such as Robins *Erithacus rubecula* and Dunnocks, in terms of egg and nest size as well as

275 concealment. Some studies have substituted model eggs made from modelling clay, both to give a

276 smaller prey item and so that when nests are not monitored by cameras it allows predator

277 identification through marks left on the eggs (Major & Kendal 1996, Burke *et al.* 2004). These studies

278 have found that rodents (not including Squirrels) cause a significant proportion of artificial nest

279 predation events. As only two nests were visited by mice and none by rats (and no feeder visits by rats

280 were recorded) either the system in this experiment is different or previous results have been skewed

281 by the attraction of these rodents to the smell and/or taste of the model eggs (Rangen *et al.* 2000).

282 While for practical and ethical reasons the use of artificial nests remains the standard approach for

283 understanding the causes and consequences of nest predation, such caveats suggest that interpreting

284 the results of artificial nest studies should be taken as indicative rather than definitive, particularly

285 when applied to bird species of different sizes or with different nesting habits such as ground or cavity

286 nesting birds.

287 The urban landscape presents a challenging environment for wild birds to live and breed (Chace &

288 Walsh 2006, Chamberlain *et al.* 2009). Together with potentially limited natural food (McKinney

289 2008) and high numbers of generalist predators (Sorace & Gustin 2009), urban areas also hold the

290 majority of the UK's estimated 10.3 million Cats (Murray *et al.* 2010) which predate millions of birds

291 annually (Thomas *et al.* 2012, Thomas *et al.* 2014). Nevertheless, significant populations of birds are

292 supported within urban environments (Bland *et al.* 2004) and species richness can be greater than in

293 adjacent rural areas (Chace & Walsh 2006), in part because of the combined efforts of millions of

294 people providing supplementary food (Fuller *et al.* 2008).

295 However, while some species are effectively human commensals, others including open-cup nesters

296 such as thrushes, are increasingly under challenge in urban habitats (Máthé & Batáry 2015) and do not

297 necessarily use the supplementary food people supply. In consequence, supplementary feeding may

298 strongly benefit one avian guild to the detriment of others through increased local nest predation. Any

299 effect we have on their demographic processes through supplementary feeding may have important

300 conservation consequences and warrants further investigation. However, while we have shown that

301 nests close to filled feeders suffer considerably higher predation rates, it is not clear if such predation

302 would affect the population dynamics of urban birds. As with other anthropogenic pressures (e.g. the

303 presence of Cats), testing this would not be straight-forward, in particular given the ubiquity of

304 supplementary feeding in urban ecosystems. Nevertheless, while difficult, this work suggests that the

305 question is worthy of further exploration.

306 Furthermore, we find that feeder type affects the assemblage of species feeding upon it. When feeders

307 are unguarded, corvids and Grey Squirrels exclude small passerines (this study; Bonnington *et al.*

308 2014a, Orros & Fellowes 2015a). We suggest that this not only reduces the volume of food available

309 to target species through competition, it may also support increased population sizes of predatory

310 species through a demographic response (Davies *et al.* 2009). We suggest that people who choose to

311 provide supplementary food for birds consider using guarded feeders to minimise opportunities to

312 support predatory species, and consider in the context of the ecology of their own gardens if feeding

313 during the breeding season is appropriate.

314 Providing supplementary food during the breeding season is widespread (Orros & Fellowes 2015a)

315 and can increase local bird population size (Peach *et al.* 2013, Smith & Smith 2013). Urban areas may

316 be important for the conservation of some bird species and species richness in suburban areas can be

317 greater than that found in adjacent urban and rural areas largely as a result of the decisions made by

318 millions of homeowners (Marzluff 2001, Chace & Walsh 2006, Väisänen 2008, Jokimäki &

319 Kaisanlahti-Jokimäki 2012). Our results suggest a possible negative indirect effect of supplementary

320 garden bird feeding on local nesting success by attracting nest predators to point sources of food. It

321 would be unfortunate if our most common act of engagement with wildlife was counter-productive

322 during the breeding season.

323 **Acknowledgements**

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329

330   **References**

331   Antonov, A. & Atanasova, D. 2003. Small-scale differences in the breeding ecology of urban and
332   rural Magpies *Pica pica. Ornis Fennica,* **80:** 21-30.

333

334   Baker, P. J. & Harris, S. 2007. Urban mammals: what does the future hold? An analysis of the factors
335   affecting patterns of use of residential gardens in Great Britain. *Mammal Review,* **37:** 297-
336   315.

337

338   Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using
339   lme4. *Journal of Statistical Software,* **67:** 1-48.

340

341   Bland, R. L., Tully, J. & Greenwood, J. J. D. 2004. Birds breeding in British gardens: an
342   underestimated population? *Bird Study,* **51:** 97-106.

343

344   Bonnington, C., Gaston, K. J. & Evans, K. L. 2014a. Squirrels in suburbia: influence of urbanisation
345   on the occurrence and distribution of a common exotic mammal. *Urban Ecosystems,* **17:** 533-
346   546.

347

348   Bonnington, C., Gaston, K. J. & Evans, K. L. 2014b. Assessing the potential for Grey Squirrels
349   *Sciurus carolinensis* to compete with birds at supplementary feeding stations. *Ibis,* **156:** 220-
350   226.

351

352   Bonnington, C., Gaston, K. J. & Evans, K. L. 2015. Ecological traps and behavioural adjustments of
353   urban songbirds to fine-scale spatial variation in predator activity. *Animal Conservation,* **16:**
354   529-538.

355

356   Borgmann, K. L., Conway, C. J. & Morrison, M. L. 2013. Breeding phenology of birds: mechanisms
357   underlying seasonal declines in the risk of nest predation. *Plos One,* **8:** 10.

358

359   Bradley, C.A. & Altizer, S. 2007. Urbanization and the ecology of wildlife diseases. *Trends in
360   Ecology and Evolution*, **22**: 95–102.

361

362   British Trust for Ornithology. 2006. We spend £200 million a year on wild bird food. In *British Trust
363   for Ornithology Press Release No. 2006/12/76.* Thetford: British Trust for Ornithology.

364

365   Brittingham, M. C. & Temple, S. A. 1988. Impacts of supplemental feeding on survival rates of
366   Black-Capped Chickadees. *Ecology,* **69:** 581-589.

367

368   Buler, J. J. & Hamilton, R. B. 2000. Predation of natural and artificial nests in a southern pine forest.
369   *Auk,* **117:** 739-747.

370

371   Burke, D. M., Eliliott, K., Moore, L., Dunford, W., Nol, E., Phillips, J., Holmes, S. & Freemark, K.
372   2004. Patterns of nest predation on artificial and natural nests in forests. *Conservation*
373   *Biology,* **18:** 381-388.

374

375   Burnham, K. P. & Anderson, D. R. (2002) *Model selection and multimodel inference: a practical*
376   *information-theoretic approach,* New York: Springer-Verlag.

377

378   Chace, J. F. & Walsh, J. J. 2006. Urban effects on native avifauna: a review. *Landscape and Urban*
379   *Planning,* **74:** 46-69.

380

381   Chamberlain, D. E., Vickery, J. A., Glue, D. E., Robinson, R. A., Conway, G. J., Woodburn, R. J. W.
382   & Cannon, A. R. 2005. Annual and seasonal trends in the use of garden feeders by birds in
383   winter. *Ibis,* **147:** 563-575.

384

385   Chamberlain, D. E., Cannon, A. R., Toms, M. P., Leech, D. I., Hatchwell, B. J. & Gaston, K. J. 2009.
386   Avian productivity in urban landscapes: a review and meta-analysis. *Ibis,* **151:** 1-18.

387

388   Cooper, S. M. & Ginnett, T. F. 2000. Potential effects of supplemental feeding of deer on nest
389   predation. *Wildlife Society Bulletin,* **28:** 660-666.

390

391   Courter, J. R., Johnson, R. J., Bridges, W. C. & Hubbard, K. G. 2013. Assessing migration of Ruby-
392   throated Hummingbirds (*Archilochus colubris*) at broad spatial and temporal scales. *Auk,* **130:**
393   107-117.

394

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

398

399   Eaton, M. A., Balmer, D. E., Bright, J., Cuthbert, R., Grice, P. V., Hall, C., Hayhow, D. B., Hearn, R.
400   D., Holt, C. A., Knipe, A., Mavor, R., Noble, D. G., Oppel, S., Risely, K., Stroud, D. A. &

401   Wotton, S. 2013. The state of the UK's birds 2013. Sandy, Bedfordshire.: The RSPB, BTO,
402   WWT, NRW, JNCC, NE, NIEA and SNH.

403

404   Fuller, R. A., Warren, P. H., Armsworth, P. R., Barbosa, O. & Gaston, K. J. 2008. Garden bird
405   feeding predicts the structure of urban avian assemblages. *Diversity and Distributions,* **14:**
406   131-137.

407

408   Gaston, K. J., Fuller, R. A., Loram, A., MacDonald, C., Power, S. & Dempsey, N. 2007. Urban
409   domestic gardens (XI): variation in urban wildlife gardening in the United Kingdom.
410   *Biodiversity and Conservation,* **16:** 3227-3238.

411

412   Gregory, R. D. & Baillie, S. R. 1998. Large-scale habitat use of some declining British birds. *Journal*
413   *of Applied Ecology,* **35:** 785-799.

414

415   Harrison, T. J. E., Smith, J. A., Martin, G. R., Chamberlain, D. E., Bearhop, S., Robb, G. N. &
416   Reynolds, S. J. 2010. Does food supplementation really enhance productivity of breeding
417   birds? *Oecologia,* **164:** 311-320.

418

419   Hill, G. E., Sargent, R. R. & Sargent, M. B. 1998. Recent change in the winter distribution of Rufous
420   Hummingbirds. *Auk,* **115:** 240-245.

421

422   Jansson, C., Ekman, J. & Anders von, B. 1981. Winter mortality and food supply in tits *Parus* spp.
423   *Oikos,* **37:** 313-322.

424

425   Jokimaki, J. & Huhta, E. 2000. Artificial nest predation and abundance of birds along an urban
426   gradient. *Condor,* **102:** 838-847.

427

428   Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Sorace, A., Fernández-Juricic, E., Rodriguez-Prieto, I. &
429   Jimenez, M. D. 2005. Evaluation of the "safe nesting zone" hypothesis across an urban
430   gradient: a multi-scale study. *Ecography,* **28:** 59-70.

431

432   Kurucz, K., Kallenberger, H., Szigeti, C. & Purger, J. J. 2010. Survival probabilities of first and
433   second clutches of blackbird (*Turdus merula*) in an urban environment. *Archives of Biological*
434   *Sciences,* **62:** 489-493.

435

436 Kurucz, K., Bertalan, L. & Purger, J. J. 2012. Survival of blackbird (*Turdus merula*) clutches in an
437   urban environment: experiment with real and artificial nests. *North-Western Journal of*
438   *Zoology,* **8:** 362-364.
439

440 Loram, A., Tratalos, J., Warren, P. H. & Gaston, K. J. 2007. Urban domestic gardens (X): the extent
441   & structure of the resource in five major cities. *Landscape Ecology,* **22:** 601-615.
442

443 Madden, C. F., Arroyo, B. & Amar, A. 2015. A review of the impacts of corvids on bird productivity
444   and abundance. *Ibis,* **157:** 1-16.
445

446 Major, R. E. & Kendal, C. E. 1996. The contribution of artificial nest experiments to understanding
447   avian reproductive success: A review of methods and conclusions. *Ibis,* **138:** 298-307.
448

449 Martin, T. E. & Li, P. 1992. Life History Traits of Open- vs. Cavity-Nesting Birds. *Ecology,* **73:** 579-
450   592.
451

452 Marzluff, J. M., Bowman, R. & Donnelly, R. 2001. A historical perspective on urban bird research:
453   trends, terms, and approaches. In *Avian Ecology and Conservation in an Urbanizing World.*
454   (eds. J. M. Marzluff, R. Bowman & R. Donnelly), pp. 1-17. New York: Springer US.
455

456 Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. In *Avian Ecology and*
457   *Conservation in an Urbanizing World.* (eds. J. M. Marzluff, R. Bowman & R. Donnelly), pp.
458   19-47. New York: Springer US.
459

460 Marzluff, J. M., Withey, J. C., Whittaker, K. A., Oleyar, M. D., Unfried, T. M., Rullman, S. & DeLap,
461   J. 2007. Consequences of habitat utilization by nest predators and breeding songbirds across
462   multiple scales in an urbanizing landscape. *Condor,* **109:** 516-534.
463

464 Máthé, O. & Batáry, P. 2015. Insectivorous and open-cup nester bird species suffer the most from
465   urbanization. *Bird Study,* **62:** 78-86.
466

467 McKinney, M. L. 2008. Effects of urbanization on species richness: A review of plants and animals.
468   *Urban Ecosystems,* **11:** 161-176.
469

470 Miller, J. R. & Hobbs, N. T. 2000. Recreational trails, human activity, and nest predation in lowland
471   riparian areas. *Landscape and Urban Planning,* **50:** 227-236.
472

473   Moore, R. P. & Robinson, W. D. 2004. Artificial bird nests, external validity, and bias in ecological
474   field studies. *Ecology,* **85:** 1562-1567.
475

476   Murray, J. K., Browne, W. J., Roberts, M. A., Whitmarsh, A. & Gruffydd-Jones, T. J. 2010. Number
477   and ownership profiles of cats and dogs in the UK. *Veterinary Record,* **166:** 163-168.
478

479   Office for National Statistics. 2013. Neighbourhood statistics. 2011 census data. HM Government.
480   Crown Copyright. In *2011 census data.* HM Government. Crown Copyright.
481

482   Orros, M. E. & Fellowes, M. D. E. 2012. Supplementary feeding of wild birds indirectly affects the
483   local abundance of arthropod prey. *Basic and Applied Ecology,* **13:** 286-293.
484

485   Orros, M. E. & Fellowes, M. D. E. 2014. Supplementary feeding of the reintroduced Red Kite *Milvus*
486   *milvus* in UK gardens. *Bird Study,* **61:** 260-263.
487

488   Orros, M. E. & Fellowes, M. D. E. 2015a. Wild bird feeding in an urban area: intensity, economics
489   and numbers of individuals supported. *Acta Ornithologica,* **50:** 43-58.
490

491   Orros, M. E. & Fellowes, M. D. E. 2015b. Widespread supplementary feeding in domestic gardens
492   explains the return of reintroduced Red Kites *Milvus milvus* to an urban area. *Ibis,* **157:** 230-
493   238.
494

495   Orros, M. E., Thomas, R. L., Holloway, G. J. & Fellowes, M. D. E. 2015. Supplementary feeding of
496   wild birds indirectly affects ground beetle populations in suburban gardens. *Urban*
497   *Ecosystems,* **18:** 465-475.
498

499   Peach, W. J., Mallord, J. W., Orsman, C. J., Ockendon, N. & Haines, W. G. 2013. Testing
500   assumptions of a supplementary feeding experiment aimed at suburban House Sparrows
501   *Passer domesticus*. *Bird Study,* **60:** 308-320.
502

503   Plummer, K. E., Bearhop, S., Leech, D. I., Chamberlain, D. E. & Blount, J. D. 2013a. Fat
504   provisioning in winter impairs egg production during the following spring: a landscape-scale
505   study of blue tits. *Journal of Animal Ecology,* **82:** 673-682.
506

507   Plummer, K. E., Bearhop, S., Leech, D. I., Chamberlain, D. E. & Blount, J. D. 2013b. Winter food
508   provisioning reduces future breeding performance in a wild bird. *Scientific Reports,* **3:** 6.
509

510 Plummer, K. E., Siriwardena, G. M., Conway, G. J., Risely, K. & Toms, M. P. 2015. Is supplementary
511   feeding in gardens a driver of evolutionary change in a migratory bird species? *Global*
512   *Change Biology,* **21:** 4353-4363.
513
514 R Core Team (2016) *R: A language and environment for statistical computing,* Vienna, Austria.: R
515   Foundation for Statistical Computing.
516
517 Rangen, S. A., Clark, R. G. & Hobson, K. A. 2000. Visual and olfactory attributes of artificial nests.
518   *Auk,* **117:** 136-146.
519
520 Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology***:**
521   1-48.
522
523 Robb, G. N., McDonald, R. A., Chamberlain, D. E., Reynolds, S. J., Harrison, T. J. E. & Bearhop, S.
524   2008. Winter feeding of birds increases productivity in the subsequent breeding season.
525   *Biology Letters,* **4:** 220-223.
526
527 Robinson, R. 2005. BirdFacts: species profiles of birds occurring in Britain and Ireland. In *BTO*
528   *Research Report.* Vol. 407. Thetford: BTO.
529
530 Robinson, R.A., Lawson, B., Toms, M.P., Peck, K.M., Kirkwood, J.K., Chantrey, J., et al. 2010.
531   Emerging infectious disease leads to rapid population declines of common British birds. *PLoS*
532   *ONE*, **5**: e12215.
533
534 Rolshausen, G., Segelbacher, G., Hobson, K. A. & Schaefer, H. M. 2009. Contemporary evolution of
535   reproductive isolation and phenotypic divergence in sympatry along a migratory divide.
536   *Current Biology,* **19:** 2097-2101.
537
538 RSPB (2009) *When to feed wild birds.,* Sandy, Bedfordshire: The Royal Society for the Protection of
539   Birds.
540
541 Selva, N., Berezowska-Cnota, T. & Elguero-Claramunt, I. 2014. Unforeseen effects of supplementary
542   feeding: ungulate baiting sites as hotspots for ground-nest predation. *Plos One,* **9**: e90740.
543
544 Shaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk,* **121:** 526-540.
545

546 Shochat, E. 2004. Credit or debit? Resource input changes population dynamics of city-slicker birds.
547   *Oikos,* **106:** 622-626.

548

549 Smith, R. M., Thompson, K., Hodgson, J. G., Warren, P. H. & Gaston, K. J. 2006. Urban domestic
550   gardens (IX): Composition and richness of the vascular plant flora, and implications for
551   native biodiversity. *Biological Conservation,* **129:** 312-322.

552

553 Smith, K. W. & Smith, L. 2013. The effect of supplementary feeding in early spring on the breeding
554   performance of the great spotted woodpecker *Dendrocopos major*. *Bird Study,* **60:** 169-175.

555

556 Soh, M. C. K., Sodhi, N. S., Seoh, R. K. H. & Brook, B. W. 2002. Nest site selection of the house
557   crow (Corvus splendens), an urban invasive bird species in Singapore and implications for its
558   management. *Landscape and Urban Planning,* **59:** 217-226.

559

560 Sorace, A. & Gustin, M. 2009. Distribution of generalist and specialist predators along urban
561   gradients. *Landscape and Urban Planning,* **90:** 111-118.

562

563 Swanson, L., Sanyaolu, R. A., Gnoske, T., Whelan, C. J., Lonsdorf, E. V. & Cordeiro, N. J. 2012.
564   Differential response of nest predators to the presence of a decoy parent in artificial nests.
565   *Bird Study,* **59:** 96-101.

566

567 Therneau, T. M. (2015) *A Package for Survival Analysis in S. R package version 2.37-7.*

568

569 Thomas, R. L., Fellowes, M. D. E. & Baker, P. J. 2012. Spatio-temporal variation in predation by
570   urban domestic cats (*Felis catus*) and the acceptability of possible management actions in the
571   UK. *Plos One,* **7:** 13.

572

573 Thomas, R. L., Baker, P. J. & Fellowes, M. D. E. 2014. Ranging characteristics of the domestic cat
574   (*Felis catus*) in an urban environment. *Urban Ecosystems,* **17:** 911-921.

575

576 Thorington, K. K. & Bowman, R. 2003. Predation rate on artificial nests increases with human
577   housing density in suburban habitats. *Ecography,* **26:** 188-196.

578

579 U.S. Fish and Wildlife Service. 2011. National Survey of Fishing, Hunting, and Wildlife-Associated
580   Recreation.

581

582   Väisänen, R. A. 2008: Talviruokintapaikkojen lintujen seuranta 1989–2007. *Linnut-vuosikirja*, **2007**:

583   60–79.

584

585

586
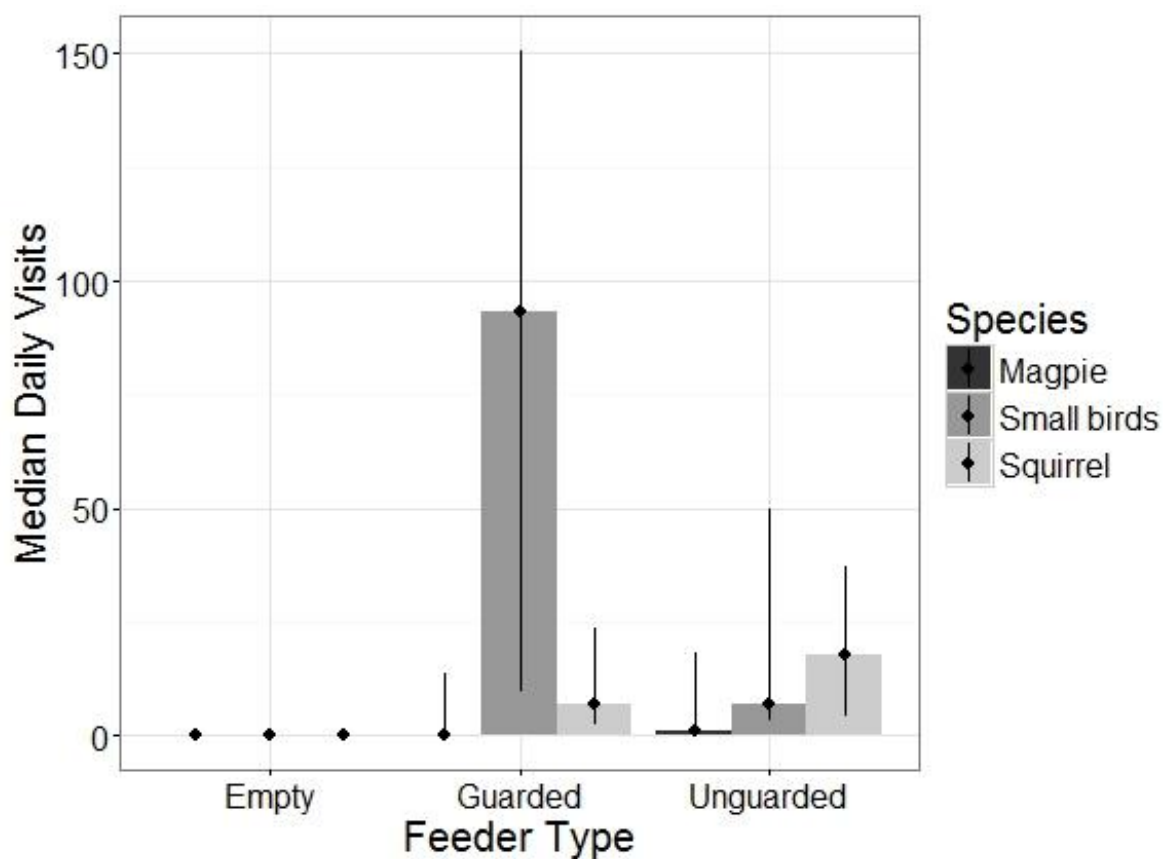
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588 **Figure 1.** Median (+/-IQR) daily animal visits to each feeder treatment by species/grouping. Only species that

589 visited at least two individual bird feeders are included. Small bird species are great tit (*Parus major*), blue tit

590 (*Cyanistes caeruleus*), nuthatch (*Sitta europaea*) and robin (*Erithacus rubecula*).
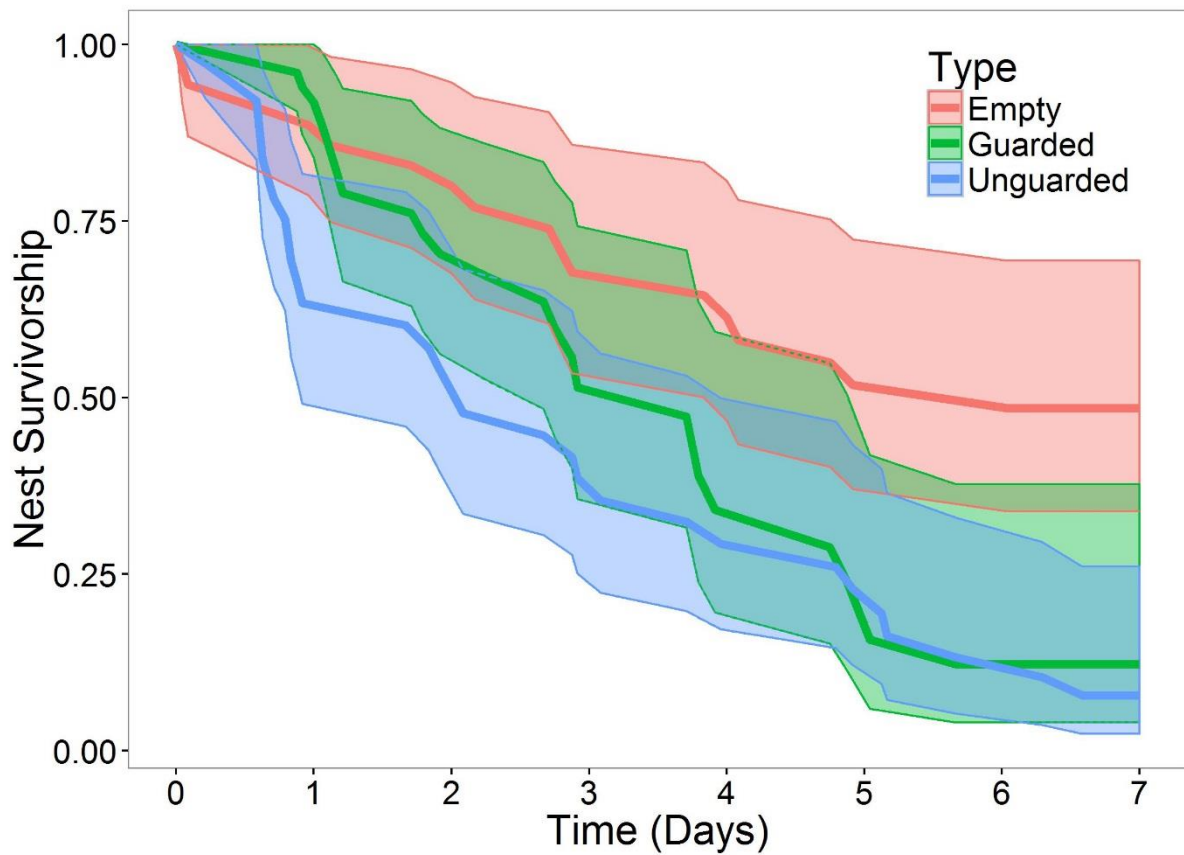
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Figure 2. Predicted Cox's proportional hazard survival distribution by feeder nest type over the course of a

mean experimental week (bold lines) with individual 95% confidence intervals (grey). Final predicted survival

rates were 0.49, 0.12 and 0.08 for empty, guarded and unguarded feeder nests respectively.

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603   **Table 1.** Median daily species visits and Kruskal-Wallis tests by feeder type (all d.f. = 2). Only common species

604   that visited at least two individual bird feeders are included.

Species	Empty median	Guarded median	Unguarded median	Kruskal-Wallis chi-squared	P	Number of feeders where species was recorded
Grey Squirrel	0.0	6.9	17.86	23.02	<0.001	26
Magpie	0.0	0.0	0.9	6.88	0.032	13
Great Tit	0.0	47.7	4.1	25.59	<0.001	27
Blue Tit	0.0	24.6	1.6	18.18	<0.001	21
Nuthatch	0.0	4.9	0.0	13.76	0.001	14
Robin	0.0	0.3	0.0	8.12	0.017	14

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607   **Table 2.** Hazard ratios (relative predation risk; +/- CI) and P values for covariates in the global model where h =

608   1 is the control (empty) feeder hazard ratio (d.f. = 6.42, AICc = 600.4, model weight = 0.210). After the removal

609   of distance from the AICc selected model (d.f. = 5.43, AICc = 598.5, model weight = 0.672) the hazard ratios,

610   CI and P values were identical after rounding.

Covariate	Hazard ratio (h)	Lower 95% CI	Upper 95% CI	P
Guarded	2.14	1.14	3.99	0.017
Unguarded	3.09	1.67	5.73	<0.001
Week (random effect)	1.00	0.58	1.73	0.010
Distance (removed in AICc selected model)	*1.08*	*0.68*	*1.71*	*0.740*

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Table 3. Binomial generalised linear mixed effect models of predation against daily visitors with model AICc values and weights. The grouped predator models consider all predator visits together while the individual predator models consider them separately. The null model includes only the intercept and study week random effect. *indicates significance at the 95% level.

Predator variables	Model	Visit Coefficients	Estimate (95% CIs)	Std. Error	P	Model AICc	Model weight
Grouped predators	Null	Intercept only	0.751 (-0.263 – 2.061)	0.4533	0.0976	84.1	0.024
	Global	All Predators	0.079 (0.022 – 0.155)	0.033	0.016*	79.4	0.255
		All small birds	0.004 (-0.012 – 0.021)	0.008	0.620		
	AICc selected	**All Predators**	**0.068 (0.025 – 0.157)**	**0.029**	**0.019***	**77.3**	**0.705**
Individual predators	Null	Intercept only	0.751 (-0.263 – 2.061)	0.4533	0.0976	84.1	0.024
	Global	Squirrel	0.068 (-0.004 – 0.141)	0.037	0.066	81.5	0.095
		Magpie	0.131 (-0.081 – 0.342)	0.108	0.225		
		All small birds	0.004 (-0.012 – 0.020)	0.008	0.645		
	Model 2	Magpie	0.178 (0.0197 – 0.414)	0.097	0.068	81.2	0.108
	Model 3	Squirrel	0.084 (0.017 – 0.174)	0.039	0.029*	80.9	0.124
		All small birds	0.005 (-0.010 – 0.219)	0.008	0.519		
	Model 4	Squirrel	0.070 (0.003 – 0.158)	0.038	0.063	79.3	0.277
		Magpie	0.061	0.084	0.469		

			(-0.045 – 0.391)				
	AICc selected	**Squirrel**	**0.090** **(0.022 – 0.179)**	**0.039**	**0.021***	**79.1**	**0.314**

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