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3 **Colour Preferences of UK Garden Birds at Supplementary Seed Feeders**

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13 **Abstract**

14 Supplementary feeding of garden birds has benefits for both bird populations and
15 human wellbeing. Birds have excellent colour vision, and show preferences for food items of
16 particular colours, but research into colour preferences associated with artificial feeders is
17 limited to hummingbirds. Here, we investigated the colour preferences of common UK
18 garden birds foraging at seed-dispensing artificial feeders containing identical food. We
19 presented birds simultaneously with an array of eight differently coloured feeders, and
20 recorded the number of visits made to each colour over 370 30-minute observation periods
21 in the winter of 2014/15. In addition, we surveyed visitors to a garden centre and science
22 festival to determine the colour preferences of likely purchasers of seed feeders. Our results
23 suggest that silver and green feeders were visited by higher numbers of individuals of
24 several common garden bird species, while red and yellow feeders received fewer visits. In
25 contrast, people preferred red, yellow, blue and green feeders.

26

27 **Introduction**

28 It has been estimated that 20-30% of people in more developed areas of the world
29 provide wild birds with additional food (supplementary feeding) at some point in the year
30 (typically during the winter months) [1,2]. In the UK, approximately 60% of households with
31 gardens provide food for birds [3], estimated at 12.6 million households [1], 7.4 million of
32 which use bird feeders [4]. As a result the UK wild bird feeding industry was estimated as
33 being worth £210m per annum [5], and the wild bird care market rose 15% in value
34 between 2014 and 2015 [6]. Levels of bird feeding vary enormously across society [7], but

35 the importance of the connection between people and nature to human well-being in urban
36 environments is well established [8]. People feed birds because it gives them a sense of
37 personal wellbeing, although the underpinning emotions, experiences and personal
38 perceptions of the people feeding birds are certainly more complex than such a simplistic
39 statement might suggest [9]. Some people (those involved in avian monitoring or research)
40 feed birds in order to attract them for capture, measurement and subsequent release.

41

42 During the northern hemisphere winter natural food resources are at their lowest
43 level of availability [10] and a bird's thermodynamic costs are at their highest [11]. Over
44 winter survival is thus highly dependent upon the characteristics and availability of food
45 supply [10]. Gaining enough energy each day to ensure overnight survival is particularly
46 important for small passerines: individuals in the tit family (Paridae) can lose up to 10% of
47 their body weight overnight in winter [12]. Supplementary feeding may off-set the effects of
48 winter resource depletion [13] and in many cases a winter feeding station may be the most
49 abundant and dependable food source in a particular area [14]. Supplementary feeding has
50 been recorded as having a number of other benefits to birds, including larger clutch sizes
51 (house sparrows *Passer domesticus* [15]), better body condition and more rapid recovery
52 from injury (Carolina chickadee *Parus carolinensis*, tufted titmice *Parus bicolor* and white-
53 breasted nuthatch *Sitta carolinensis* [16]). Supplementary feeding increases both the range
54 of species and number of individuals visiting gardens [1,17] and increases abundance at a
55 landscape scale [1]. In the UK, for example, supplementary feeding has been implicated in
56 population increases of both house sparrow and starling (*Sturnus vulgaris* [18]) and may be

57 important in the evolution of 'new' migration strategies amongst over-wintering blackcap
58 (*Sylvia atricapilla* [19]).

59

60 In order that the benefits of supplementary feeding to both birds and the people
61 who feed them are realised it is essential that food be provided in a way that makes it
62 accessible to birds. In the case of the seed based foods provided to passerines
63 supplementary feeding most often involves the use of commercially available tubular seed
64 dispensers. These feeders commonly consist of a transparent plastic tube through which
65 seeds are visible to birds and coloured metal or plastic lids, bases, perches and feeder ports.
66 Here, we report an investigation into whether the colour of these metal or plastic parts
67 affected the number of birds choosing to feed at a particular feeder. For a feeder to attract
68 larger numbers of birds, something likely to be seen as preferable by those that purchase
69 feeders, the colour should be attractive or neutral to either a particular target species, or
70 seed feeding birds more generally. A feeder the colour of which birds avoid would not be an
71 effective feeder.

72

73 Birds have excellent colour vision and exhibit the ability to distinguish and choose
74 between different colours and shades [e.g. 20-22]. Here, we focus on colour preferences in
75 relation to foraging. Multiple studies report preferences of birds for food items of a
76 particular colour. Great tits (*Parus major*) blue tits (*Cyanistes caeruleus*) and Eurasian
77 nuthatches (*Sitta europaea*) all preferred uncoloured (natural) peanuts over those that had
78 been dyed white [23]. Willson et al. [24] reviewed a number of studies demonstrating that
79 frugivorous birds prefer black or red grapes or cherries over other colours such as green and

80 yellow, but point out that preference for colour here is confounded by preference for other
81 factors associated with colour, such as ripeness, size and nutritional value [24]. Other
82 studies have used artificial or novel foods dyed different colours and found colour-based
83 preferences [24-26]. Wilson et al [24] reported a preference for red, and avoidance of
84 yellow in three species of frugivorous bird, while North Island robins (*Petroica longipes*)
85 preferred yellow and avoid blue and brown [26] for example.

86

87 Preferences for colour associated with supplementary feeders, rather than food,
88 have exclusively focused on the preferences of hummingbirds (Trochillidae) at feeders
89 designed to provide sugar syrup. While hummingbird-pollinated flowers tend to be red
90 [27,28], and birds tend to prefer red-pigmented flowers over those lacking red pigments (e.g.
91 [29-31], reviewed in [28]), experimental studies on feeders do not show a consistent
92 preference for any particular colour (e.g. [32-34], reviewed in [28]). Instead, factors such as
93 location [35,36], previous experience [37-39] and nectar quality [35,39] appear to be more
94 important in determining choice. We have been unable to find any peer-reviewed studies of
95 the impact of seed dispensing feeder colour on bird feeding behaviour. One anecdotal
96 report [40] suggested that work carried out by the British Trust for Ornithology
97 demonstrated colour-based preferences for birds visiting seed and peanut feeders, namely
98 that blue seed feeders are preferred during the summer, while silver feeders are preferred
99 in winter (although goldfinches preferred green), and red peanut feeders are preferred over
100 other colours. The primary aim of our research was to investigate the effect of feeder colour
101 on the feeding preferences of wild birds. As an additional aim we investigated the level to

102 which birds and the humans who feed them agreed on their preferred feeder colour, an
103 important consideration for those who make and sell feeders and those who use them.

104

105 **Methods**

106 **Bird colour preference**

107 To explore the effect of colour on the number of visits by birds, we recorded bird
108 visit rates to 8 different coloured feeders at three sites on 78 sampling days during the
109 winter/spring of 2014/15 (November 2014 to May 2015).

110 Data were collected at Tophill Low Nature Reserve (Driffield, East Yorkshire TA
111 075,492), The University of Hull Botanic Garden (Cottingham, East Yorkshire TA 050,329)
112 and a suburban garden in Otley (West Yorkshire SE 195,472). These sites were chosen due
113 to accessibility and the presence of existing artificial feeders with regular avian visitors. The
114 feeders used (Natures Feast Royal Seed Feeders, Westland Horticulture) were of
115 transparent tubular design with metal lids, two metal ports and two straight metal perches.
116 The metal parts of each feeder were painted a single colour using Hammerite Metal Paint.
117 The proprietary colours used were *Smooth Black*, *Smooth Blue*, *Smooth Dark Green*, *Smooth*
118 *Red*, *Smooth White*, *Smooth Yellow*, *Hammered Silver* and Purple (achieved by mixing
119 *Smooth Blue*, *Smooth Red* and *Smooth White* at a ratio of 3:2:1). Analysis of the feeder
120 colours can be found in the section below. Throughout the experiment the feeders were
121 filled with "Nature's Feast High energy No Mess 12 Seed Blend" (Westland Horticulture, UK).

122 At each site the feeders were suspended in a line from a metal cross-bar, 30 cm
123 apart from one another and 1.5m above the ground. At any time, one feeder of each of the
124 8 colours used was available (see supporting information: Fig S1). The order of the feeders
125 along the cross-bar was changed after every 30 minute observation period according to a
126 pre-determined random pattern to control for any preferences based on feeder position
127 rather than colour. Feeders were filled at the beginning of each observation period and
128 cleaned thoroughly every 14 days. During each data collection session the numbers of
129 feeding visits by birds to each of the feeders in the array were recorded over 30 minutes. A
130 feeding visit was defined as a bird landing on the perch and taking food from the feeder port.
131 Birds were identified to species level, but as it was not possible to distinguish between
132 individuals of the same species, each visit to the feeders was counted as an independent
133 data point. All observations periods were video recorded (Sony Handycam HDR-CX240E)
134 mounted on a tripod approximately 10m from the feeders. Identification and counting of
135 birds either took place in real-time in the field or later using the video recordings (where the
136 number of visits was too high to allow for accurate real-time recording).

137 Data were collected across a total of 370 observation periods (Otley: 208; Tophill; 26
138 Botanic Gardens: 136), and a total of 7535 visits to the feeders were recorded (table 1).

139

140 **Table 1:** Summary of data, showing the total number of visits by each species at each site,
141 and the number of sample periods in which that species was observed at least once.

Species	Thwaite Gardens	Tophill Low	Otley	Total	Sample periods
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Blue tit <i>Cyanistes caeruleus</i>	810	1824	629	3263	108
Great tit <i>Parus major</i>	833	1564	13	2410	38
House sparrow <i>Passer domesticus</i>	-	-	701	701	58
Coal tit <i>Periparus ater</i>	311	116	109	536	48
Robin <i>Erithacus rubecula</i>	171	12	105	288	75
Starling <i>Sturnus vulgaris</i>	-	-	172	172	13
Greenfinch <i>Chloris chloris</i>	-	1	135	136	21
Marsh tit <i>Poecile palustris</i>	-	16	-	16	3
Long tailed tit <i>Aegithalos caudatus</i>	2	3	-	5	2
Bullfinch <i>Pyrrhula pyrrhula</i>	5	-	-	5	3
Goldfinch <i>Carduelis carduelis</i>	-	3	-	3	1
Total	2132	3539	1864	7535	370

142

143

144 **Human colour preference**

145 To assess the preferences of likely purchasers of bird feeders, we collected data in a
146 garden centre (Hornsea Garden Centre, Sigglesthorne, Hornsea, UK) where similar feeders
147 were sold (3 days, 8 2-hour sample periods) and at the University of Hull Science Festival (1
148 day as a single sample period). At each venue we explained to adult volunteers that we
149 were investigating the choices made by birds and people but we did not provide any
150 information on actual bird preferences (supporting information: Fig S2). People were shown

151 the coloured feeders used in the study and asked simply to indicate (by placing a token in an
152 appropriately coloured container) which they would be most likely to buy for their own
153 garden. Containers were emptied and tokens counted at the end of each sample period. In
154 total, 587 'votes' were cast during the poll.

155

156 **Data analysis**

157 All analysis was carried out using R v3.2.3 [41]. The total number of visits (across all
158 species, to give a measure of the overall preference for particular colours) to the feeders
159 were analysed using a generalised linear mixed effects model with a Poisson error
160 distribution (as appropriate for count data). Observation period and site were added as
161 random effects to account for non-independence of visits to feeders displayed at the same
162 time, and overall differences in bird populations at a given site. An observation-level
163 random effect was included to account for overdispersion in the data [42]. Re-leveling the
164 data within the model allowed for all pairwise comparisons between colours to be made,
165 and p-values were corrected for multiple testing across pairwise comparisons using the false
166 discovery rate control method [43]. The same analysis was used for the number of visits for
167 each species with more than 100 total visits to the feeders (see supplementary tables S1-S5),
168 to evaluate whether different species had different colour preferences. Preferences
169 expressed by visitors to the garden centre and science festival were also analysed using the
170 same methodology.

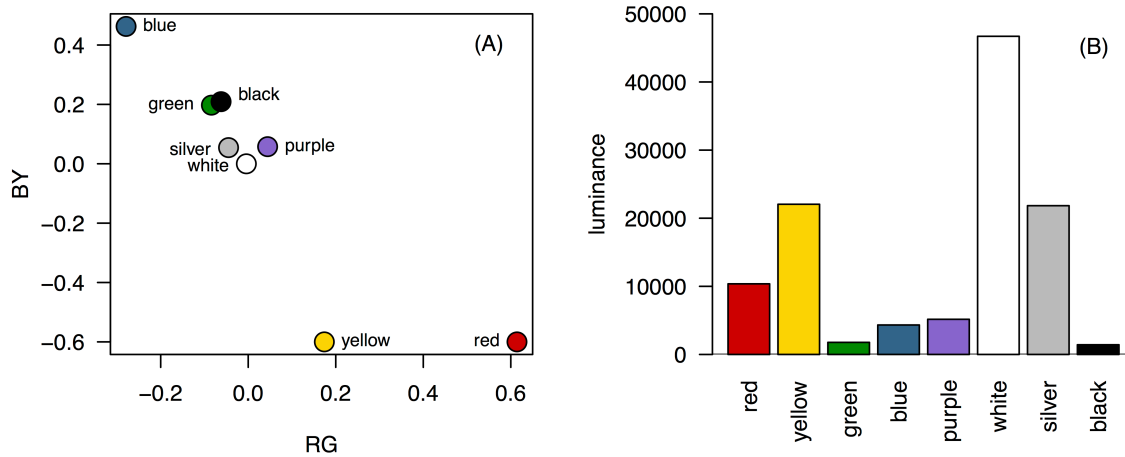
171

172 **Feeder colour analysis**

173 To objectively describe the colour of the feeders, photographs of the feeder lids
174 were taken in RAW format using a Canon Powershot G12 camera. Lids were placed into a
175 light tent (EZCube, Ventura, CA, USA) under daylight spectrum illumination with a white
176 reflectance standard (Ocean Optics, Dunedin, FL, USA).

177 Images were processed using the Image Calibration and Analysis Toolbox [44] plugin
178 for ImageJ 1.50i [45]. After using the toolbox to linearise and standardise the image against
179 the white standard, a patch on each feeder that was approximately the same distance and
180 orientation as the reflectance standard and free from specular reflections, was selected, and
181 the mean camera-specific RGB values of the patch were recorded (16-bit colour depth).

182 To summarise the luminance independent colour measures, RG and BY ratios were
183 calculated ($RG = (R-G)/(R+G)$; $BY = B - ((R+G)/2) / B + ((R+G)/2)$; Fig 1A). These ratios describe
184 the redness versus greenness (RG), and blueness versus yellowness (BY) of a stimulus and
185 approximate human and potential avian opponent colour channels [46]. Additionally,
186 luminance $((R+G+B)/3)$ is shown in Fig 1B. As the camera was not UV sensitive and had not
187 been characterised (i.e. the spectral sensitivity of each sensor measured), it was not
188 possible to measure reflectance in the UV range or transform the RGB values into avian
189 colour space [44].



190

191 **Fig 1: Analysis of feeder colour.** (A) RG and BY ratios, and (B) luminance for the 8 different

192 feeder colours

193

194 Ethical statement

195 Experiments were approved by the University of Hull's School of Biological,
196 Biomedical and Environmental Sciences and Faculty of Science and Engineering ethical
197 review committees before commencement. All avian work was observational, and carried
198 out at locations where supplementary feeding of birds already occurred and would continue
199 after data collection was completed. Permission to carry out fieldwork was granted by the
200 University of Hull (Thwaite Gardens), Richard Hampshire (Tophill Low Reserve Warden) and
201 Mark Rothery (Otley site owner). The field studies did not involve endangered or protected
202 species. All participation in the human colour preference was entirely voluntary and the
203 purpose of the experiment was explained to the participants either verbally or via an A4
204 poster displayed near the stand (Fig S2). Written consent was not obtained to ensure
205 participation was simple and to maximise the number of participants, and approved by the

206 institutional review boards above. No data on the participants (other than their choice of
207 colour) was collected.

208

209 **Results**

210 **Bird colour preference**

211 There was a significant effect of feeder colour on the number of visits to the feeders
212 ($F_{7, 875}=6.120$, $p < 0.001$; Fig 2A). Birds made significantly more visits to the silver feeder and
213 significantly fewer visits to the red and yellow feeders than any other colour (all $p < 0.05$;
214 table 2). Green was visited significantly more often than any other colour except silver, but
215 there was no difference in the number of visits to blue, purple, white and black.

216

217 **Table 2: Pairwise comparisons of visits to feeders.**

218 *Please see end of document for table 2 (landscape format)*

219 The cells above the diagonal show the z- and p-values, while the estimate \pm standard error is
220 below the diagonal. Significant p-values are highlighted in bold. Adjusted p-values following
221 false discovery rate control are presented.

222

223 For blue tits (Fig 2B, supporting table S1), there was a significant effect of colour on
224 number of visits ($F_{7, 749.73}=4.3575$, $P < 0.001$). Yellow and red were the least visited colours,
225 and were visited with similar regularity (table S1, $p > 0.05$). Yellow was visited significantly

226 less than all other colours except white ($p > 0.050$), while visits to red were not different
227 from white or green ($p > 0.05$). There were no differences in the number of visits between
228 the other colours ($p > 0.05$; table S1).

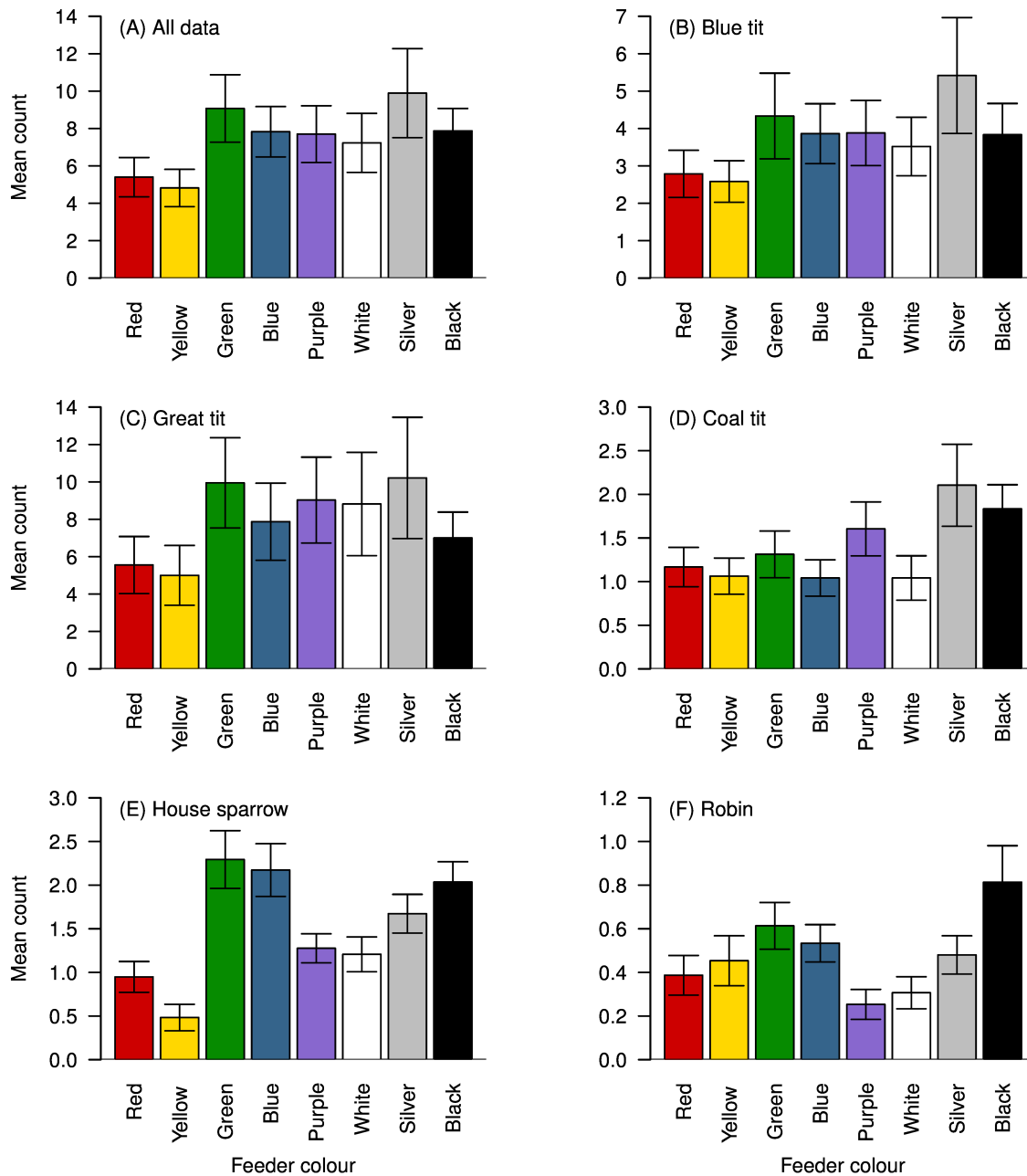
229 For great tits (Fig 2C, table S2), there was a significant effect of colour on number of
230 visits ($F_{7,259} = 2.671$, $p = 0.011$). There were significantly fewer visits to yellow than to all
231 other colours except red ($p < 0.05$ in all cases), while red was visited significantly less often
232 than green ($p = 0.017$). There were no other significant pairwise differences (table S2).

233 For coal tits, there was a significant overall effect of colour on visits ($F_{7,329}=3.796$, $p < 0.001$),
234 but no significant pairwise comparisons were found after correction for multiple testing (Fig
235 2D; table S3).

236 For house sparrows, there was a significant effect of colour on visits ($F_{7,399} = 11.139$,
237 $P < 0.001$). The yellow feeder was visited significantly less often than all other colours (Fig
238 2E, table S4, $p < 0.05$ in all cases), and red was visited less often than blue, green, silver and
239 black ($p < 0.05$). White and purple were visited less often than blue, green and black ($p <$
240 0.05) which were the colours visited most (although not significantly more than silver; table
241 S4)

242 For robins, there was a significant effect of colour on visits ($F_{7,518}=3.1033$, $p = 0.003$;
243 Fig 2F). Black, the most visited colour, was visited significantly more often than purple and
244 white ($p < 0.05$, table S5), the least visited colours, but no other pairwise comparisons were
245 significant.

246 There was no significant effect of colour on visits for greenfinch ($F_{7,140} = 1.3.383, p = 0.217$)
 247 or starling ($F_{7,84} = 1.232, P = 0.294$), and no other species was recorded more than 100 times
 248 during the sample period, so their preferences have not been analysed.



249

250 **Fig 2: Bird colour preferences.** Mean numbers of visits per observation period to feeders of
 251 each colour, for (A) all species combined, (B) Blue tit *Cyanistes caeruleus* (C) Great tit *Parus*

252 *major (D) Coal tit *Periparus ater* (E) House sparrow *Passer domesticus* and (F) Robin*

253 *Erithacus rubecula*. Error bars represent +/- 1 S.E.

254

255 **Human colour preference**

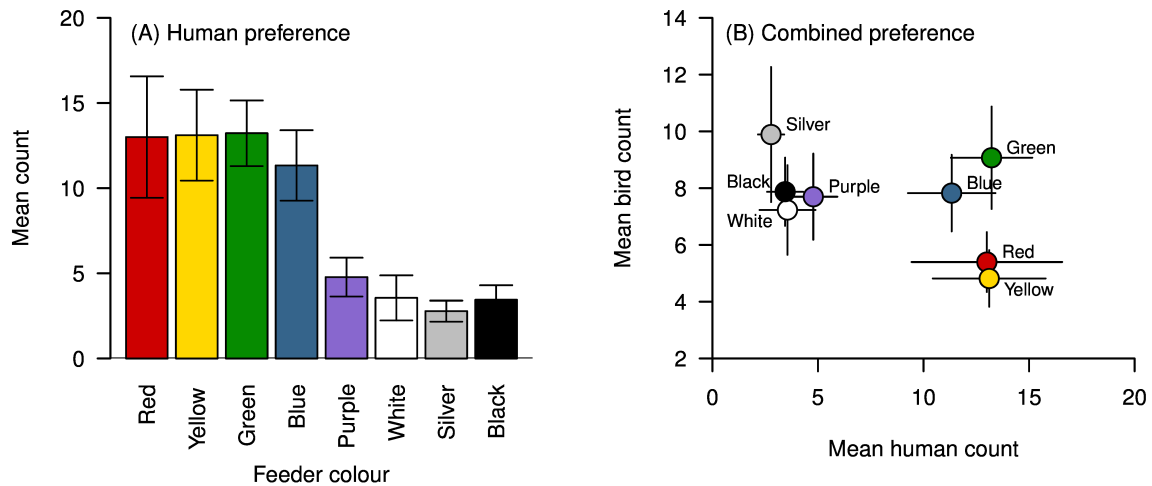
256 There was a significant effect of colour on the preferences observed in our survey
257 ($F_{1,7}=10.485$, $P<0.001$; Fig 3a). Pairwise comparisons revealed that red, yellow, green and
258 blue were preferred over purple, white, silver and black (table 3). Fig 3B shows the mean
259 number of visits by birds plotted against the mean number of votes from visitors, and
260 suggests that human and bird preferences do not necessarily align. Colours in the top right
261 of Fig 3B are those that received high visit rates from birds and high numbers of votes from
262 visitors, and we suggest those colours (green and to a lesser extent, blue) may be
263 simultaneously marketable and well-visited by birds. While red and yellow received high
264 numbers of votes from visitors, these are the colours that received the lowest numbers of
265 visits from birds.

266

267 **Table 3: Pairwise comparisons of numbers of votes for each colour.**

268 *Please see end of document for table 3 (landscape format)*

269 The cells above the diagonal show the z- and p-values, while the estimate \pm standard error is
270 below the diagonal. Significant p-values are highlighted in bold.



271

272 **Fig 3: Human colour preferences. (A)** Mean number of tokens placed into the container
273 corresponding to each coloured feeder by potential purchasers of bird feeders. **(B)** The
274 combined preferences of potential purchasers (x axis) and visits by all birds (y axis) for each
275 colour feeder. Error bars represent +/- 1 S.E.

276

277 Discussion

278 Overall, birds preferentially visited the silver feeders, followed by green, and made
279 fewer visits to the red and yellow feeders when all feeders were displayed simultaneously.
280 These patterns are likely driven by the preferences of the most abundant species at the
281 feeders (blue tits and great tits), which showed similar preferences to the overall patterns.
282 These patterns contrast with the preferences expressed by the potential purchasers of
283 feeders, who preferred red, yellow, green and blue, but rarely voted for silver. In terms of
284 feeder design, this suggests that green (and to a lesser extent, blue) may be simultaneously
285 marketable and well visited by birds. Our findings also suggest that different species of
286 birds may have different colour preferences, although the total number of visits by some
287 species was too low to evaluate this.

288

289 Silver and green feeders may be preferred over red and yellow for a variety of
290 reasons. Green and silver are common colours for birdfeeders, and familiarity with
291 particular colours may have played a role in determining preferences. In hummingbirds,
292 previous experience of particular colours plays a role in colour choice. Anna's (*Calypte anna*)
293 and rufous (*Salasphorus rufus*) hummingbirds preferentially choose red feeders if captured
294 from red-flowered *Ribes speciosum* plants, but prefer yellow if captured near yellow-
295 flowered *Nicotiana glauca* [38]. Hummingbirds can also be trained to prefer particular
296 colours when that colour is associated with higher quality rewards [31,35,39]. As the seed
297 quality in our feeders was identical, the preferences exhibited by the birds could have been
298 due to our choice of locations where birds were regularly fed, and thus familiar with
299 commonly coloured feeders.

300

301 In contrast, red and yellow are uncommon colours for seed dispensing bird feeders.
302 Neophobia in relation to food colour has been well documented in both birds (e.g. [47-51])
303 and other species [52,53]. Red and yellow are also associated with warning colouration and
304 aposematism, and may be avoided by foraging birds [54,55]. Red and yellow feeders may
305 also be more conspicuous against the background (while green and silver are more cryptic),
306 which may increase perceived predation risk [56]. However, these colours may also make
307 the resource more conspicuous from a distance [57] and thus brightly coloured feeders may
308 be effective in attracting birds to new foraging sites more rapidly: some evidence from
309 Anna's hummingbirds suggests that red feeders placed in novel locations initially attract
310 more birds than other colours [36], but red is a common colour of the nectar resource for

311 this species, and so may not be applicable to seed-feeding birds. Our experiment does not
312 allow us to speculate on whether particular colours would be more or less attractive to birds
313 if put out alone.

314

315 During data collection, we observed (but did not record) multiple events where a
316 competitor displaced feeding individuals from one feeder to another. This may mask feeding
317 preferences as individuals are then recorded at less preferred feeder colours, a limitation of
318 presenting all colours together. The ways in which different options are presented often
319 affects the choices that animals make. Hummingbirds offered a choice between red and
320 yellow-flowered *Mimulus aurantiacus* prefer to feed at the red morph [58], but in a hybrid
321 population where orange morphs occur, visit orange flowers more often than expected by
322 chance, given their prevalence in the population [28]. Preferences between two option may
323 also be affected by the addition of a third option (e.g. if A is preferred over B, and B over C,
324 then A is not necessarily preferred over C), violating the principle that choices are ‘rational’
325 and preferences are transitive [59,60]. Evidence suggests that the principle of rational
326 choice is violated by a range of species, including humans (e.g. [61-63]), honeybees (*Apis*
327 *mellifera* [64]), rufous hummingbirds [59,65], starlings [66] and grey jays (*Perisoreus*
328 *canadensis* [64]). By presenting all colours together (and covering a wide range of colour
329 options) we were able to overcome some of these issues associated with animal decision-
330 making.

331

332 Further work is needed to explore interspecific differences in colour preference: for
333 the bird feeder industry, it may be desirable to design and market feeders for particular

334 target species or groups of species - those that are seen as desirable by the people that feed
335 birds. Further questions include whether feeder colour is important for attracting birds to a
336 new feeding site, increasing avian visitor numbers at existing feeding sites, and whether
337 different types of feeders, such as those designed to dispense seeds, peanuts or nyjer seeds,
338 would attract more birds if they were different colours. Finally, other factors, such as
339 distance to cover, or the type and quality of food provided, may be more important in
340 determining the 'success' of a particular feeder than the colour, as in hummingbirds (e.g.
341 [35-39]) or these factors, and others, may trade off with colour in determining the number
342 of visits by birds, as they forage optimally [67].

343

344 **Acknowledgements**

345 We thank Rose Bull and Adam Lea for assistance with data collection, William Allen
346 for assistance with the feeder colour analysis, Martin McDaid and Lorrion Bright for useful
347 discussions, and Hornsea Garden Centre for allowing us to collect data on human choices.
348 Roland Ennos, Sue Hull and Katherine Jones provided useful feedback on earlier versions of
349 this manuscript.

350

351 **Supporting information**



352

353 **Fig S1: Birdfeeders in the field.** An example array of filled birdfeeders ready for
354 observations in the field. The colour order (from left to right) is: red, yellow, blue, silver,
355 green, purple, white, black. Colour order was randomised between trials.

356

357 **Fig S2: Poster explaining the project.** A copy of the poster explaining the project, as
358 displayed at the Science Festival and in the garden centre.

359

360 **Table S1: Pairwise comparisons of visits to feeders by blue tits.** The cells above the
361 diagonal show the z- and p-values, while the estimate \pm standard error is below the diagonal.
362 Significant p-values are highlighted in bold.

363

364 **Table S2: Pairwise comparisons of visits to feeders by great tits.** The cells above the
365 diagonal show the z- and p-values, while the estimate \pm standard error is below the diagonal.
366 Significant p-values are highlighted in bold.

367

368 **Table S3: Pairwise comparisons of visits to feeders by coal tits.** The cells above the diagonal
369 show the z- and p-values, while the estimate \pm standard error is below the diagonal.
370 Significant p-values are highlighted in bold.

371

372 **Table S4: Pairwise comparisons of visits to feeders by house sparrows.** The cells above the
373 diagonal show the z- and p-values, while the estimate \pm standard error is below the diagonal.
374 Significant p-values are highlighted in bold.

375

376 **Table S5: Pairwise comparisons of visits to feeders by robins.** The cells above the diagonal
377 show the z- and p-values, while the estimate \pm standard error is below the diagonal.
378 Significant p-values are highlighted in bold.

379 **References**

- 380 1. Fuller RA, Warren PH, Armsworth PR, Barbosa O, Gaston KJ. Garden bird feeding
381 predicts the structure of urban avian assemblages. *Divers Distrib.* 2008;14: 131–137.
382 doi:10.1111/j.1472-4642.2007.00439.x
- 383 2. Galbraith JA, Beggs JR, Jones DN, Stanley MC. Supplementary feeding restructures
384 urban bird communities. *P Natl Acad Sci. National Acad Sciences;* 2015;112: E2648–57.
385 doi:10.1073/pnas.1501489112
- 386 3. Department for Environment, Food and Rural Affairs (DEFRA). *Working with the grain*
387 *of nature: A biodiversity strategy for England.* London; 2002;: 180.

- 388 4. Davies ZG, Fuller RA, Loram A, Irvine KN, Sims V, Gaston KJ. A national scale inventory
389 of resource provision for biodiversity within domestic gardens. *Biol Cons.* 2009;142:
390 761–771. doi:10.1016/j.biocon.2008.12.016
- 391 5. Pet Food Manufacturers' Association. Annual Report 2015. In:
392 www.pfma.org.ukannual-reports. 2015.
- 393 6. Foy S. Enduring affection for birds as spend on wild bird care products increases
394 despite the mild weather. GfK Point of Sales Tracking Great Britain 2015. In:
395 [www.gfk.com/en-gb/insights/news/enduring-affection-for-birds-as-spend-on-wild-](http://www.gfk.com/en-gb/insights/news/enduring-affection-for-birds-as-spend-on-wild-bird-care-products-increases-despite-the-mild-weather/)
396 [bird-care-products-increases-despite-the-mild-weather/](http://www.gfk.com/en-gb/insights/news/enduring-affection-for-birds-as-spend-on-wild-bird-care-products-increases-despite-the-mild-weather/). 2016.
- 397 7. Gaston KJ, Fuller RA, Loram A, MacDonald C, Power S, Dempsey N. Urban domestic
398 gardens (XI): variation in urban wildlife gardening in the United Kingdom. *Biodivers*
399 *Conserv.* Springer Netherlands; 2007;16: 3227–3238. doi:10.1007/s10531-007-9174-6
- 400 8. Maller C, Townsend M, Pryor A, Brown P, St Leger L. Healthy nature healthy people:
401 “contact with nature” as an upstream health promotion intervention for populations.
402 *Health Promot Int.* 2006;21: 45–54. doi:10.1093/heapro/dai032
- 403 9. Jones DN, Reynolds SJ. Feeding birds in our towns and cities: a global research
404 opportunity. *J Avian Biol.* 2008;39: 265–271.
- 405 10. Brittingham MC, Temple SA. Impacts of supplemental feeding on survival rates of
406 black-capped chickadees. *Ecology.* Ecological Society of America; 1988;69: 581–589.
407 doi:10.2307/1941007
- 408 11. Martin TE, Karr JR. Behavioral plasticity of foraging maneuvers of migratory warblers:
409 multiple selection periods for niches. *Studies in Avian Biology.* 1990;13: 353–359.
- 410 12. Olsson O, Wiktander U, Nilsson SG. Daily foraging routines and feeding effort of a
411 small bird feeding on a predictable resource. *Proc Roy Soc Lond B. The Royal Society;*
412 2000;267: 1457–1461. doi:10.1098/rspb.2000.1164
- 413 13. Stephens DW. Decision ecology: Foraging and the ecology of animal decision making.
414 *Cogn Affect Behav Neurosci.* Springer-Verlag; 2008;8: 475–484.
415 doi:10.3758/CABN.8.4.475
- 416 14. Cowie RJ, Hinsley SA. Feeding ecology of great tits (*Parus major*) and blue tits (*Parus*
417 *caeruleus*), breeding in suburban gardens. *J Anim Ecol.* 1988;57: 611.
418 doi:10.2307/4928
- 419 15. Peach WJ, Sheehan DK, Kirby WB. Supplementary feeding of mealworms enhances
420 reproductive success in garden nesting house sparrows *Passer domesticus*. *Bird Study.*
421 Taylor & Francis; 2014;61: 378–385. doi:10.1080/00063657.2014.918577
- 422 16. Grubb TC, Cimprich DA. Supplementary food Improves the nutritional condition of
423 wintering woodland birds: Evidence from ptilochronology. *Ornis Scandinavica.*
424 1990;21: 277. doi:10.2307/3676392

- 425 17. Daniels GD, Kirkpatrick JB. Does variation in garden characteristics influence the
426 conservation of birds in suburbia? *Biol Cons.* 2006;133: 326–335.
- 427 18. Robinson RA, Siriwardena GM, Crick H. The population decline of the starling, *Sturnus*
428 *vulgaris*, in Great Britain: patterns and causes. *Acta Zoologica Sinica.* 2006;52 (suppl):
429 550–553.
- 430 19. Rolshausen G, Segelbacher G, Hobson KA, Schaefer HM. Contemporary evolution of
431 reproductive isolation and phenotypic divergence in sympatry along a migratory
432 divide. *Current Biology.* 2009;19: 2097–2101. doi:10.1016/j.cub.2009.10.061
- 433 20. Kelber A, Vorobyev M, Osorio D. Animal colour vision--behavioural tests and
434 physiological concepts. *Biological Reviews of the Cambridge Philosophical Society.*
435 2003;78: 81–118.
- 436 21. Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, et al. An
437 integrative framework for the appraisal of coloration in nature. *Am Nat.* 2015;185:
438 705–724. doi:10.1086/681021
- 439 22. Endler J, Mielke P. Comparing entire colour patterns as birds see them. *Biological*
440 *Journal of the Linnean Society.* 2005;86: 405–431.
- 441 23. Marples G. Experiments on colour sense in birds. *British Birds.* 1933;26: 238–243.
- 442 24. Willson MF, Graff DA, Whelan CJ. Color preferences of frugivorous birds in relation to
443 the colors of fleshy fruits. *Condor. JSTOR;* 1990;92: 545–555.
- 444 25. Duan Q, Quan R-C. The effect of color on fruit selection in six tropical Asian birds.
445 *Condor. University of California Press;* 2013;115: 623–629.
446 doi:10.1525/cond.2013.120111
- 447 26. Hartley L, O'Connor C, Waas J, Matthews L. Colour preferences in North Island robins
448 (*Petroica australis*): implications for deterring birds from poisonous baits. *New Zeal J*
449 *Ecol.* 1999;23: 255–259. doi:10.2307/24054779
- 450 27. Lunau K, Papiorek S, Eltz T, Sazima M. Avoidance of achromatic colours by bees
451 provides a private niche for hummingbirds. *J Exp Biol. The Company of Biologists Ltd;*
452 2011;214: 1607–1612. doi:10.1242/jeb.052688
- 453 28. Handelman C, Kohn JR. Hummingbird color preference within a natural hybrid
454 population of *Mimulus aurantiacus* (Phrymaceae). *Plant Species Biology.* 2014;29:
455 65–72. doi:10.1111/j.1442-1984.2012.00393.x
- 456 29. Vickery RK Jr, Vickery PK Jr. Pollinator preferences for yellow, orange, and red flowers
457 of *Mimulus verbenaceus* and *M. cardinalis*. *The Great Basin Naturalist.* 1992;52: 145–
458 148. doi:10.2307/41712708
- 459 30. Vickery RK. Speciation in *Mimulus*, or, can a simple flower color mutant lead to
460 species divergence? *The Great Basin Naturalist.* 1995;55: 177–180.
461 doi:10.2307/41712884

- 462 31. Meléndez-Ackerman E, Campbell DR, Waser NM. Hummingbird behavior and
463 mechanisms of selection on flower colour in *Ipomopsis*. *Ecology*. Ecological Society of
464 America; 1997;78: 2532–2541. Available: <http://www.jstor.org/stable/2265912>
- 465 32. Grant KA. A hypothesis concerning the prevalence of red coloration in California
466 hummingbird flowers. *American Naturalist*. 1966;100: 85–97. doi:10.2307/2459422
- 467 33. Bené F. Experiments on the color preference of black-chinned hummingbirds. *Condor*.
468 *The Condor*; 1941;43: 237–242. doi:10.2307/1364506
- 469 34. Miller RS, Miller RE. Feeding activity and color preference of ruby-throated
470 hummingbirds. *Condor*. 1971;73: 309–313. doi:10.2307/1365757
- 471 35. Collias NE, Collias EC. Anna's hummingbirds trained to select different colors in
472 feeding. *Condor*. *The Condor*; 1968;70: 273–274. Available:
473 <https://sora.unm.edu/sites/default/files/journals/condor/v070n03/p0273-p0274.pdf>
- 474 36. Wheeler TG. Experiments in feeding behavior of the Anna hummingbird. *The Wilson*
475 *Bulletin*. 1980;92: 53–62. doi:10.2307/4161293
- 476 37. Wagner HO. Food and feeding habits of Mexican hummingbirds. *The Wilson Bulletin*.
477 1946;58: 69–93. doi:10.2307/4157484
- 478 38. Stiles FG. Taste preferences, color preferences, and flower choice in hummingbirds.
479 *Condor*. 1976;78: 10–26.
- 480 39. Goldsmith TH, Goldsmith KM. Discrimination of colors by the black-chinned
481 hummingbird, *Archilochus alexandri*. *J Comp Physiol*. Springer-Verlag; 1979;130: 209–
482 220. doi:10.1007/BF00614607
- 483 40. Thomas C. Do different coloured feeders attract different birds? In:
484 www.rspb.org.uk/makeahomeforwildlifeadviceexpertpreviousfeedercolour.aspx. 2007.
- 485 41. R Core Team. R: A language and environment for statistical computing. v 3.2.1.
486 Vienna: R Foundation for Statistical Computing; 2015.
- 487 42. Harrison XA. Using observation-level random effects to model overdispersion in count
488 data in ecology and evolution. *PeerJ*. *PeerJ Inc*; 2014;2: e616. doi:10.7717/peerj.616
- 489 43. Benjamini Y, Hochberg Y. Controlling the false discovery rate: a practical and powerful
490 approach to multiple testing. *J R Stat Soc Series B Stat Methodol*. 1995;57: 289–300.
- 491 44. Troscianko J, Stevens M. Image calibration and analysis toolbox - a free software suite
492 for objectively measuring reflectance, colour and pattern. Rands S, editor. *Methods in*
493 *Ecology and Evolution*. 2015;6: 1320–1331. doi:10.1111/2041-210X.12439
- 494 45. Schneider CA, Rasband WS, Eliceiri KW. NIH Image to ImageJ: 25 years of image
495 analysis. *Nat Meth*. 2012;9: 671–675.
- 496 46. Cuthill IC. Colour Perception. In: McGraw KJ, editor. *Bird Colouration: Mechanisms*

- 497 and measurements. 2006.
- 498 47. Brigham AJ, Sibly RM. A review of the phenomenon of neophobia. In: Cowan DP,
499 Feare CJ, editors. Advances in vertebrate pest management. Furth: Advances in
500 vertebrate pest management. Filander ...; 1999. pp. 67–84.
- 501 48. Roper TJ, Marples NM. Colour preferences of domestic chicks in relation to food and
502 water presentation. Appl Anim Behav Sci. 1997;54: 207–213.
- 503 49. Roper TJ. Responses of domestic chicks to artificially coloured insect prey: effects of
504 previous experience and background colour. Anim Behav. 1990;39: 466–473.
505 doi:10.1016/S0003-3472(05)80410-5
- 506 50. Kelly DJ, Marples NM. The effects of novel odour and colour cues on food acceptance
507 by the zebra finch, *Taeniopygia guttata*. Anim Behav. 2004;68: 1049–1054.
508 doi:10.1016/j.anbehav.2004.07.001
- 509 51. Boogert N, Reader S, Laland K. The relation between social rank, neophobia and
510 individual learning in starlings. Anim Behav. 2006;72: 1229–1239.
- 511 52. Thomas RJ, King TA, Forshaw HE, Marples NM, Speed MP, Cable J. The response of
512 fish to novel prey: evidence that dietary conservatism is not restricted to birds. Behav
513 Ecol. 2010;21: 669–675. doi:10.1093/beheco/arq037
- 514 53. Richards EL, Thomas RJ, Marples NM, Snellgrove DL, Cable J. The expression of dietary
515 conservatism in solitary and shoaling 3-spined sticklebacks *Gasterosteus aculeatus*.
516 Behav Ecol. 2011;22: 738–744. doi:10.1093/beheco/arr047
- 517 54. Ruxton G, Sherratt T, Speed M. Avoiding attack: The evolutionary ecology of crypsis,
518 warning signals, and mimicry. Oxford: Oxford University Press; 2004.
- 519 55. Exnerova A, Stys P, Fucikova E, Vesela S, Svadova K, Prokopova M, et al. Avoidance of
520 aposematic prey in European tits (Paridae): learned or innate? Behav Ecol. Oxford
521 University Press; 2006;18: 148–156. doi:10.1093/beheco/arl061
- 522 56. Ruiz-Rodríguez M, Avilés JM, Cuervo JJ, Parejo D, Ruano F, Zamora-Muñoz C, et al.
523 Does avian conspicuous colouration increase or reduce predation risk? Oecologia.
524 2013;173: 83–93. doi:10.1007/s00442-013-2599-6
- 525 57. Willson MF, Whelan CJ. The evolution of fruit color in fleshy-fruited plants . American
526 Naturalist. 1990;136: 790–809. doi:10.2307/2462168
- 527 58. Streisfeld MA, Kohn JR. Environment and pollinator-mediated selection on parapatric
528 floral races of *Mimulus aurantiacus*. J Evol Biol. Blackwell Publishing Ltd; 2007;20:
529 122–132. doi:10.1111/j.1420-9101.2006.01216.x
- 530 59. Bateson M, Healy SD, Hurly TA. Irrational choices in hummingbird foraging behaviour.
531 Anim Behav. 2002;63: 587–596. doi:10.1006/anbe.2001.1925
- 532 60. Schuck-Paim C, Pompilio L, Kacelnik A. State-dependent decisions cause apparent

- 533 violations of rationality in animal choice. PLoS Biology. Public Library of Science;
534 2004;2: e402. doi:10.1371/journal.pbio.0020402
- 535 61. Tversky A, Simonson I. Context-Dependent Preferences. Management Science.
536 INFORMS; 1993;39: 1179–1189. doi:10.1287/mnsc.39.10.1179
- 537 62. Tversky A. Intransitivity of preferences. Psychol Rev. American Psychological
538 Association; 1969;76: 31–48. doi:10.1037/h0026750
- 539 63. Simonson I, Tversky A. Choice in context: Tradeoff contrast and extremeness aversion.
540 J Mark Res. 1992;29: 281–295.
- 541 64. Shafir S, Waite T, Smith B. Context-dependent violations of rational choice in
542 honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*). Behav Ecol Sociobiol.
543 2002;51: 180–187. doi:10.1007/s00265-001-0420-8
- 544 65. Bateson M, Healy SD, Hurly TA. Context-dependent foraging decisions in rufous
545 hummingbirds. Proc Roy Soc Lond B. 2003;270: 1271–1276.
546 doi:10.1098/rspb.2003.2365
- 547 66. Schuck-Paim C. Rationality in risk-sensitive foraging choices by starlings. Anim Behav.
548 2002;64: 869–879. doi:10.1006/anbe.2003.2003
- 549 67. Davies NB, Krebs JR, West SA. An Introduction to Behavioural Ecology. 4 ed.
550 Chichester: Wiley-Blackwell; 2012.
- 551
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553 **Table 2:** Pairwise comparisons of visits to feeders.

	Red	Yellow	Green	Blue	Purple	White	Silver	Black
Red	-	z = -2.042 p = 0.052	z = -10.765 p < 0.001	z = -7.383 p < 0.001	z = -7.129 p < 0.001	z = 5.793 p < 0.001	z = 12.751 p < 0.001	z = -7.614 p < 0.001
Yellow	-0.114±0.056	-	z = -12.650 p < 0.001	z = -9.440 p < 0.001	z = -9.093 p < 0.001	z = -7.779 p < 0.001	z = -14.586 p < 0.001	z = -9.569 p < 0.001
Green	-0.519±0.048	-0.633±0.050	-	z = 3.413 p = 0.001	z = -3.774 p < 0.001	z = -5.128 p < 0.001	z = 2.115 p = 0.046	z = 3.278 p = 0.001
Blue	-0.372±0.050	-0.485±0.051	0.148±0.043	-	z = -0.363 p = 0.743	z = -1.728 p = 0.098	z = 5.512 p < 0.001	z = -0.135 p = 0.892
Purple	-0.355±0.050	-0.469±0.052	-0.164±0.043	-0.016±0.045	-	z = -1.365 p = 0.193	z = 5.870 p < 0.001	z = -0.499 p = 0.666
White	0.292±0.050	-0.406±0.052	-0.277±0.044	-0.079±0.046	-0.063±0.046	-	z = -7.212 p < 0.001	z = -1.863 p = 0.076
Silver	0.606±0.047	-0.719±0.049	0.086±0.041	0.234±0.042	0.250±0.043	-0.313±0.043	-	z = 5.378 p < 0.001
Black	-0.378±0.005	-0.491±0.051	0.142±0.043	-0.006±0.045	-0.022±0.045	-0.085±0.046	0.228±0.042	-

554 The cells above the diagonal show the z- and p-values, while the estimate ± standard error is below the diagonal. Significant p-values are

555 highlighted in bold.

556 **Table 3:** Pairwise comparisons of votes by visitors to the garden centre and science festival.

	Red	Yellow	Green	Blue	Purple	White	Silver	Black
Red	-	z = -0.474 p = 0.810	z = 0.620 p = 0.715	z = -0.182 p = 0.0.887	z = 3.285 p = 0.003	z = -4.014 p < 0.001	z = -4.234 p < 0.001	z = 3.759 p = 0.001
Yellow	-0.722±1.522	-	z = 0.146 p = 0.884	z = -0.657 p = 0.718	z = 2.810 p = 0.011	z = 3.540 p = 0.002	z = 3.759 p = 0.001	z = 3.285 p = 0.003
Green	0.944±1.522	0.222±1.522	-	z = -0.803 p = 0.659	z = -2.664 p = 0.015	z = -3.394 p = 0.002	z = -3.613 p = 0.001	z = 3.139 p = 0.004
Blue	-0.278±1.522	-1.000±1.522	-1.222±1.522	-	z = -3.467 p = 0.002	z = -4.197 p < 0.001	z = -4.416 p < 0.001	z = 3.942 p < 0.001
Purple	5.000±1.522	4.278±1.522	-4.056±1.522	-5.278±1.522	-	z = -0.730 p = 0.688	z = -0.949 p = 0.568	z = 0.474 p = 0.810
White	-6.111±1.522	5.389±1.522	-5.167±1.522	-6.389±1.522	-1.111±1.522	-	z = 0.219 p = 0.891	z = -0.255 p = 0.895
Silver	-6.444±1.522	5.722±1.522	-5.500±1.522	-6.722±1.522	1.444±1.522	0.333±1.522	-	z = -0.474 p = 0.810
Black	5.722±1.522	5.000±1.522	4.778±1.522	6.000±1.522	0.722±1.522	-0.389±1.522	-0.722±1.522	-

557 The cells above the diagonal show the t- and p-values, while the estimate ± standard error is below the diagonal. Significant p-values are

558 highlighted in bold.