

1 **Personality in blue tits (*Cyanistes caeruleus*) and its effect on their**
2 **breeding success**

3 Claire Colchester (Anglia Ruskin University, East Road, Cambridge, CB1
4 1PT) claire.colchester@rocketmail.com (corresponding author)

5 Nancy M Harrison (Anglia Ruskin University, East Road, Cambridge, CB1
6 1PT) nancy.harrison@anglia.ac.uk

7 **Contributions** Both authors designed the research, CC collected the data,
8 both authors analysed the data, CC wrote the first draft and both authors
9 contributed substantially to revisions.

10 **Running title** Neophobia in blue tits

11 **Keywords** Personality, behavioural syndrome, neophobia, breeding
12 success, *Cyanistes caeruleus*

13 **Abstract** 100 words

14 **Main text** 3236 words

15 35 references and 4 figures

16

17

18

19

20

21 **ABSTRACT**

22 In this study, we investigated whether blue tits (*Cyanistes caeruleus*) showed
23 consistent variation in neophobia responses. The experiment represents a
24 test of how personality, consistent individual differences in behaviour, may
25 have fitness consequences. The experimental design consisted of a control
26 observation followed by two neophobia tests, during which the parent's
27 behaviour was recorded using the instantaneous sampling method. Blue tits
28 showed consistent variation in neophobia responses, which was related to
29 total offspring biomass, but not to mean offspring weight or fledging success.
30 GLMM analyses suggest that there may be ideal neophobia trait
31 combinations in breeding pairs that maximises breeding success.

32

33

34

35

36

37

38

39

40

41

42 INTRODUCTION

43 Neophobia is the fear of novelty and is an indicator of an animal's internal
44 state of risk perception as well as its inclination to take risks (Echeverría &
45 Vassallo 2008). The tendency of individuals to take risks, particularly in novel
46 contexts is termed as boldness (Azevedo & Young 2006; Atwell *et al.* 2012).
47 Boldness is a component of behavioural syndromes, which are combinations
48 of behavioural axes that are consistent over time and functional contexts
49 (Lendvai *et al.* 2011; Gabriel & Black 2012b). Examples of these behavioural
50 axes include: bold-shy, aggressive-docile, risk adverse, extrovert-cautious
51 and slow-fast (Gabriel & Black 2010; Lendvai *et al.* 2011). For example, in a
52 study of Stellar's Jay (*Cyanocitta stelleri*) bold individuals showed fast
53 exploratory and aggressive behaviours, whereas shy individuals showed
54 slow exploratory and docile behaviours (Gabriel & Black 2012b).

55 Scientific methods have been applied to experiments to eliminate subjective
56 assessments and prevent anthropomorphism (Tetley & O'Hara 2012). Many
57 previous studies have used wild caught great tits (*Parus major*) under
58 laboratory conditions to control environmental conditions, but it is not known
59 if the results reflect how the individuals behave in a wild environment
60 (Dingemanse *et al.* 2002; Klueen *et al.* 2012). Moreover, captured birds will
61 generally be bolder, so the sampled population will be homogeneous as
62 shown in collared flycatchers *Ficedula albicollis* (Garamszegi *et al.* 2009).
63 Captivity testing may exaggerate behaviour differences as handling and
64 capture stress may cause shy individuals to take longer to eat or explore in a
65 novel environment (Herborn *et al.* 2010). However, it is important to

66 understand how an animal behaves in one context because that may
67 influence how it behaves in another; for example how it cares for its offspring
68 might reflect how it reacts towards mates and predators (Dall *et al.* 2012).

69 Comparing cautious, shy slow-exploring individuals with aggressive, bold,
70 fast-exploring individuals highlights a trade-off between the predator-adverse
71 prioritising survival and the more risk-prone behaviour that boosts
72 productivity (Aplin *et al.* 2013). Exploratory behaviour varies depending on
73 the time of year and reflects the current environmental conditions; for
74 example, faster exploratory behaviour during spring may be a response to
75 the reproductive season (Dingemanse *et al.* 2012). Fluctuating pressures on
76 personality from competition for food and territory causes differing
77 exploratory tendencies in great tit, which can predict survival between the
78 sexes and over time (Dingemanse *et al.* 2004; David *et al.* 2011). Boldness
79 may affect fitness because it influences the way individuals explore novel
80 environments, interact with conspecifics and react to predators, showing that
81 personality and life history strategies are linked (Réale *et al.* 2000).

82 Monogamous animals, such as barnacle geese (*Branta leucopsis*), often
83 achieve higher reproductive success when their partner has similar traits to
84 their own (Black, 2001; Gabriel & Black, 2012b). Choosing a partner of
85 similar traits allows individuals to engage in similar activities and spend more
86 time together, strengthening their bond and co-ordinating their behaviour
87 (Gabriel & Black, 2010, 2012b). In great tit, slow-exploring females that are
88 more successful at nesting and produce larger offspring are attracted to fast-
89 exploring males that hold higher quality territories (Both *et al.* 2005).

90 Assortative pairings in great tits (e.g. pairing between parents of the same
91 personality type) had the highest number of recruits compared to other
92 combinations and produced offspring with the highest body mass
93 (Dingemanse *et al.* 2004; Dingemanse & Reale 2005). However, disassortive
94 pairings may be favoured over an entire lifespan because it allows birds at
95 the personality extremes to increase fitness (Both *et al.* 2005).

96 Personality differences could play a key role in explaining the lack of true
97 genetic monogamy in socially monogamous species, such as blue tits
98 (*Cyanistes caeruleus*) as male promiscuity can be predicted by his mates'
99 personality (Patrick *et al.* 2012). In great tits, bolder, faster, highly exploratory
100 individuals have higher rates of extra-pair copulations and therefore a greater
101 chance of increased lifetime reproductive success and fitness if all offspring
102 survive to breed themselves (Both *et al.* 2005; Patrick *et al.* 2012). Slow
103 exploring, shy individuals may be better parents because they respond to
104 more easily to environmental change and do not take unnecessary risks
105 (Both *et al.* 2005; Boon *et al.* 2007).

106 The aim of this study was to investigate if there was a consistent individual
107 variation in neophobia responses in blue tits. We used the neophobia data
108 collected to explore if different combinations of personality traits in breeding
109 pairs affected their breeding success.

110

111

112

113 **METHODS**

114 This study took place in the Cambridge University Botanic Garden (CUBG),
115 which is situated less than a mile from Cambridge city centre in the United
116 Kingdom (52° 11' 39.422" N, 0° 07' 33.933" E). The CUBG is ≈16.5ha in size
117 and contains varied garden and parkland habitat holding a collection of over
118 8000 labelled plant species in different settings (CUBG, 2005). The blue tits
119 and great tits breeding in nest boxes in the CUBG have been the subject of
120 study for 15 years; 42 nest boxes have been maintained in the gardens and
121 the majority have been utilised by birds each year (Mackenzie 2010). The
122 nest boxes varied in design with half being 'blue tit specific', meaning that the
123 hole size excludes great tits (Mackenzie *et al.* 2014).

124

125 **Measurement of breeding success**

126 To evaluate breeding success nest boxes were regularly checked beginning
127 1st April each year by the research team to obtain first egg date, clutch size
128 and hatch date for each nest. Offspring were ringed (by qualified licence
129 holders) and weighed at 11 days old. Finally, following the breeding season,
130 nest boxes were checked for dead offspring to score fledging success; some
131 error existed as a result of predation, or adults removing dead offspring, but
132 this was minimal

133 Knowing the age of the offspring was crucial for the current study in order to
134 establish equivalent data on brood biomass and mean offspring weight (the
135 primary measure of breeding success), but also for ethical reasons as the
136 experiment was only carried out after the offspring were 6 days old (when

137 desertion becomes unlikely). Each nest was under observation throughout
138 incubation and early brood provisioning, and as such it became apparent if
139 there was a missing parent or if a brood was highly vulnerable and likely to
140 perish. These unhealthy/weak broods were excluded from the study. They
141 may have been interesting in the context of the study but it was deemed
142 unethical to include them in the experimental trials. Observations were not
143 carried out on day 11 when the offspring were weighed and ringed.

144 **Field Experiments**

145 Tests for neophobia were carried out on pairs breeding in the nest boxes
146 after their offspring were 6 days old and healthy. During the 2013 season,
147 data collection took place from 20th May 2013 until 9th June 2013 as the
148 weather delayed the breeding season by several weeks. Data collection in
149 2014 took place from 26th April 2014 until 17th May 2014. Data were not
150 collected in extreme weather conditions, such as heavy rain and strong
151 winds. Thirty-four individuals or seventeen breeding pairs were tested during
152 this study.

153 The behaviour of the parent birds was recorded using instantaneous
154 sampling method (Martin & Bateson 2007), permitting the collection of data
155 on provisioning rate and time taken to return to the nest box following initial
156 disturbance (latency). This sampling method allowed the recording of
157 behavioural states at a given point in time, but did not take into account
158 event or rare behaviours. There was an interval of thirty seconds between
159 sampling points, at which time the behaviour of both individuals was
160 recorded (“Nest box”, “In sight” and “Out of sight”). During the breeding

161 season, parent birds are constantly provisioning for their offspring, whether
162 travelling to or from a foraging site or feeding their offspring. During the short
163 experimental trials, we rarely saw the parents at the nest box at the same
164 time, so we believe that the risk of one parent influencing the other to be low.

165 The study was carried out on a population of colour ringed birds, however
166 the observations of birds during the experimental trials did not always permit
167 reading colour rings. Furthermore, not all birds in the study were ringed
168 (30% were known individuals). Identifying the male and female within a pair
169 when making observations depended on our knowledge of the different
170 behaviours of males and females at the nest. Based on years of experience
171 of watching known (marked) birds, we (N Harrison) have learned that the
172 approach to the nest box of females differs from males consistently; females
173 approach the nest box rapidly, flying directly into the hole, not stopping to
174 perch. Males usually pause on a perch, or the box itself, before entering the
175 hole. There are some cases in which the birds interact, and the pattern
176 changes, but in these instances the identity or sex of the individuals
177 becomes evident. Our knowledge of the differences between sexes in their
178 behaviour at the nest is unpublished, but in this study we confidently
179 identified most of the birds as either the male or female within the pair. (Out
180 of a total of 602 observations, 51 individuals were unidentifiable distributed
181 across 35 nest boxes).

182 The control observation took place first. The nest box was approached with a
183 ladder as if a nest box check was taking place. The roof of the nest box was
184 touched to simulate the placement of a novel object, but no object was left

185 during the control. The observer retreated 20m-30m away from the nest box,
186 preferably to a public place (such as a footpath) where birds are habituated
187 to human presence. Minas (2015) showed that Eurasian coot (*Fulica atra*) in
188 urban areas paid little or no attention to human presence. Aided by
189 binoculars, the observer recorded the parent's behaviour every thirty
190 seconds for a twenty minute observation period.

191 The above was repeated with two novel object trials to test the repeatability
192 of each individual's responses. Each object was placed on the roof of the
193 nest box. The order in which the birds were exposed to novel objects was
194 randomly changed with each nest box. The novel object was removed as
195 soon as the observation was completed. All observations (one control and
196 two neophobia tests) took place on the same day to control for provisioning
197 differences depending on the age of the offspring, with an interval of one
198 hour between experimental trials, more than enough time for pairs to return
199 fully to provisioning behaviour (see Hinsley *et al.* 2011). All observations
200 were carried out by the same observer (C. Colchester).

201 Fig. 1 shows the four novel objects (two from 2013 and two from 2014) used
202 in this study. The novel objects were chosen because it was thought that
203 they were not something the birds would normally encounter.

204 Individual neophobia trait was allocated using changes in provisioning rate in
205 response to the novel object. The difference of each trial from the control for
206 each individual was recorded and an average taken. If the value was
207 between 5 and 2, the response to the novel object was higher than in the
208 control and therefore the individual was bold. If the value was between -5

209 and -2, the response to the novel object was lower than in the control and
210 therefore the individual was shy. Individuals in the middle of the spectrum
211 (between 2 and -2) were referred to as mid.

212 **Analysis**

213 In the first instance, paired t-tests were used to compare the differences in
214 the neophobia responses (provisioning and latency) for each individual
215 between the control and trials to test whether an individual responded to the
216 novel object. The distribution of the data for latency was non-normal and
217 required transformation (ln); provisioning data had a normal distribution.
218 General Linear Mixed Models (GLMM) were used to test for individual
219 consistency to novel objects (provisioning, latency) with nest box as a
220 random variable, including sex and clutch size as fixed factors, and
221 responses to the control and the alternative trial as covariates. The
222 relationship between neophobia trait and breeding success was also tested
223 using GLMMs. The response variable was brood biomass or mean offspring
224 mass, with nest box as a random variable and neophobia trait for the male
225 and the female at a nest box as fixed factors. A further test of breeding
226 success was carried out with fledging success (% eggs to leave nest as
227 fledglings) as the response variable with General Estimating Equations
228 (GEE) using a Poisson distribution with nest box as a repeated measure and
229 neophobia trait for the male and female as fixed factors.

230 The computer software used for statistical analysis was IBM SPSS Statistics
231 20.0 (IBM Corporation 2012).

232 For all statistical tests $\alpha = 0.05$, indication of a 95% confidence level.

233 **RESULTS**

234 **Consistent individual variation in neophobia responses**

235 The results of the paired t-tests indicated the field experiments was
236 effectively testing for responses to novel objects, with significant differences
237 between the trials and the control. In repeat observations of individuals at
238 nest boxes ($n = 34$), there was a difference in provisioning rate between the
239 control and trial 1 (paired t-test: $t_{33} = 5.235$, $P = <0.001$; Fig 2.) and between
240 the control and trial 2 (paired t-test: $t_{33} = 3.071$, $P = 0.004$; Fig. 2). There was
241 a difference in provisioning rate between trial 1 and trial 2 (paired t-test: $t_{33} =$
242 -2.231 , $P = 0.033$; Fig. 2).

243 There was a difference in latency between the control and trial 1 (paired t-
244 test: $t_{33} = -3.420$, $P = 0.002$; Fig. 3), but not between the control and trial 2
245 (paired t-test: $t_{33} = -1.392$, $P = 0.173$; Fig. 3). There was a difference in
246 latency between trial 1 and trial 2 (paired t-test: $t_{33} = 2.242$, $P = 0.032$; Fig.
247 3).

248 Further analysis using mixed models showed that provisioning rates for the
249 two trials were significantly related for each individual bird (GLMM: $F_{1,1} =$
250 7.968 , $P = 0.009$) and not related to clutch size (GLMM: $F_{1,4} = 0.871$, $P =$
251 0.510), sex (GLMM: $F_{1,1} = 0.005$, $P = 0.947$) or control trial (GLMM: $F_{1,1} =$
252 0.000 , $P = 0.986$). Latency for trial 2 was significantly related to the control
253 (GLMM: $F_{1,1} = 7.613$, $P = 0.010$) and trial 1 (GLMM: $F_{1,1} = 4.773$, $P = 0.038$)
254 for each individual, but not related to clutch size (GLMM: $F_{1,4} = 0.373$, $P =$
255 0.826) or sex (GLMM: $F_{1,1} = 2.737$, $P = 0.110$).

256 **The relationship between individual neophobia trait and breeding**
257 **success**

258 Neophobia traits were significant in explaining the pattern in total offspring
259 biomass (n=17) in both males (GLMM: $F_{1,2} = 8.033$, $P = 0.006$, Fig. 4a) and
260 females (GLMM: $F_{1,2} = 4.026$, $P = 0.046$, Fig. 4a). Interaction between the
261 two variables was tested and was not significant (GLMM: $F_{1,2} = 1.396$, $P =$
262 0.296).

263 For females, the biomass of the broods raised by bold individuals was
264 significantly greater than those raised by shy individuals (GLMM: $t_{12} = -2.735$,
265 $P = 0.018$) and 'mid' (GLMM: $t_{12} = -2.566$, $P = 0.025$). For males, the
266 biomass of the broods raised by shy individuals was greater than the
267 biomass of those raised by bold individuals (GLMM: $t_{12} = 2.318$, $P = 0.039$),
268 but there was no significant difference between the biomass of bold and 'mid'
269 individuals (GLMM: $t_{12} = -0.350$, $P = 0.732$).

270 Male (GLMM: $F_{1,2} = 0.039$, $P = 0.962$, Fig. 4b) and female (GLMM: $F_{1,2} =$
271 0.031, $P = 0.969$, Fig. 4b) neophobia traits were not significant in explaining
272 the pattern in mean offspring weight. Nor was fledging success found to
273 relate to neophobia trait (GEE model – male: Wald $X^2 = 0.856$, $df = 2$, $P =$
274 0.652; female: Wald $X^2 = 0.623$, $df = 2$, $P = 0.732$).

275

276 **DISCUSSION**

277 This study showed that there was consistent variation in the neophobia
278 responses of blue tits to a novel object placed on their nest box. This can be

279 concluded from the significant differences of both trials from the control. For
280 both provisioning and latency data, clutch size and sex did not explain the
281 differences in behaviour.

282 Individual neophobia trait may have had an effect on the productivity of a pair
283 as measured by total offspring biomass, but not on mean offspring weight
284 and fledging success. The pattern was not the same for each sex, with larger
285 broods raised by shy males, and by bold females. Although there was no
286 significant interaction between the sexes, these results suggest that there
287 may exist favourable pair combination for neophobia trait that merits further
288 research. If neophobia trait has significant implications for lifetime
289 reproductive success, then the personality of partner has important
290 consequences.

291 Both *et al.* (2005) showed that assortative pairs at the extremes of
292 exploratory and aggression axes had the highest reproductive success in
293 terms of the amount of offspring produced. Yet, intermediate exploring birds
294 had the highest survival and recruitment across years and sexes (Both *et al.*
295 2005; Mutzel *et al.* 2013). Disassortative mating can be successful when fast
296 exploring males that hold high quality habitats pair with slow exploring
297 females that nested well and had larger offspring (Both *et al.* 2005).

298 However, bold individuals had higher rates of extra-pair copulations and
299 sired more offspring through promiscuity, whilst shyer individuals sired more
300 young at the social nest (Patrick *et al.* 2012). Each partner is invested into
301 the breeding attempt and each sex carried out different reproductive
302 behaviours to care for their offspring (Sanz *et al.* 2000). Also, assortative

303 pairings produced more recruits compared to other pair combinations
304 (Dingemanse *et al.* 2004), highlighting the link between personality within
305 breeding pairs and their breeding success.

306 These results for birds studied in the urban habitat of Cambridge University
307 Botanic Gardens point to the potential importance of individual personalities
308 to the fitness of birds breeding in novel environments. The urban
309 environment represents a particular challenge, individuals struggling to
310 complete their breeding attempt in a harsh habitat (Drent *et al.* 2003). It can
311 be hard to survive in a fluctuating environment and as it is difficult to raise
312 offspring to fledging (Mackenzie *et al.* 2014), parents may act “out of
313 character” for any chance to increase its lifetime reproductive success
314 (Echeverría & Vassallo 2008; Dingemanse *et al.* 2010). For example, shy
315 individuals may be more flexible in a stochastic environment and bold
316 individuals seemed to benefit in a constant environment (Frost *et al.* 2007;
317 Atwell *et al.* 2012). Also, unpredictable environmental factors were often
318 exacerbated in urban habitats (Gabriel & Black 2012a), meaning that urban
319 individuals are challenged far more greatly than those in rural habitats
320 (Echeverría & Vassallo 2008). A recent study on Eurasian coots showed that
321 individuals who recently founded an urban population changed their
322 behaviour to be more aggressive, but less stressed to the anthropogenic
323 environment (Minas 2015).

324 It can be concluded that blue tits show consistent variation in neophobia
325 responses to a novel object. Individual neophobia trait was linked to total
326 offspring biomass and suggests that there may be an ideal pair combination

327 for neophobia trait because of the biparental care strategy used by the study
328 species. This study further showed that changes in provisioning rate could be
329 used as a measure of neophobia response. Great tits are the species of
330 choice for many avian personality studies, so it was noteworthy to illustrate
331 consistent variation in blue tits.

332 **ACKNOWLEDGEMENTS**

333 We thank Julia Mackenzie for her guidance and help with fieldwork, Dawn
334 Hawkins for advice on statistics, Mick Whitehouse for help preparing the
335 manuscript and the Cambridge University Botanic Garden for access and
336 permission to carry out the research.

337

338 **LITERATURE CITED**

- 339 1. Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cole, E.F., Cockburn, A. &
340 Sheldon, B.C. 2013: Individual personalities predict social behaviour in
341 wild networks of great tits (*Parus major*). *Ecol. Lett.* **16**, 1365-1372.
- 342
- 343 2. Atwell, J.W., Cardoso, G.C., Whittaker, D.J., Campbell-Nelson, S.,
344 Robertson, K.W. & Ketterson, E.D. 2012: Boldness behavior and stress
345 physiology in a novel urban environment suggest rapid correlated
346 evolutionary adaptation. *Behav. Ecol.* **23**, 960–969.
- 347
- 348 3. de Azevedo, C.S. & Young, R.J. 2006: Shyness and boldness in greater
349 rheas *Rhea americana* Linnaeus (Rheiformes, Rheidae): the effects of

- 350 antipredator training on the personality of the birds. *Rev. Bras. Zool.* **23**,
351 202–210.
- 352
- 353 4. Black, J. M. 2001: Fitness consequences of long-term pair bonds in
354 barnacle geese: monogamy in the extreme. *Behav. Ecol.* **12**, 640–645.
- 355
- 356 5. Boon, A.K., Réale, D. & Boutin, S. 2007: The interaction between
357 personality, offspring fitness and food abundance in North American red
358 squirrels. *Ecol. Lett.* **10**, 1094–104.
- 359
- 360 6. Both, C. Dingemanse, N.J, Drent, P.J. & Tinbergen, J.M. 2005: Pairs of
361 extreme avian personalities have highest reproductive success. *J. Anim.*
362 *Ecol.* **74**, 667–674.
- 363
- 364 7. Cambridge University Botanic Garden. 2005: *Cambridge University*
365 *Botanic Garden "Gardens & Plantings"* Available at:
366 [http://www.botanic.cam.ac.uk/Botanic/Page.aspx?p=27&ix=2705&pid=27](http://www.botanic.cam.ac.uk/Botanic/Page.aspx?p=27&ix=2705&pid=2702&prcid=4&ppid=2702)
367 [02&prcid=4&ppid=2702](http://www.botanic.cam.ac.uk/Botanic/Page.aspx?p=27&ix=2705&pid=2702&prcid=4&ppid=2702). Last accessed 11 September 2014.
- 368
- 369 8. Dall, S.R.X., Bell, A.M., Bolnick, B.I. & Ratnieks, F.L.W. 2012: An
370 evolutionary ecology of individual differences. *Ecol. Lett.* **15**, 1189–98.
- 371
- 372 9. David, M., Cézilly, F. & Giraldeau, L-A. 2011: Personality affects zebra
373 finch feeding success in a producer–scrounger game. *Anim. Behav.* **82**,

374 61–67.

375

376 10. Dingemanse, N.J., Both, C., Drent, P.J. & Tinbergen, J.M. 2004: Fitness
377 consequences of avian personalities in a fluctuating environment. *P. Roy.*
378 *Soc. B-Biol. Sci.* **271**, 847–852.

379

380 11. Dingemanse, N.J., Both, C., Drent, P.J., van Oers, K. & van Noordwijk,
381 A.J. 2002: Repeatability and heritability of exploratory behaviour in great
382 tits from the wild. *Anim. Behav.* **64**, 929–938.

383

384 12. Dingemanse, N.J., Both, C., van Noordwijk, A.J., Rutten, A.L. & Drent,
385 P.J. 2003: Natal dispersal and personalities in great tits (*Parus major*). *P.*
386 *Roy. Soc. B-Biol. Sci.* **270**, 741–747.

387

388 13. Dingemanse, N.J., Kazem, A.J.N., Reale, D. & Wright, J. 2010:
389 Behavioural reaction norms: animal personality meets individual plasticity.
390 *Trends. Ecol. Evol.* **25**, 81–89.

391

392 14. Dingemanse, N.J., Bouwman, K.M., van de Pol., M., van Overveld, T.,
393 Patrick, S.C. Matthysen, E., *et al.* 2012: Variation in personality and
394 behavioural plasticity across four populations of the great tit *Parus major*.
395 *J. Anim. Ecol.* **81**, 116–26.

396

- 397 15. Dingemanse, N.J. & Réale, D. 2005: Natural selection and personality.
398 *Behaviour* **142**, 1159-1184.
399
- 400 16. Drent, P.J., van Oers, K. & van Noordwijk, A.J. 2003: Realized heritability
401 of personalities in the great tit (*Parus major*). *P. Roy. Soc. B-Biol. Sci.*
402 **260**, 45-51.
403
- 404 17. Echeverría, A.I. & Vassallo, A.I. 2008: Novelty responses in a bird
405 assemblage inhabiting an urban area. *Ethology* **114**, 616–624.
406
- 407 18. Frost, A.J., Winrow-Giffen, A., Ashley, P.J. & Sneddon, L.U. 2007:
408 Plasticity in animal personality traits: does prior experience alter the
409 degree of boldness. *P. Roy. Soc. B-Biol. Sci.* **274**, 333-339.
410
- 411 19. Gabriel, P.O. & Black, J.M. 2010: Behavioural syndromes in Steller's jays:
412 the role of time frames in the assessment of behavioural traits. *Anim.*
413 *Behav.* **80**, 689–697.
414
- 415 20. Gabriel, P.O. & Black, J.M. 2012a: Reproduction in Stellar's Jays
416 (*Cyanocitta stelleri*): Individual characteristics and behavioral strategies.
417 *Auk* **129**, 377-386.
418
- 419 21. Gabriel, P.O. & Black, J.M. 2012b: Behavioural syndromes, partner
420 compatibility and reproductive performance in Steller's Jays. *Ethology*

- 421 **118**, 76–86.
- 422
- 423 22. Garamszegi, L.Z., Eens, M. & Török, J. 2009: Behavioural syndromes
424 and trappability in free-living collared flycatchers, *Ficedula albicollis*.
425 *Anim. Behav.* **77**, 803–812.
- 426
- 427 23. Herborn, K.A., Macleod, R., Miles, W.T.S., Schofield, A.N.B., Alexander,
428 L. & Arnold, K.E. 2010: Personality in captivity reflects personality in the
429 wild. *Anim. Behav.* **79**, 835-843.
- 430
- 431 24. Hinsley, S.A., Bellamy, P.E., Rothery, P., Redman, P., Furness, L.,
432 Speakman, J.R. 2011: Effects of the doubly labelled water procedure on
433 Great Tits *Parus major* feeding young. *Bird Study* **58**, 151-159.
- 434
- 435 25. Klun, E., Kuhn, S., Kempenaers, B. & Brommer J.E. 2012: A simple
436 cage test captures intrinsic differences in aspects of personality across
437 individuals in a passerine bird. *Anim. Behav.* **84**, 279–287.
- 438
- 439 26. Lendvai, A.Z., Bókony, V. & Chastel, O. 2011: Coping with novelty and
440 stress in free-living house sparrows. *J. Exp. Biol.* **214**, 821–828.
- 441
- 442 27. Mackenzie, J. 2010: Impact of floral origin, floral composition and
443 structural fragmentation on breeding success of blue tits (*Cyanistes*
444 *caeruleus*) and great tits (*Parus major*). PhD Thesis, Anglia Ruskin
445 University, Cambridge, UK. Available at:

- 446 <http://angliaruskin.openrepository.com/arro/handle/10540/123186> [Last
447 accessed 6 June 2013].
448
- 449 28. Mackenzie, J.A., Hinsley, S.A. & Harrison, N.M. 2014: Parid foraging
450 choices in urban habitat and their consequences for fitness. *Ibis* **156**,
451 591-605.
452
- 453 29. Martin, P. & Bateson, P. 2007: *Measuring Behaviour: An Introductory*
454 *Guide*, 3rd edition. Cambridge University Press, Cambridge, UK.
455
- 456 30. Minas, P. 2015: Successful colonization of a novel urban environment is
457 associated with an urban behavioural syndrome in a reed-nesting
458 waterbird. *Ethology* **121**, 1178-1190.
459
- 460 31. Mutzel, A., Dingemanse, N.J., Araya-Ajoy, Y.G. & Kempenaers, B. 2013:
461 Parental provisioning behaviour plays a key role in linking personality with
462 reproductive success. *P. Roy. Soc. B-Biol. Sci.* **280**, 20131019.
463
- 464 32. Patrick, S.C., Chapman, J.R., Dugdale, H.L., Quinn, J.L. & Sheldon B.C.
465 2012: Promiscuity, paternity and personality in the great tit. *P. Roy. Soc.*
466 *B-Biol. Sci.* **279**, 1724–1730.
467
- 468 33. Réale, D., Gallant, B.Y., Leblanc, M. & Festa-Bianchet, M. 2000:
469 Consistency of temperament in bighorn ewes and correlates with

470 behaviour and life history. *Anim. Behav.* **60**, 589-597.

471

472 34. Sanz, J.J., Kranenbarg, S. & Tinbergen, J.M. 2000: Differential response
473 by males and females to manipulation of partner contribution in the great
474 tit (*Parus major*). *J. Anim. Ecol.* **69**, 74–84.

475

476 35. Tetley, C. & O'Hara, S. 2012: Ratings of animal personality as a tool for
477 improving the breeding, management and welfare of zoo mammals.
478 *Anim. Welfare.* **21**, 463–476.

479

480

481

482

483

484

485

486

487

488

489

490 **Figure 1 – The novel objects used in this study**

491 **Figure 2 shows the difference in provisioning rate between control, trial 1 and trial 2**

492 **Figure 3 shows the difference in latency between control, trial 1 and trial 2**

493 **Figure 4 shows the relationship between (a) neophobia trait and total biomass of**

494 **offspring and (b) neophobia trait and mean offspring weight at day 11; where O**

495 **represents shy individuals, Δ represents mid individuals, and \square represents bold**

496 **individuals**

497

2013



1. Shiny silver jar lid



2. Blue plastic milk bottle top

2014



1. Shiny blue battery



2. Red Lego brick





