1   **Inhibitory control, personality, and manipulated ecological conditions influence foraging**

2   **plasticity in the great tit**

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19   **Abstract**

20   1. Organisms are consistently under selection to respond effectively to a diversity of,

21   sometimes rapid, changes in their environment. Behavioural plasticity can allow

22   individuals to do so instantaneously, but why individuals vary in this respect is poorly

23   understood. Although personality and cognitive traits are often hypothesised to

24   influence plasticity, the effects reported are highly inconsistent, which we hypothesise

25   is because ecological context is usually not considered.

26   2. Here we explore the roles of individual cognitive and personality variation – assayed

27   using standard tasks for inhibitory control, a measure of self-control, and 'reactive-

28   proactive' personality axis (RPPA), respectively – in driving foraging plasticity, and asked

29   how these effects varied across two experimentally manipulated ecological contexts:

30   food value and predation risk.

31   3. After great tits (*Parus major)* had initially been trained to retrieve high value food

32   hidden in sand, they were then simultaneously offered the hidden food and an

33   alternative food choice on the surface, that was either high or low value. Their choices

34   were further examined under high and low perceived predation risk treatments.

35   Individuals' choices were classified in terms of whether they continued to forage on the

36   hidden but familiar food source, or instead switched to the new visible food source. We

37   defined the latter option as the plastic response.

38   4. Our assays captured consistent differences among individuals in foraging behaviour.

39   Both inhibitory control and exploration influenced whether birds switched from the

40   familiar but hidden food source to the new alternative visible food on the surface. These

41   effects depended on the relative value of the food items available and on the perceived

42   level of predation risk, but also on the time scale over which the response was

43   measured.

44   5. Our results demonstrate how an executive cognitive function and one specific

45   personality axis can simultaneously influence plasticity in a key functional behaviour.

46   That their effects on foraging were primarily observed as interactions with food value or

47   predation risk treatments also suggest that the population level consequences of

48   behavioural mechanisms, such as these, may only be revealed across key ecological

49   conditions or gradients.

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51   **Introduction**

52   Organisms are consistently under pressure to adapt to changes in their environment, such as,

53   changes in climate, food availability, and predation risk. Behavioural plasticity allows individuals

54   to respond to environmental change by adjusting their behaviour (Gross, Pasinelli and Kunc,

55   2010; Snell-Rood, 2013), but behavioural plasticity is constrained by the costs of sampling

56   information (Dall and Johnstone, 2002; Snell-Rood, 2013) and adjusting behaviour (Komers,

57   1997). Although these costs are ubiquitous, some individuals are more plastic than others

58   (Dingemanse *et al.*, 2009; Coppens, De Boer and Koolhaas, 2010). Why individuals vary in their

59   plasticity is a major focus of research in evolutionary ecological studies of behaviour (Wolf, Van

60   Doorn and Weissing, 2008; Dingemanse *et al.*, 2009). Cognition and personality have the

61   potential to influence behavioural plasticity (Dingemanse *et al.*, 2009; Snell-Rood, 2013) but

62   their role in doing so under realistic ecological scenarios is poorly understood.

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64   A major focus in cognitive ecology has been to explore the cognitive traits that influence fitness (Cole

65   *et al.*, 2012; Shaw *et al.*, 2019; Sonnenberg *et al.*, 2019), and in particular, foraging success (Balda and

66   Kamil, 1992; Healy and Hurly, 1995). Most of the focus has been on the role of learning, memory, or

67   innovation (Laland and Reader, 1999; Raine and Chittka, 2008; Morand-Ferron *et al.*, 2011).

68   Inhibitory control, an executive cognitive function defined as the suppression of a dominant

69   (prepotent) behaviour in favour of a more beneficial or appropriate behaviour (Diamond, 2013), is

70   likely also an important mechanism because foraging success relies on making optimal choices

71   among different options. One study demonstrated that cotton-top tamarins discount future high-

72   quality rewards in favour of immediate lower-quality rewards, a strategy that may be beneficial given

73   the temporal availability of their natural diet (Stevens *et al.*, 2005). Other studies show that

74   inhibitory control predicts dietary breath, although the direction of this relationship varies; primate

75   species with higher self-control had greater dietary breath (MacLean *et al.*, 2014), while pheasants

76   with greater dietary breadth had poor performance on inhibitory control tasks (van Horik *et al.*,

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77   2018). In general, however, there is a dearth of empirical evidence to support the expectation that

78   inhibitory control influences foraging decisions in ecologically-relevant contexts.

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80   In addition, cognitive performance can vary dramatically depending on the specific conditions

81   (Cauchoix, Chaine and Barragan-Jason, 2020). In particular, the risk of predation may influence

82   the extent to which individuals can suppress the prepotent response and choose an alternative,

83   more rewarding behaviour (Schwabe and Wolf, 2009), as stress in humans promotes habitual

84   behaviours and reduces goal-directed behaviour (Schwabe and Wolf, 2009). Similarly, in the

85   presence of a predator, individuals might be expected to minimize predation risk rather than

86   expending time and resources inhibiting a prepotent response. Therefore, an individuals'

87   "ability" to perform alternative behaviours may not only be dependent on their inhibitory

88   control abilities, but also on the environmental context: when under predation risk, individuals

89   may focus on avoiding predation and show little variation in behavioural plasticity, and when

90   not under predation risk, individuals may focus on the task at hand, and show variation in

91   behavioural plasticity (MacLean *et al.*, 2014; Rosati, 2017). Nevertheless, the effects of

92   inhibitory control on behavioural plasticity remain poorly understood, especially when

93   individuals are under predation risk.

94   Personality refers to consistent differences between individuals in behaviour or behavioural

95   correlations (Sih *et al.*, 2004), and is an increasingly common paradigm for examining the

96   evolutionary ecology of behaviour and constraints on behavioural plasticity (Dingemanse *et al.*,

97   2009; Herborn *et al.*, 2014). The 'reactive-proactive personality axis' (RPPA), for example,

98   contrasts 'proactive' individuals, who are more exploratory and risk-prone at one end of the

99   continuum, with 'reactive' individuals at the other end, who are less exploratory and more risk-

100   averse (Groothuis and Carere, 2005; Réale *et al.*, 2007). Two contrasting hypotheses can explain

101   how the reactive-proactive axis might influence individual behavioural plasticity when

102   conditions change (Arvidsson and Matthysen, 2016; Rojas-Ferrer, Thompson and Morand-

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103   Ferron, 2019). The information-gathering strategy (IGS) hypothesis posits that individuals vary in

104   how they collect information from the environment: proactive individuals explore their

105   environment more and sample in novel areas, while reactive individuals explore less and sample

106   known areas (Arvidsson and Matthysen, 2016; Rojas-Ferrer, Thompson and Morand-Ferron,

107   2019). This leads to the expectation that proactive individuals should display greater

108   behavioural plasticity than reactive individuals, when ecological conditions change. In contrast,

109   the behavioural flexibility (BF) hypothesis states that proactive individuals are more routine-like

110   in their behaviour (Arvidsson and Matthysen, 2016) and are less responsive to changes in their

111   environment (Coppens, De Boer and Koolhaas, 2010); so for example, proactive individuals are

112   less plastic in their behaviour than reactive individuals when faced with a depleted food patch

113   (Verbeek, Drent and Wiepkema, 1994). The conditions under which these divergent predictions

114   are supported are poorly known.

115   Our aim was to investigate whether inhibitory control and the reactive-proactive personality

116   axis influenced foraging plasticity in a realistic scenario, and whether these effects varied

117   depending on the relative value of alternative food options, and perceived predation risk. We

118   tested this in great tits (*Parus major*), a model species for studies on individual variation in

119   cognition (Cole, Cram and Quinn, 2011; Amy, van Oers and Naguib, 2012; Morand-Ferron *et al.*,

120   2015) and personality (Verbeek, Drent and Wiepkema, 1994; Marchetti and Drent, 2000;

121   Dingemanse *et al.*, 2012). First, we performed standard assays for inhibitory control and the

122   RPPA. Next, we trained individuals to retrieve hidden, patchy, high-value food underneath sand,

123   and examined how cognition and personality affected whether individuals continued to use this

124   foraging strategy or instead switched to an alternative, more obvious food source introduced on

125   the surface, while manipulating two variables: 1) the value of the alternative food source, and 2)

126   the risk of predation. Rather than predetermine the adaptive value of each choice, which is

127   difficult to quantify because of context and state dependency, we simply considered the sand or

128   surface food options as alternative choices that were freely available to all individuals.

129   Our prediction for how inhibitory control could influence whether individuals switched to the

130   visible food source varied depending on which of the choices became the prepotent (dominant)

131   response. In realistic ecological scenarios, the prepotent response is difficult to predict due to

132   conflicts between how the brain simultaneously processes information from past and present

133   stimuli (Anderson and Weaver, 2009). On the one hand, the prepotent behaviour could be to

134   continue the sand foraging technique the birds had been trained to do. In this case, we

135   expected individuals with poor inhibitory control, as measured by the detour-reaching task, to

136   continue to search for hidden food items, even when there were similar food items on the

137   surface (see Table 1). We also predicted in this case that individuals with good inhibitory control

138   could suppress their prepotent foraging technique and instead choose the visible food item

139   when it was of similar value to the hidden food. On the other hand, if the prepotent behaviour

140   is to immediately forage on visible food items, then we expected individuals with poor inhibitory

141   control to feed on the visible food, even when of lower value than the hidden food. Additionally,

142   individuals with good inhibitory control should be able to resist the prepotent response to the

143   visible food when it is low value and instead continue to search for the hidden food. When the

144   visible food is of similar value to the hidden food however, all individuals are likely to choose the

145   visible food.

146   We predicted personality could also influence foraging plasticity in one of two contrasting ways

147   (Table 1). In line with the IGS hypothesis (Arvidsson and Matthysen, 2016; Rojas-Ferrer,

148   Thompson and Morand-Ferron, 2019), we expected proactive birds would be more likely to

149   switch to an alternative, novel, visible food source, primarily when the alternative food source

150   was of high value, whereas reactive birds would be less likely to utilize the alternative food.

151   Alternatively, according to the BF hypothesis, we predicted reactive birds to be more responsive

152   to the sudden availability of a new food source and to switch to the alternative visible food,

153   especially when it was high value. With the high value food on the surface, there would no

154   longer be a trade-off between food value and searching time. Additionally, we expected the

155   proactive birds to continue foraging on the hidden food source irrespective of the value of

156   alternatives. Finally, given the expectation that the influence of inhibitory control and the RPPA

157   could be context dependent (Stevens *et al.*, 2005; Sih and Del Giudice, 2012; Tsukayama,

158   Duckworth and Kim, 2012; Bray, Maclean and Hare, 2014), and that individual differences in

159   behaviour are sometimes only exposed under stress (Suomi, 2004; Quinn and Cresswell, 2005),

160   we explored whether the association between foraging plasticity and inhibitory control, and

161   between foraging plasticity and exploration behaviour, varied depending on predation risk. We

162   expected the great tits, under predation risk, to perform their trained behaviour of searching for

163   the hidden food. To demonstrate the evolutionary validity of our measure of foraging, we also

164   estimated the repeatability of food choices across treatments, which sets the upper limit of

165   heritability, and examined whether any observed between individual variation changed after

166   controlling for potentially confounding effects of the main treatments, or by inhibitory control

167   and exploration.

168

169   **Materials and methods**

170   <u>Aviary housing</u>

171   We caught wild great tits at seven field sites (three mixed deciduous and four coniferous) in County

172   Cork, Ireland and held them in the aviary on the university campus for a maximum of two weeks

173   from January to March 2018. We fitted birds with a colour ring and a British Trust for Ornithology

174   ring for identification, before placing them in individual cages (62 x 50 x 60cm, H x W x D). When not

175   participating in experiments, birds were fed ad-libitum sunflower seeds, peanuts and water with

176   added vitamin drops (AviMix®). Mealworms (*Tenebrio molitor*) were provided three times a day and

177   during experimental training and tests. Before each experiment, we deprived birds of food, but not

178   water, for one hour.

179   <u>Exploration assay and inhibitory control assays</u>

180   On the day after their arrival to the aviary, we released the birds into an experimental room (4.60 x

181   3.10 x 2.65m, W x L x H) to run the open field 'exploration of a novel environment' assay (Verbeek,

182   Drent and Wiepkema, 1994). The experimental room was adjacent to the birds' individual cages and

183   had five artificial trees (1.53m tall) spaced two metres apart from one another. The number of hops

184   and flights made on the 'trees' within two minutes of entering the room was totalled to give each

185   bird an 'exploration' score.

186   On the following day, we assayed inhibitory control using a detour-reaching task in the individual

187   cages, following the methods described in MacLean *et al.* (2014). The detour-reaching task involved

188   presenting a plastic cylinder (3.5 x 3cm, D x L) laterally to the bird, 20 cm in front of a perch that was

189   5 cm high, so that the bird was positioned in the middle of the long edge of the cylinder before

190   making an approach towards the cylinder. The assay had three phases: 1) Habituation – the birds had

191   to acquire half a waxworm (*Galleria mellonella*) from the open end of an opaque cylinder three

192   times; 2) Training – half a waxworm was placed in the centre of the cylinder and to complete

193   training, birds had to retrieve the food without pecking at the cylinder, in four out of five consecutive

194   attempts; and 3) Test – the opaque cylinder was replaced with a transparent cylinder, and birds were

195   given 10 trials to attempt to retrieve half a waxworm from the centre. During the test phase, any

196   contact a bird had with the cylinder was scored as a fail, and following a failure, the cylinder was

197   removed from the cage. Birds that pecked at the barrier could still access the reward (>90% of failed

198   trials resulted in the bird immediately moving to the side to access the worm). A successful trial was

199   when the bird moved around to the side of the tube and took the waxworm from the open end, as in

200   training. The birds' final score was the proportion of trials that were successful i.e., high values

201   indicate high inhibitory control (Davidson G.L. unpublished data).

202   <u>Experiment pre-training and training</u>

203   We gave the birds a food preference test consisting of three mealworms and three dehusked

204   sunflower seeds, and recorded the first food they ate. Four individuals did not choose either food in

205   5 minutes, so were given the preference test again but with waxworms instead of mealworms. Of 41

206   individuals, 85% chose and ate a worm (either waxworm or mealworm) as their first choice,

207   demonstrating that the birds preferred worms to seeds. For the four birds that preferred waxworms

208   they received waxworms for all of their following experimental trials and the other birds all received

209   mealworms. After the preference test, we gave the birds a pre-training task consisting of a 24-well

210   tray filled with sand. We buried mealworms underneath the sand in ten randomly chosen wells,

211   scattered ten sunflower seeds (dehusked) randomly on the surface (Fig. 1a) and recorded the first

212   food chosen. We ran this task to confirm that the birds would forage on the tray, that the seeds were

213   easier to access than the worms, and that the birds could not detect the buried worms either visually

214   or through smell. 38 of the 39 birds tested chose a seed as their first choice, instead of searching in

215   the sand, suggesting that the birds had to be trained to find the buried worms. Next, we trained the

216   birds to forage for high-value food in sand. The purpose of this training was to teach them that when

217   they were presented with a tray with sand, their preferred food item (i.e. worms) could be found

218   under the sand, and in a patchy distribution. We acknowledge this training does not necessarily

219   mean that foraging in the sand became habitual. Nevertheless, because birds became familiar with

220   searching through the sand in the context of this novel foraging situation, we considered foraging in

221   the sand as being their trained behaviour, and a switch to eating food on the surface of the tray was

222   considered a plastic response. Birds were trained in a step-wise progression. In the first step, we

223   baited all 24-wells with hidden worms, two of which were partially visible to encourage birds to

224   search. Birds progressed to the next step if they ate five worms within one hour (n = 40). The second

225   step was similar to the first, except only ten wells were baited (i.e. patchy distribution), one of which

226   was partially visible. Birds progressed if they ate three worms in one hour. The final step was the

227   same as the second but the worms were hidden in different wells compared to step two. The birds

228   completed training if they ate three worms from this tray. Steps were repeated until birds progressed

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229   and completed the training (n = 35). Of the 41 individuals who received the food preference test, six

230   did not complete training due to welfare concerns or time constraints.

231   Food choice tasks

232   After completion of training, all birds received four treatments in a 2 x 2 factorial design (Fig. 1).

233   The first factor was the type of visible food and the second was the presence of a predator. In all

234   four treatments, we placed the 24-well tray, baited with ten buried mealworms (high-value) in

235   randomly assigned wells, on a stool in the centre of the experimental room and provided two

236   artificial trees (1.53m H) as perches, each a metre from the stool. Visible food on the surface of

237   the tray was one of two types: low-value (ten randomly scattered sunflower hearts), or high-

238   value, where mealworms were encased in two transparent, sealed case (Fig. 1). They were

239   encased for two reasons: one, to stop them burrowing in the sand and, two, to ensure that

240   some individual variation in surface choice would likely arise when a high quality but difficult to

241   access food item became available, otherwise all birds would have chosen the surface food. To

242   avoid a carry-over effect of birds choosing high-value surface food leading to them by default

243   choosing the visible option, the low-value visible food was always presented first. We assumed

244   that the birds did not know that the worm inside the case was inaccessible, and expected the

245   birds to attempt to get at the encased worm because it would be visible.

246   The first two treatments (visible low-value; visible high-value) were run in the absence of a

247   predator and the third and fourth treatments were run in the presence of a taxidermy

248   sparrowhawk (*Accipiter nisus*) to simulate an increased perception of predation risk (Fig. 1).

249   Taxidermic mounts are an effective way to simulate predation risk (Carlson, Pargeter and

250   Templeton, 2017), and have been used effectively on similar experiments in great tits (Kalb,

251   Anger and Randler, 2019). During the third and fourth treatment, when an individual first

252   landed on the tray to make a food choice, we released the 'hawk' from behind a sheet via a

253   pulley system, to 'fly' across the room and 'hide' in a cardboard box. The order in which the

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254   visible food alternatives were presented during the two predator trials was chosen randomly to

255   account for possible carry-over effects of the predator attack on food choice in subsequent

256   trials.

257   For the four treatments, we determined all the food choices made by the birds in four minutes from

258   video recordings. We scored food choices as 'hidden' (two or more pecks in the sand in the same

259   well), or 'visible' (choose a seed and remove it from the tray, or touch the transparent case with foot

260   or beak). To examine the possibility that the effects of either inhibitory control or exploration

261   behaviour were short-lived rather than persistent, we analysed both 1) first food choice only, and 2)

262   the proportion of visible choices out of the total number of choices made over the four minutes

263   (henceforth, total choices). Additionally, these separate analyses were important for the visible high-

264   value food because individuals' choices in this experiment may have depended on their experience

265   with the transparent casing. On their first choice, we could not assume that the birds were aware of

266   the encased worm being inaccessible and if inhibitory control or exploration behaviour were involved

267   in their choice, they may have required time to learn about the contingencies of this food item. Great

268   tits sometimes flicked over the seeds with their beaks, which we did not count as a choice. A second

269   coder (C.A.T) watched 20% of the videos to ensure the records of food choice were not biased.

270   Strong agreement was found between raters (intraclass correlation coefficient: first choice; 100%

271   similarity; total choices; ICC = 0.977, 95% confidence interval = 0.938-0.994).

272   Statistical analysis

273   Data were analysed in R version 3.6.0 (R Core Team 2019). To investigate if individuals were

274   consistent in their food choices across treatments we performed a repeatability analysis using the

275   rptR package (Stoffel, Nakagawa and Schielzeth, 2017). Unadjusted (single variable of individual as a

276   random effect) and adjusted (all variables contained in the model average) repeatabilities were

277   measured for the four models mentioned below: first choice and total choices, with separate models

278   for the effects of detour-reaching and exploration. The two unadjusted models used different

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279   datasets, due to differences in sample size. If the observed individual differences in foraging

280   behaviour reflected intrinsic differences among individuals, then we expected the adjusted and

281   unadjusted values to be similar. If the observed differences were caused by environmental

282   covariation with the experimental conditions, then we expected adjusted repeatability to be lower

283   than unadjusted values. Finally, the adjusted repeatability should be higher than the unadjusted if

284   the experimental conditions masked among individual differences in the foraging behaviour.

285   For the main analyses, we used the *lme4* package (Bates *et al.*, 2015) to create four models: two

286   were based on the first choice (models 1 and 3) and two on the proportion of total choices (models 2

287   and 4), with either detour-reaching score (models 1 and 2, n = 29) or exploration score (models 3 and

288   4, n = 35) as the main explanatory variables. We included inhibitory control and exploration

289   behaviour in separate models to avoid over-parameterisation, and because they are not correlated in

290   this population and likely have independent effects on behaviour (Davidson G. L. unpublished data).

291   The response variable for the first choice models was a binary 'hidden' (0) or 'visible' (1), and for the

292   total choice models was the proportion of visible food choices out of the total number of choices

293   made. All models were generalised linear mixed models (GLMM) with a binomial error distribution

294   and a logit link function, with individual ID fitted as a random effect. All models had predator

295   treatment (yes or no), visible food type (seed or encased worm), age (adult or juvenile), resident

296   habitat (deciduous or coniferous), sex and the interaction effect between predator treatment and

297   visible food, included as explanatory variables. We included resident habitat because habitat origin

298   affects food choice in our populations (Serrano-Davies, O'Shea and Quinn, 2017). The results for age,

299   habitat and sex are included in the supplementary material. Our predictions were tested by the

300   inclusion of detour-reaching score (a proportion out of ten, treated as continuous) in models 1 and 2,

301   and exploration score (continuous) in models 3 and 4, and their interactions with both visible food

302   type and predation risk.

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303   We used the *DHARMa* package (Hartig 2019) to check model fit and to test model assumptions. We

304   used the *dredge* function from the MuMIn package (Barton 2019) and an information-theoretic

305   approach in combination with model averaging (Grueber *et al.*, 2011) to generate the models with

306   the most support, taken from the global model. The information-theoretic approach compares

307   multiple models (i.e. hypotheses) simultaneously and we calculated the amount of support for each

308   model using Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham and

309   Anderson, 2002). Models with a ΔAICc <2 were retained as the 'top' models that included the most

310   important explanatory variables. We report the averaged weighted parameter estimates across all

311   models in the top set.

312

313   **Results**

314   Adjusted and unadjusted repeatabilities

315   Repeatability analyses confirmed that individuals differed consistently from one another in their first and total

316   choices (Table 2). The model's fixed effects masked the between individual differences in the first choice made

317   because adjusted repeatability was higher when these effects were controlled (Table 2). Repeatability estimates

318   for the total choices analyses were unaffected by whether or not the fixed effects were included.

319

320   Food choice and predation risk

321   Whether birds switched to the visible food depended on both the value of the visible food and the

322   predation risk treatment. This was true for both the first choice (Tables 3 and 4; Fig. 2a) and total

323   choices (Tables 5 and 6; Fig. 2b), and there was a similar pattern of response across both (compare

324   Fig. 2a and 2b). Birds were more likely to switch to the visible food when it was high value, and when

325   there was no predator present. Despite this, some birds switched to feeding on the surface even

326   when the value of the visible food was low compared to the hidden food, and even when the

327   predator was present, demonstrating individual variation in foraging plasticity.

328

329   Detour-reaching and inhibitory control

330   Our assay of inhibitory control, the detour reaching score, did not predict whether birds switched to

331   the visible food in their first choice, either as a main effect, or in either of the interactions with food

332   value or predation risk (Table 3; for weights of the top models see Table S1). An interaction between

333   detour reaching with visible food type did predict choices in the total choice analysis (Detour*Visible

334   food; Table 5; Fig. 3; for weights of the top models see Table S2). Birds that had a high score on the

335   detour-reaching task were more likely to choose the visible food than birds that had a low score, and

336   only when the visible food was high value (Tukey posthoc test: Estimate= 0.73, St. Error = 0.24, z =

337   3.02, P = 0.0025; Fig. 3). The interaction between detour-reaching score and predation risk on food

338   choice did not appear in the average of the top models.

339   Exploration behaviour

340   Exploration behaviour, a proxy of the RPPA, had a positive main effect on whether birds switched to the visible

341   food for first choice but not total choices (Tables 4 and 6). Exploration behaviour especially influenced first

342   choice when the visible food was high value (Exploration*Visible food; Table 4; Fig. 4; for weights of the top

343   models see Table S3); fast explorers were more likely than slow explorers to switch to the visible food (Tukey

344   posthoc test: Estimate: 0.12, St. Error = 0.053, z = 2.27, P = 0.023; this model only converged when age, sex,

345   predator treatment and habitat were excluded). This interaction was non-significant for total choices

346   (Exploration*Visible food; Table 6). The effect of exploration on whether birds switched from the hidden to the

347   visible food was not affected by predation risk in the first choice analysis (Exploration*Predator, Table 4).

348   However, in the total choice analysis, an interaction between exploration and predator treatment did influence

349   the switch to the visible food (Exploration*Predator; Table 6; Fig. 5; for weights of the top models see Table S4).

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350   Fast explorers were more likely to choose the visible food than slow explorers, but only in the presence of a

351   predator (Tukey posthoc test: Estimate = 0.19, St. Error = 0.06, z = 3.02, *P* = 0.003; Fig. 5).

352

353   **Discussion**

354   There were consistent differences in individuals' foraging behaviour. In the first choice analysis,

355   the repeatability estimate adjusted for the two ecological factors, predation risk and surface

356   food value, was twice as high as the unadjusted estimate. This demonstrates that failing to

357   control for ecological variation can underestimate the potential population level consequences

358   of this variation, although this was not true for the total choice repeatability estimate. Birds

359   were more likely to show plasticity in their choice (to switch to the surface food) when both of

360   the food rewards were of high value and when there was no risk of predation. Foraging

361   plasticity was influenced by both inhibitory control and exploration behaviour, to some extent in

362   the first choice, but especially in the total choices analysis. Fast explorers and birds with good

363   inhibitory control were more plastic than slow explorers and birds with poor inhibitory control

364   respectively, but only when the visible food was high-value. Fast explorers were also more

365   plastic than slow explorers when under risk. Together these results reveal the complex

366   interactions between foraging strategies, cognition, personality and environmental context,

367   which we discuss in more detail below.

368

369   <u>Food value and predation risk</u>

370   Foraging plasticity, here defined as switching from feeding on a familiar but hidden food source

371   to an alternative visible food source, was influenced by the value of the alternative food that

372   was available, and by predation risk. Although these were, or tended towards, significant main

373   effects, for both the first choice and total choices, their interaction was especially important.

16

374   Birds showed greater plasticity when the visible food was high value and there was no risk from

375   a predator. These choices are consistent with optimal foraging theory, in which animals are

376   expected to switch foraging tactics when the costs (e.g. of predation) start to outweigh the

377   benefits of the current option (e.g. of energy gain on the patch) (MacArthur and Pianka, 1966;

378   Milinski and Heller, 1978; Lima and Dill, 1990). In our experiment, the absence of a predator and

379   the option of a high-value food, that seemed to be easier to access than the hidden food, meant

380   that great tits chose to switch their food choice during this combination of treatments.

381

382   Even though great tits could not acquire the encased worm (high-value surface food) after their

383   first attempt, they still persisted strongly for the duration of the trial. This may be because great

384   tits are innovative and acquire food from challenging places (Aplin *et al.*, 2015; Serrano-Davies,

385   O'Shea and Quinn, 2017). As they did not know that the worm could not be accessed, and it was

386   a desirable reward, they were willing to expend energy and time trying to acquire it. It could

387   also be that the great tits were acquiring information about this new, unknown reward, in order

388   to reduce their uncertainty about it, which is beneficial for survival and fitness (Stephens and

389   Krebs, 1986; Mathot *et al.*, 2012).

390

391   When there was a predator present, behavioural plasticity was supressed: most individuals

392   foraged on the familiar, if hidden, food source. In contrast, there was no effect of risk on food

393   choice when the low-value seeds were visible. This suggests that the great tits feel safer feeding

394   on the familiar food, despite it taking more time to locate than the visible, surface food.

395   Whether animals are likely to disregard high quality foods depends on risk, certainty and reward

396   value (Holbrook and Schmitt, 1988; Mazur, 1988; Green and Myerson, 1996). In our study, the

397   worm in the case was likely too costly to choose when there is heightened risk because it was

398   too difficult to obtain. An alternative explanation for why individuals chose to feed on the

399   hidden worms in the presence of a predator is that stress reduces the ability to perform goal-

17

400   directed behaviour because of the inability to assess changes in food value, as seen in a study on

401   humans (Schwabe and Wolf, 2009). As such, when great tits were in the presence of a perceived

402   predator, perhaps they could not accurately assess the relative value of the foods and so fell

403   back on their trained behaviour of searching in the sand for the hidden worms. Whatever the

404   explanation, the effect of predation and food type in combination demonstrates the ecological

405   relevance of our treatment.

406

407   Inhibitory control

408   We found support for the general hypothesis that the executive cognitive function of inhibitory

409   control influences foraging plasticity. This influence depended on the value of the visible food:

410   individuals with a high detour-reaching score were more likely to switch from the hidden food to

411   the visible food when both were of a similarly high value. This outcome fits the prediction that the

412   hidden food reward was the prepotent stimulus (Table 1): individuals with good inhibitory control

413   were able to resist the prepotent response of continuing to feed with their learned foraging

414   technique for the hidden food, in order to feed on a visible, apparently more accessible, and

415   therefore more immediately rewarding, food source. Birds with poor inhibitory control were less

416   plastic in their response and therefore did not attempt to feed on the visible food, even when it

417   was the preferred, high-value mealworm. These results suggest that individual differences in

418   inhibitory control will influence foraging success, particularly when food differs in value and

419   accessibility. We also predicted that predation risk could modify effects of inhibitory control on

420   foraging plasticity because individual differences, and/or habitual behaviour, are sometimes more

421   pronounced under stress (Suomi, 2004; Schwabe and Wolf, 2009), or because severe predation

422   risk could over-ride any effects of inhibitory control on behaviour (Quinn and Cresswell, 2005).

423   However, we found no interaction between predation risk and inhibitory control, suggesting that

424   the functional significance of this executive cognitive function is not influenced by an immediate

425   extrinsic stressor like predation risk, although whether this extends to other kinds of stressors

18

426   remains to be determined. Taken together, our results suggest that differences in foraging niches

427   and environmentally-determined food availability, rather than an immediate stressor like

428   predation risk, can provide insight into individual differences in inhibitory control.

429

430   The effect of inhibitory control on foraging plasticity was observed when measuring total choices, rather

431   than the first choice only, suggesting perhaps that the interaction with the encased worm influenced

432   their subsequent choices. One might have expected birds with good inhibitory control to quickly realise

433   that the visible food, though similar in value and ostensibly more obtainable, was in reality inaccessible,

434   and to switch back to the hidden food, but we found the opposite. Because there was a trade-off

435   between perceived accessibility (visible and on the surface) and searching time (not visible and patchy),

436   birds with higher inhibitory control may have weighed this cost differently than birds with low inhibitory

437   control. Another possibility is that individuals with high detour-reaching scores may also differ in their

438   motivation for food, or be more persistent than those with low scores, either because the detour-

439   reaching task measured these traits (eg. van Horik *et al.*, 2018), or because these traits co-vary with

440   inhibitory control. A further possible explanation for birds with high inhibitory control continuing to

441   peck at the inaccessible encased worm may be due to carry-over effects from the detour task to the

442   food choice tasks, for example, learning that food could be accessed from the side, despite a barrier. We

443   note that although the validity of the detour-reaching task as a measure for inhibitory control has been

444   questioned (van Horik *et al.*, 2018), we chose to use it because it remains a widely used approach, and

445   no assay of putative underlying cognitive processes is without its limitations. Additionally, we measured

446   success/failure on a per-trial basis, repeated ten times (as opposed to counting the number of pecks on

447   a barrier over four trials (van Horik *et al.*, 2018)), and found our measure of inhibitory control to be

448   robust against a similar task performed in the wild (Davidson G. L. unpublished data, preliminary

449   analysis available on request).

450

451   Personality

19

452   We found a positive main effect of exploration behaviour on the choice for the visible food for

453   first choice only; fast explorers were more likely than slow explorers to choose the visible food.

454   This relationship was especially pronounced when the visible food was high value. The influence

455   of predation risk and exploration on a choice for the visible food was not dependent on the

456   value of the visible food. When considering choices made over the entire trial (as opposed to

457   the first choice), fast explorers were more likely to choose the visible food, regardless of its

458   value, under predation risk. Thus the influence of exploration behaviour on plasticity was time

459   and predation risk dependent, but not food value dependent.

460

461   Empirical studies predict that the reactive-proactive personality axis correlates with plasticity, with

462   some suggesting a positive relationship between plasticity and proactive personalities (information

463   gaterhing hypothesis; Frost *et al.*, 2007; Mathot *et al.*, 2012; Rojas-Ferrer, Thompson and Morand-

464   Ferron, 2019), while others suggest a negative relationship between the two (behavioural flexibility

465   hypothesis; Verbeek, Drent and Wiepkema, 1994; Wolf, Van Doorn and Weissing, 2008; Coppens, De

466   Boer and Koolhaas, 2010). We found that fast (proactive) explorers are more plastic, supporting the

467   information-gathering strategy (IGS) hypothesis. Our observation that overall, birds tended to forage

468   on the familiar food option (i.e. in the sand) when under predation risk suggests they perceived the

469   hidden food to be a safer option, despite it being more time-consuming to acquire (even if not to

470   consume). At least in the total choice analysis, slow individuals were unlikely to feed on the visible

471   food source under risk of predation (Fig. 5), whereas fast individuals were more likely to prioritise the

472   visible high value food. This also supports the pace of life syndrome hypothesis (Réale *et al.*, 2010; Hall

473   *et al.*, 2015), where fast individuals prioritise immediate foraging at the risk of increased predation,

474   and slow individuals do the opposite (Stamps, 2007; Biro and Stamps, 2008; Mazza *et al.*, 2019).

475   Moreover, if stress causes individuals to perform habitual actions (Schwabe and Wolf, 2009), perhaps

476   slow explorers, as well as being more risk-averse (Koolhaas *et al.*, 1999; Groothuis and Carere, 2005;

20

477   Reale *et al.*, 2007), are also affected more strongly and negatively by stress than fast individuals (Baugh

478   *et al.*, 2013), and this could be another reason that they chose the familiar option when under risk.

479

480   Our results clearly suggest that this major constraint on behavioural variation, the reactive-proactive

481   personality axis, had an effect on foraging plasticity in our experimental setup. Several studies have

482   found personality to have different effects in different contexts (Frost *et al.*, 2007; Sih and Del Giudice,

483   2012). In our experiment, the association between our measure of personality on behavioural

484   plasticity was context-dependent, but the timescale in which the behaviour was expressed was also an

485   important variable for detecting these context-dependent responses. The value of the visible food was

486   important in the first choice, and the presence of a predator was important for total choices, which we

487   speculate could be related to the first choice representing sampling behaviour and their total choices

488   over four minutes representing their average choice.

489

490   Although we previously demonstrated that exploration behaviour is repeatable in our study

491   population (O'Shea, Serrano-Davies and Quinn, 2017), and many have shown it is also heritable (e.g.

492   (Quinn *et al.*, 2009), simultaneous repeat measures of exploration score and of foraging success (or

493   indeed of inhibitory control and foraging success), would be necessary to establish whether

494   correlations between these pairs of behaviour occur at the between-individual level, and really do

495   constrain plasticity (Dingemanse and Dochtermann, 2013). Estimating behavioural covariance is

496   challenging in general, and two factors make this especially impractical in the context of this study.

497   One is that the sample sizes would be prohibitory, not just because they are particularly high when

498   measuring covariation (Dingemanse and Dochtermann, 2013), but also because here the covariation

499   occurred in the context of an interaction. Another is that arguably it would be unethical to do so, since

500   the repeat measures would have to be separated by lengthy periods of time for them to reflect

501   anything other than temporary environmental effects. Despite this limitation in our approach, our

21

502   results demonstrate that constraints on plasticity caused by behavioural mechanisms like the RPPA are

503   likely important, if difficult to detect.

504

505   **Conclusion**

506   Individual variation in behavioural plasticity is an important mechanism facilitating adaptation to

507   ecological or environmental change. Our results show substantial variation in foraging plasticity, and

508   suggest that individual differences in cognition and personality both play context-dependent roles, that

509   are nevertheless independent of one another. We emphasise that the population level consequences of

510   behavioural variation may only be revealed in the light of very specific ecological conditions or gradients

511   experienced by individuals, but that very large sample sizes are going to be needed to demonstrate

512   phenotypic or genotypic covariance among behavioural traits.

513

517   **Author contributions:** JRC, IGK, GLD and JQ designed the study, JRC and GLD collected the data

518   with help from IGK, JRC analysed the data with help from MSR and CAT. JRC, JQ, MSR and GLD

519   wrote the manuscript with input from IGK. All authors approve the final manuscript and agree

520   to be held accountable for the contents.

526   **Competing interests:** We declare no competing interests.

527   **Ethics statement:** This study was conducted under licences from the Health Products Regulatory

528   Authority (AE19130_P017), the National Parks and Wildlife Service (C02/2018) and the British

529   Trust for Ornithology. The research project received ethical approval from the Animal Welfare

530   Body at University College Cork, and was in accordance with the ASAB (Association for the Study

531   of Animal Behaviour) Guidelines for the Treatment of Animals in Behavioural Research and

532   Teaching.

533   **Data accessibility:** R Code and Data are available as supplementary material, and will be

534   uploaded to Dryad upon acceptance.

535

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537   **Bibliography**

538   Amy, M., van Oers, K. & Naguib, M. (2012) 'Worms under cover: Relationships between

539   performance in learning tasks and personality in great tits (Parus major)', *Animal Cognition*,

540   15(5), 763–770. doi: 10.1007/s10071-012-0500-3.

541   Anderson, M. C. & Weaver, C. (2009) 'Inhibitory Control over Action and Memory', *Encyclopedia*

542   *of Neuroscience*, 5, 153–163. doi: 10.1016/B978-008045046-9.00421-6.

543   Aplin, L. M. Farine, D., R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B., C. (2015)

544   'Experimentally induced innovations lead to persistent culture via conformity in wild birds',

545   *Nature*. 518, 538–541. doi: 10.1038/nature13998.

546   Arvidsson, L. K. & Matthysen, E. (2016) 'Individual differences in foraging decisions: Information-

547   gathering strategies or flexibility?', *Behavioral Ecology*, 27(5), 1353–1361. doi:

548   10.1093/beheco/arw054.

549   Balda, R. P. & Kamil, A. C. (1992) 'Long-term spatial memory in clark's nutcracker, Nucifraga

550   columbiana', *Animal Behaviour*, 44(4), 761–769. doi: 10.1016/S0003-3472(05)80302-1.

551   Barton, K. (2019) Mu-MIn: Multi-model inference. R package Version 0.12.2/r18. http://R-

552   Forge.R-project.org/projects/mumin/

553   Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015) 'Fitting Linear Mixed-Effects Models Using

554   **lme4**', *Journal of Statistical Software*, 67(1). 1-48. doi: 10.18637/jss.v067.i01.

555   Baugh, A. T. van Oers, K., Naguib, M. & Hau, M. (2013) 'Initial reactivity and magnitude of the

556   acute stress response associated with personality in wild great tits (Parus major)', *General and*

557   *Comparative Endocrinology*. 189. 96–104. doi: 10.1016/j.ygcen.2013.04.030.

558   Biro, P. A. & Stamps, J. A. (2008) 'Are animal personality traits linked to life-history

559   productivity?', *Trends in Ecology and Evolution*, 23(7), 361–368. doi:

560   10.1016/j.tree.2008.04.003.

561   Bray, E. E., Maclean, E. L. & Hare, B. A. (2014) 'Context specificity of inhibitory control in dogs',

562   15–31. doi: 10.1007/s10071-013-0633-z.

563   Burnham, K. P. & Anderson, D. R. (2002) *Model Selection and multimodel inference - a practical*

564   *information-theoretic approach*. 2nd Edition, Springer-Verlag, New York. doi: 10.1007/b97636

565   Carlson, N. V., Pargeter, H. M. & Templeton, C. N. (2017) 'Sparrowhawk movement, calling, and

566   presence of dead conspecifics differentially impact blue tit (Cyanistes caeruleus) vocal and

567   behavioral mobbing responses', *Behavioral Ecology and Sociobiology*. Behavioral Ecology and

568   Sociobiology, 71(9). doi: 10.1007/s00265-017-2361-x.

569   Cauchoix, M., Chaine, A. S. & Barragan-Jason, G. (2020) 'Cognition in Context: Plasticity in

570   Cognitive Performance in Response to Ongoing Environmental Variables', *Frontiers in Ecology*

571   *and Evolution*. 8. 1–8. doi: 10.3389/fevo.2020.00106.

572   Cole, E. F., Morand-Ferron, J., Hinks, A. E. & Quinn, J. L. (2012) 'Cognitive ability influences

573   reproductive life history variation in the wild', *Current Biology*. 22(19), 1808–1812. doi:

574   10.1016/j.cub.2012.07.051.

575   Cole, E. F., Cram, D. L. & Quinn, J. L. (2011) 'Individual variation in spontaneous problem-solving

576   performance among wild great tits', *Animal Behaviour*. 81(2), 491–498. doi:

577   10.1016/j.anbehav.2010.11.025.

578   Coomes, J. R., Davidson, G. L., Reichert, M. S., Kulahci, I. G., Troisi, C. A., & Quinn, J. L. (2020)

579   Data from: Inhibitory control, personality and changing ecological conditions influencing

580   foraging plasticity in the great tit. Dryad Digital Repository.

581   Coppens, C. M., De Boer, S. F. & Koolhaas, J. M. (2010) 'Coping styles and behavioural flexibility:

582   Towards underlying mechanisms', *Philosophical Transactions of the Royal Society B: Biological*

583   *Sciences*, 365(1560), 4021–4028. doi: 10.1098/rstb.2010.0217.

584   Dall, S. R. X. & Johnstone, R. A. (2002) 'Managing uncertainty: information and insurance under

585   the risk of starvation', *Philosophical Transactions of the Royal Society of London. Series B,*

586   *Biological Sciences*, 357. 1519–26. doi: 10.1098/rstb.2002.1061.

587   Diamond, A. (2013) 'Executive Functions', *Annual Review of Psychology*, 64(1), 135–168. doi:

588   10.1146/annurev-psych-113011-143750.

589   Dingemanse, N. J., Kazem, A. J. N., Réale, D. & Wright, J. (2009) 'Behavioural reaction norms:

590   animal personality meets individual plasticity', *Trends in Ecology and Evolution*, 25(2), 81–89.

591   doi: 10.1016/j.tree.2009.07.013.

592   Dingemanse, N. J., Bouwman, K. M., van de Pol, M., van Overveld, T., Patrick, S. C., Matthysen E.

593   & Quinn, J. L. (2012) 'Variation in personality and behavioural plasticity across four populations

594   of the great tit Parus major', *Journal of Animal Ecology*, 81(1), 116–126. doi: 10.1111/j.1365-

595   2656.2011.01877.x.

596   Dingemanse, N. J. & Dochtermann, N. A. (2013) 'Quantifying individual variation in behaviour:

597   Mixed-effect modelling approaches', *Journal of Animal Ecology*, 82(1), 39–54. doi:

598   10.1111/1365-2656.12013.

599   Frost, A. J., Winrow-Giffen, A., Ashley, P. J. & Sneddon, L. U. (2007) 'Plasticity in animal

600   personality traits: Does prior experience alter the degree of boldness?', *Proceedings of the Royal*

601   *Society B: Biological Sciences*, 274(1608), 333–339. doi: 10.1098/rspb.2006.3751.

602   Green, L. & Myerson, J. (1996) 'Exponential versus hyperbolic discounting of delayed outcomes:

603   Risk and waiting time', *American Zoologist*, 36(4), 496–505. doi: 10.1093/icb/36.4.496.

604   Groothuis, T. G. G. & Carere, C. (2005) 'Avian personalities: Characterization and epigenesis',

605   *Neuroscience and Biobehavioral Reviews*, 29, 137–150. doi: 10.1016/j.neubiorev.2004.06.010.

606   Gross, K., Pasinelli, G. & Kunc, H. P. (2010) 'Behavioral Plasticity Allows Short-Term Adjustment

607   to a Novel Environment', *The American Naturalist,* 176(4). doi: 10.1086/655428.

608   Grueber, C. E., Nakagawa, S., Laws, R. J. & Jamieson, I. G. (2011) 'Multimodel inference in

609   ecology and evolution : challenges and solutions', *Journal of Evolutionary* Biology, 24, 699–711.

610   doi: 10.1111/j.1420-9101.2010.02210.x.

611   Hall, M. L., van Asten, T., Katsis, A. C., Dingemanse, N. J., Magrath, M. J. L. & Mulder, R. A. (2015)

612   'Animal personality and pace-of-life syndromes: Do fast-exploring fairy-wrens die young?',

613   *Frontiers in Ecology and Evolution*, 3, 1–14. doi: 10.3389/fevo.2015.00028.

614   Hartig. F. (2020) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression

615   Models. R package version 0.3.3.0. http://florianhartig.github.io/DHARMa/

616   Healy, S. D. & Hurly, T. A. (1995) 'Spatial memory in rufous hummingbirds (Selasphorus rufus): A

617   field test', *Animal Learning & Behavior*, 23(1), 63–68. doi: 10.3758/BF03198016.

618   Herborn, K. A., Heidinger, B. J., Alexander, L. & Arnold, K. E. (2014) 'Personality predicts

619   behavioral flexibility in a fluctuating, natural environment', *Behavioral Ecology*, 25(6), 1374–

620   1379. doi: 10.1093/beheco/aru131.

621   Holbrook, S. J. & Schmitt, R. J. (1988) 'The Combined Effects of Predation Risk and Food Reward

622   on Patch Selection', *Ecology*, 69(1), 125–134. doi: 10.2307/1943167.

623   van Horik, J. O., Langley, E. J. G., Whiteside, M. A., Laker, P. R., Beardsworth, C. E. & Madden, J.

624   R. (2018) 'Do detour tasks provide accurate assays of inhibitory control?', *Proceedings of the*

625   *Royal Society B: Biological Sciences*, 285. 20180150. doi: 10.1098/rspb.2018.0150.

626   Kalb, N., Anger, F. & Randler, C. (2019) 'Subtle variations in mobbing calls are predator-specific

627   in great tits (Parus major)', *Scientific Reports*. 9(1), 1–7. doi: 10.1038/s41598-019-43087-9.

628   Komers, P. E. (1997) 'Behavioural plasticity in variable environments', *Canadian Journal of*

629   *Zoology*, 75(2), 161–169. doi: 10.1139/z97-023.

630   Koolhaas, J. M., Korte, S. M., de Boer, S. F., van der Vegt, B. J., van Reenen, C. G., Hopster, H. …

631   Blokhuis, H. J. (1999) 'Coping styles in animals: Current status in behavior and stress-

632   physiology', *Neuroscience and Biobehavioral Reviews*, 23(7), 925–935. doi: 10.1016/S0149-

633   7634(99)00026-3.

634   Laland, K. N. & Reader, S. M. (1999) 'Foraging innovation in the guppy', *Animal Behaviour*, 57(2),

635   331–340. doi: 10.1006/anbe.1998.0967.

636   Lima, S. L. & Dill, L. M. (1990) 'Behavioral decisions made under the risk of predation: a review

637   and prospectus', *Canadian Journal of Zoology*, 68, 619–640. doi: 10.1139/z90-092.

638   MacArthur, R. H. & Pianka, E. R. (1966) 'On Optimal Use of a Patchy Environment Author', *The

639   American Naturalist*, 100(916), 603–609.

640   MacLean, E. L., Hare, B., Nunn, C. L., Adessi, E. Amici, F., Anderson, R. C., … Zhao, Y. (2014) 'The

641   evolution of self-control', *Proceedings of the National Academy of Sciences*, 111(20), E2140–

642   E2148. doi: 10.1073/pnas.1323533111.

643   Marchetti, C. & Drent, P. J. (2000) 'Individual differences in the use of social information in

644   foraging by captive great tits', *Animal Behaviour*. 60, 131-140. doi: 10.1006/anbe.2000.1443.

645   Mathot, K. J., Wright, J., Kempenaers, B. & Dingemanse, N. J. (2012) 'Adaptive strategies for

646   managing uncertainty may explain personality-related differences in behavioural plasticity',

647   *Oikos*. 121. 1009–1020. doi: 10.1111/j.1600-0706.2012.20339.x.

648   Mazur, J. E. (1988) 'Choice between small certain and large uncertain reinforcers', *Animal

649   Learning & Behavior*, 16(2), 199–205. doi: 10.3758/BF03209066.

650   Mazza, V., Jacob, J., Dammhahn, M., Zaccaroni, M. & Eccard, J. A. (2019) 'Individual variation in

651   cognitive style reflects foraging and anti-predator strategies in a small mammal', *Scientific

652   Reports*. 9(1), 1–9. doi: 10.1038/s41598-019-46582-1.

653   Milinski, M. & Heller, R. (1978) 'Influence of a predator on the optimal foraging behaviour of

654   sticklebacks (Gasterosteus aculeatus L.)', *Nature*. 275. 642-644.

655   Morand-Ferron, J., Cole, E. F., Rawles, J. E. C. & Quinn, J. L. (2011) 'Who are the innovators? A

656   field experiment with 2 passerine species', *Behavioral Ecology*, 22(6), 1241–1248. doi:

657   10.1093/beheco/arr120.

658   Morand-Ferron, J., Hamblin, S., Cole, E. F., Aplin, L. M. & Quinn, J. L. (2015) 'Taking the operant

659   paradigm into the field: Associative learning in wild great tits', *PLoS ONE*, 10(8), 1–16. doi:

660   10.1371/journal.pone.0133821.

661   O'Shea, W., Serrano-Davies, E. & Quinn, J. L. (2017) 'Do personality and innovativeness influence

662   competitive ability? An experimental test in the great tit', *Behavioral Ecology*, 00, 1–10. doi:

663   10.1093/beheco/arx104.

664   Quinn, J. L., Patrick, S. C., Bouwhuis, S., Wilkin, T. A. & Sheldon, B. C. (2009) 'Heterogeneous

665   selection on a heritable temperament trait in a variable environment', *Journal of Animal*

666   *Ecology*, 78(6), 1203–1215. doi: 10.1111/j.1365-2656.2009.01585.x.

667   Quinn, J. L. & Cresswell, W. (2005) 'Personality, Anti-Predation Behaviour and Behavioural

668   Plasticity in the Chaffinch Fringilla coelebs', *Behaviour*, 142(9), 1377–1402.

669   R Core Team (2013). R: A language and environment for statistical computing. R Foundation for

670   Statistical Computing, Vienna, Austria. http://www.R-project.org/

671   Raine, N. E. & Chittka, L. (2008) 'The correlation of learning speed and natural foraging success

672   in bumble-bees.', *Proceedings of the Royal Society B: Biological Sciences*, 275(1636), 803–808.

673   doi: 10.1098/rspb.2007.1652.

674   Réale, D. Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. (2007) 'Integrating animal

675   temperament within ecology and evolution', 82, 291–318. doi: 10.1111/j.1469-

676   185X.2007.00010.x.

677   Réale, D., Garant, D., Humpheries, M. M., Bergeron, P., Careau, V. and Montiglio, P-O. (2010)

678   'Personality and the emergence of the pace-of-life syndrome concept at the population level',

679   *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4051–4063.

680   doi: 10.1098/rstb.2010.0208.

681   Rojas-Ferrer, I., Thompson, M. J. & Morand-Ferron, J. (2019) 'Is exploration a metric for

682   information gathering ? Attraction to novelty and plasticity in black - capped chickadees',

683   *Ethology*, 00:1–10. doi: 10.1111/eth.12982.

684   Rosati, A. G. (2017) 'Foraging Cognition: Reviving the Ecological Intelligence Hypothesis', *Trends*

685   *in Cognitive Sciences*. 21(9), 691–702. doi: 10.1016/j.tics.2017.05.011.

686   Schwabe, L. & Wolf, O. T. (2009) 'Stress prompts habit behavior in humans', *Journal of*

687   *Neuroscience*, 29(22), 7191–7198. doi: 10.1523/JNEUROSCI.0979-09.2009.

688   Serrano-Davies, E., O'Shea, W. & Quinn, J. L. (2017) 'Individual foraging preferences are linked to

689   innovativeness and personality in the great tit', *Behavioral Ecology and Sociobiology*. 71(161).

690   doi: 10.1007/s00265-017-2389-y.

691   Shaw, R. C., MacKinlay, R. D., Clayton, N. S. & Burns, K. C. (2019) 'Memory Performance

692   Influences Male Reproductive Success in a Wild Bird', *Current Biology*. 29(9), 1498-1502.e3. doi:

693   10.1016/j.cub.2019.03.027.

694   Sih, A., Bell, A. M., Chadwick Johnson, J. & Ziemba, R. E. (2004) 'Behavioural Syndromes, an

695   integrative overview', *The Quarterly Review of Biology*, 79(3).

696   Sih, A. & Del Giudice, M. (2012) 'Linking behavioural syndromes and cognition: A behavioural

697   ecology perspective', *Philosophical Transactions of the Royal Society B: Biological Sciences*,

698   367(1603), 2762–2772. doi: 10.1098/rstb.2012.0216.

699   Snell-Rood, E. C. (2013) 'An overview of the evolutionary causes and consequences of

700   behavioural plasticity', *Animal Behaviour*. 85(5), 1004–1011. doi:

701   10.1016/j.anbehav.2012.12.031.

702   Sonnenberg, B. R., Branch, C. L., Pitera, A. M., Bridge, E. & Pravosudov, V. V. (2019) 'Natural

703   Selection and Spatial Cognition in Wild Food- Caching Mountain Chickadees', *Current Biology*.

704   29(4), 670-676.e3. doi: 10.1016/j.cub.2019.01.006.

705   Stamps, J. A. (2007) 'Growth-mortality tradeoffs and "personality traits" in animals', *Ecology*

706   *Letters*, 10(5), 355–363. doi: 10.1111/j.1461-0248.2007.01034.x.

707   Stephens, D. W. & Krebs, J. R. (1986) *Foraging Theory*. Princeton University Press, Princeton

708   Stevens, J. R., Rosati, A. G., Ross, K. R. & Hauser, M. D. (2005) 'Will travel for food: Spatial

709   discounting in two New World monkeys', *Current Biology*, 15(20), 1855–1860. doi:

710   10.1016/j.cub.2005.09.016.

711   Stoffel, M. A., Nakagawa, S. & Schielzeth, H. (2017) 'rptR: repeatability estimation and variance

712   decomposition by generalized linear mixed-effects models', *Methods in Ecology and Evolution*,

713   8(11), 1639–1644. doi: 10.1111/2041-210X.12797.

714   Suomi, S. J. (2004) 'Research in Human Development Civic Engagement, Political Identity, and

715   Generation in Developmental Context Civic Engagement, Political Identity and Generation in

716   Developmental Context', *Research in Human Development*, 1(3), 205–222. doi:

717   10.1207/s15427617rhd0103.

718   Tsukayama, E., Duckworth, A. L. & Kim, B. (2012) 'Resisting everything except temptation:

719   evidence and an explanation for domain-specific impulsivity', *European Journal of Personality*,

720   26, 318–334. doi: 10.1002/per.841.

721   Verbeek, M. E. M., Drent, P. J. & Wiepkema, P. R. (1994) 'Consistent individual differences in

722   early exploratory behaviour of male great tits', *Animal Behaviour*, 1113–1121. doi:

723   10.1006/anbe.1994.1344.

31

724   Wolf, M., Van Doorn, G. S. & Weissing, F. J. (2008) 'Evolutionary emergence of responsive and

725   unresponsive personalities', *Proceedings of the National Academy of Sciences of the United*

726   *States of America*, 105(41), 15825–15830. doi: 10.1073/pnas.0805473105.

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729   **Figures and Tables**

730   Figure 1. The four treatments are illustrated. In each treatment, we presented great tits with a

731   24-well tray filled with sand (six wells are shown here for illustrative purposes) and buried

732   mealworms underneath the sand in ten of the 24 wells. The first treatment (a) had ten

733   sunflower seeds (dehusked) on the surface and was presented as the pre-training task. The

734   second (b) had two mealworms in transparent cases on the surface. The third (c) and fourth (d)

735   treatments were as in (a) and (b) but had the addition of a simulated attack by a model

736   sparrowhawk.
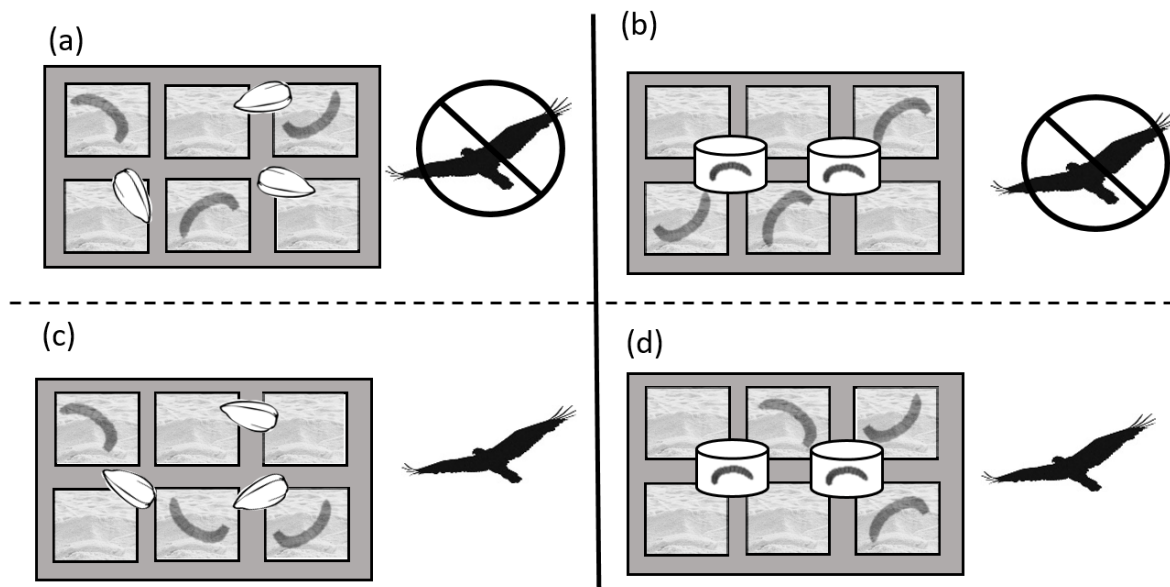
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739   Figure 2. The four treatments with (a) the proportion of birds that chose the visible food and

740   that chose the hidden food on their first choice and (b), the proportion of choices for the visible

741   food out of the total number of choices made in four minutes. For (a), sample sizes are given on

742   each bar and for (b) the 25th and 75th quartiles and median are shown and the whiskers are

743   ±1.5*IQR.

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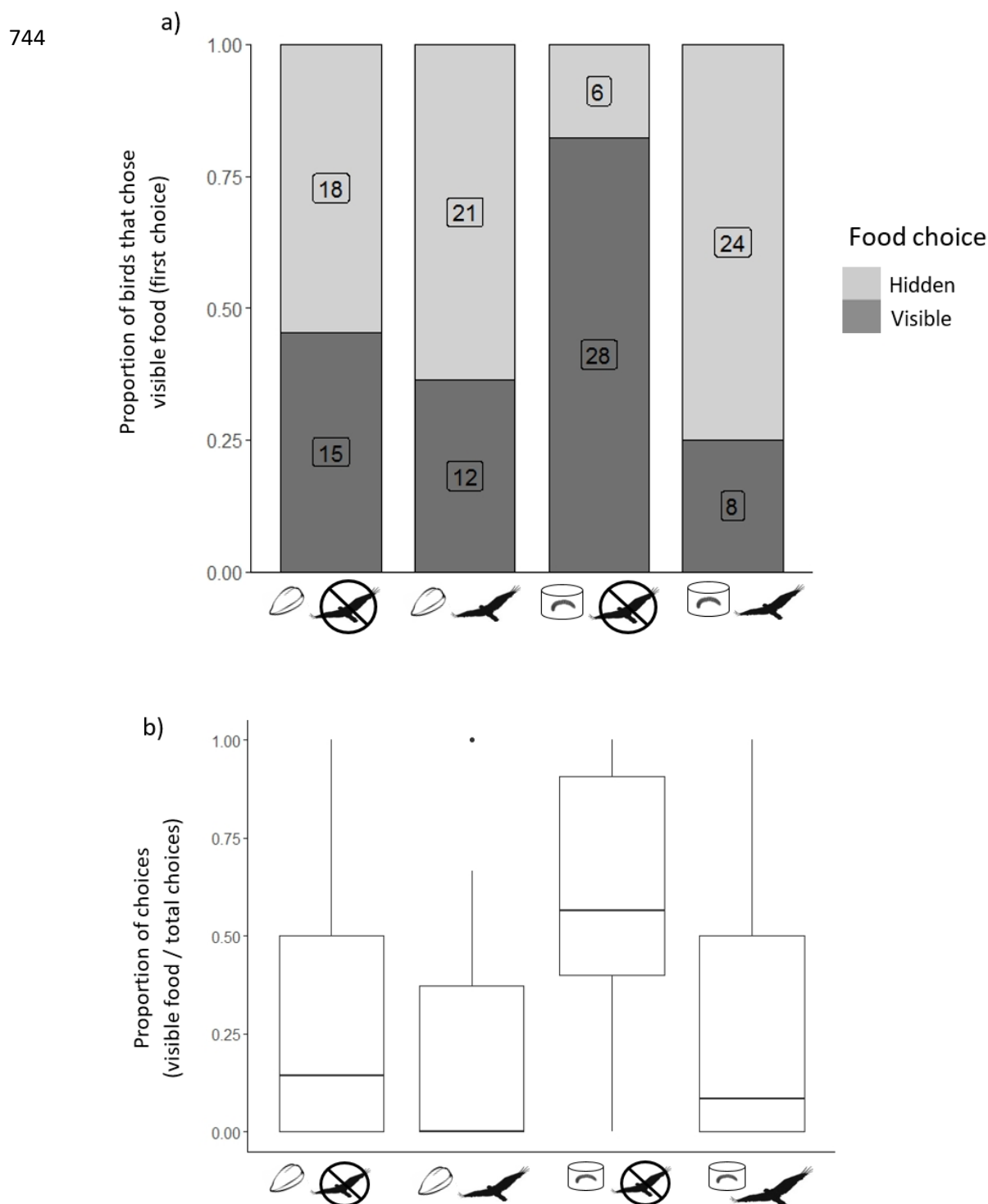
745   Figure 3. Proportion of choices for the visible food out of the total number of choices made in

746   four minutes, against detour-reaching score, for each visible food type (averaged for the two

747   treatments with the same visible food type). For illustrative purposes, the detour-reaching score

748   has been split into three groups; Low, Medium and High (Range, median, mean: Low: 0 – 0.3,

749   0.2, 0.2, n = 10; Medium: 0.4-0.5, 0.4, n = 8, 0.41; High: 0.6-0.8, 0.7, 0.69, n = 11).

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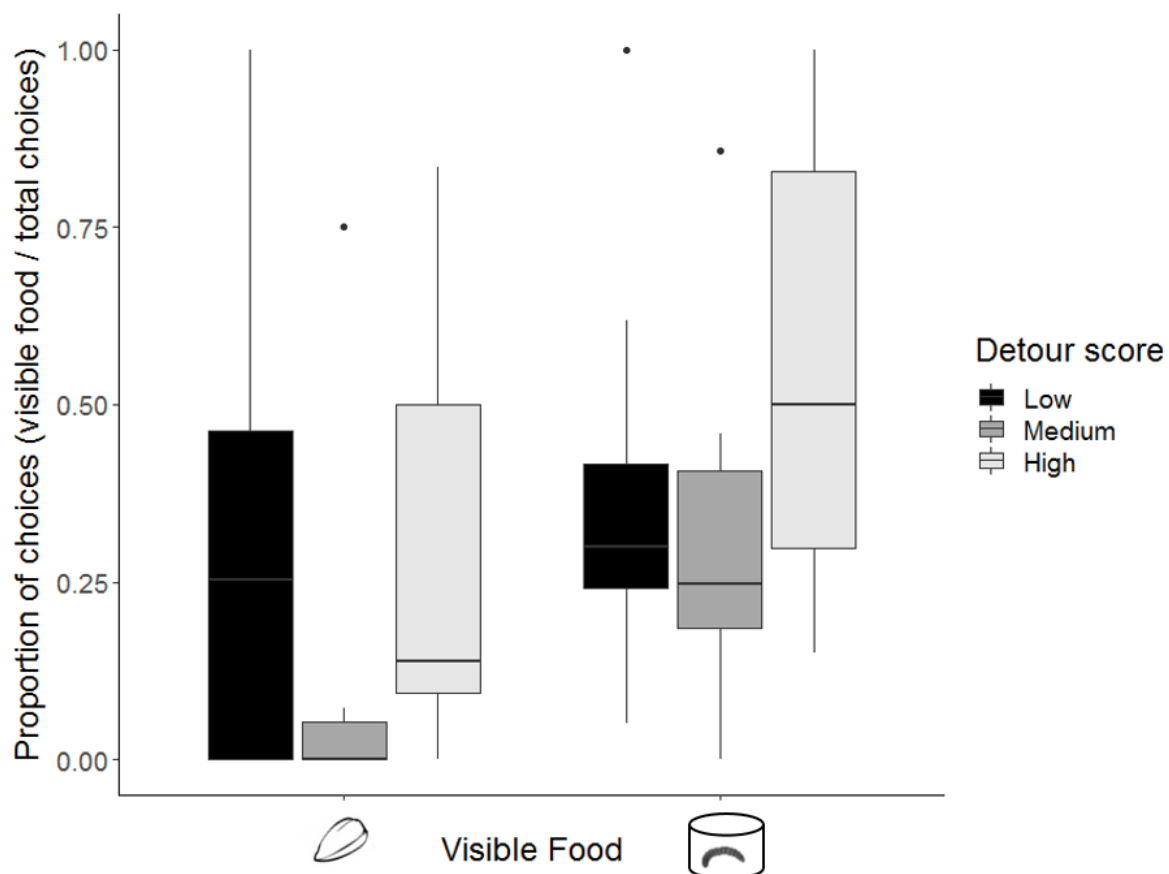
Figure 4. Proportion of birds that chose visible food depending on their exploration score, for first choice only. For illustrative purposes, the continuous exploration score has been split into three categories slow, medium and fast (Range, median, mean: Slow: 1-2, 1, 1.43, n = 14; Medium: 3-10, 7, 6.38, n = 13; Fast: 12-29, 15.5, 18.5, n = 8). Sample sizes are given on each bar.
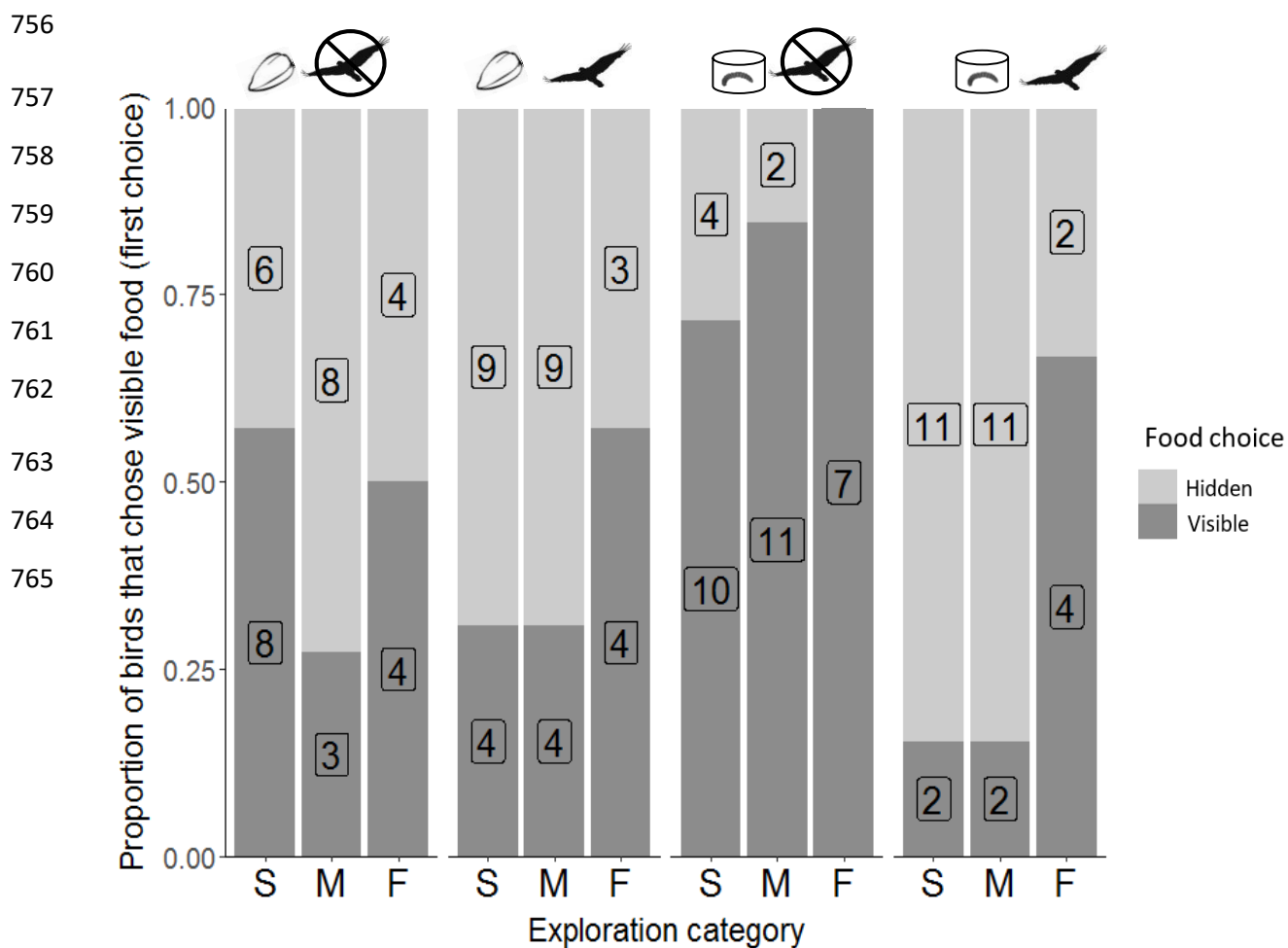
766   Figure 5. Proportion of choices for the visible food out of the total number of choices made in

767   four minutes, against exploration score, for each predator treatment (averaged across the two

768   food types). For illustrative purposes, the continuous exploration score has been split into three

769   categories; slow, medium and fast (Range, median, mean: Slow: 1-2, 1, 1.43, n = 14; Medium: 3-

770   10, 7, 6.38, n = 13; Fast: 12-29, 15.5, 18.5, n = 8).
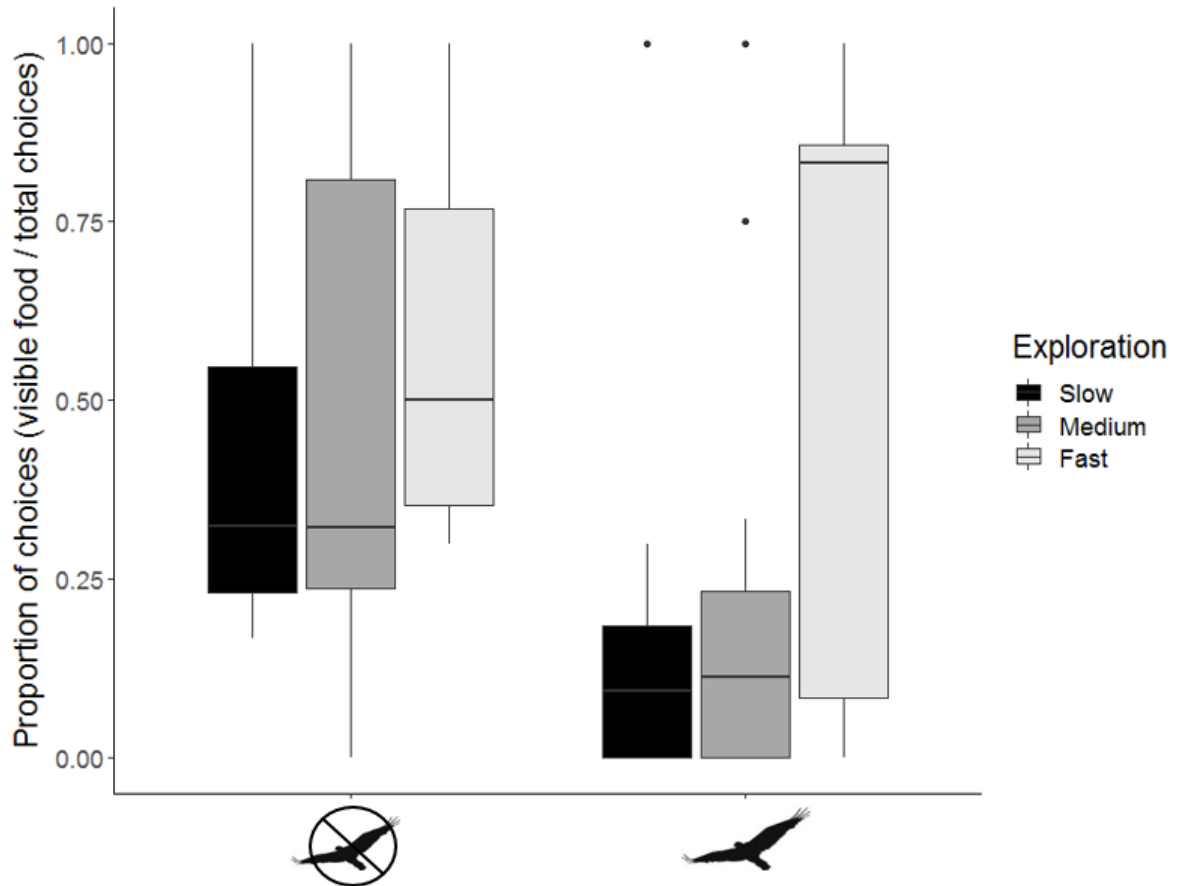
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773   Table 1. Predictions of how inhibitory control (IC), as measured from the detour-reaching task,

774   and personality, as measured from the 'reactive-proactive personality axis' (RPPA), influence

775   whether individuals switch from feeding on the hidden high-value food to feeding on the visible

776   low-value (scenario 1) or high-value (scenario 2) surface food. Note that for illustrative

777   purposes, our continuous measure of IC has been changed to a binary 'good' or 'poor'. We refer

778   to visible food choices as representing a plastic response (i.e. a switch) relative to their trained

779   behaviour of foraging in the sand.

| | | Food choice | |
| | | Scenario 1 | Scenario 2 |
	Individual phenotype	Visible low-value, hidden high-value	Visible high-value, hidden high-value
a) IC hypotheses			
i) Hidden food is the prepotent response	Good IC	Choose hidden	Switch to visible
	Poor IC	Choose hidden	Choose hidden
ii) Visible food is the prepotent response	Good IC	Choose hidden	Switch to visible
	Poor IC	Switch to visible	Switch to visible
b) RPPA hypothesis			
i) Behavioural flexibility	Proactive	Choose hidden	Choose hidden
	Reactive	Choose hidden	Switch to visible
ii) Information gathering	Proactive	Switch to visible	Switch to visible
	Reactive	Choose hidden	Choose hidden

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781   Table 2. R value, p value and confidence intervals for repeatability analysis calculated in R using

782   the rptR package. The first choice and total choices for detour reaching and exploration were

783   analysed in two models. Unadjusted: single variable of individual as a random effect, and

784   Adjusted: all variables from the model average. All values are from the link-scale approximation.

785   Due to the smaller number of birds that completed the detour-reaching task than completed

786   the exploration behaviour, the sample size for the models including detour-reaching are smaller.

Dataset	N	Model	R value	P value	95% Confidence interval
First choice					
Detour reaching data subset	29	Unadjusted	0.16	0.041	0; 0.37
		Adjusted	0.32	0.01	0; 0.74
Exploration data subset	35	Unadjusted	0.22	0.006	0.02; 0.41
		Adjusted	0.47	<0.001	0.08; 0.84
Total choices					
Detour reaching data subset	29	Unadjusted	0.30	<0.001	0.10; 0.48
		Adjusted	0.32	<0.001	0.10; 0.47
Exploration data subset	35	Unadjusted	0.31	<0.001	0.11; 0.47
		Adjusted	0.27	<0.001	0.10; 0.41

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789 Table 3. Analysis for first choice made by the great tits including detour-reaching score as an

790 explanatory variable. The values shown are the average of all the top models within two AICc of

791 the best model. A positive value for the estimate means the visible food is more likely to be

792 selected than the hidden food. The relative importance (averaged weight: sum of Akaike

793 weights) for each parameter is shown. 'Age' as a fixed effect and two interactions,

794 'Detour*Visible food' and 'Detour*Predator' are excluded because they did not appear in any of

795 the top models.

Inhibitory control First choice	Estimate	Stan. Error	95% Confidence interval	Averaged weight	P value
Intercept	2.31	0.99	0.37; 4.25		0.02
Fixed effects					
Predator					
No	0	0			
Yes	-4.14	1.03	-6.16; -2.11	1.0	<0.001
Visible food					
Encased worm	0	0			
Seed	-3.01	0.92	-4.80; -1.21	1.0	0.001
Detour	-0.45	1.16	-2.72; 1.81	0.26	0.70
Sex					
Female	0	0			
Male	-0.18	0.51	-1.19; 0.82	0.24	0.72
Habitat					
Coniferous	0	0			
Deciduous	1.67	0.83	0.05; 3.29	1.0	0.05
Interactions					
Predator*Visible food	3.68	1.22	1.28; 6.08	1.0	0.003

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798   Table 4*:* Analysis for first choice made by the great tits including exploration score as an

799   explanatory variable. The values shown are the average of all the top models within two AICc of

800   the best model. A positive value for the estimate means the visible food is more likely to be

801   selected than the hidden food. The relative importance (averaged weight: sum of Akaike

802   weights) for each parameter is shown.

Exploration *First choice*	Estimate	Stan. Error	95% Confidence interval	Averaged weight	P value
Intercept	0.54	1.07	-1.56; 2.63		0.62
Fixed effects					
Predator					
No	0	0			
Yes	-5.21	1.25	-7.66; -2.76	1.0	< 0.001
Visible food					
Encased worm	0	0			
Seed	-1.70	0.95	-3.57; 0.17	1.0	0.08
Exploration	0.29	0.12	0.05; 0.53	1.0	0.02
Sex					
Female	0	0			
Male	-0.12	0.45	-0.99; 0.75	0.15	0.79
Age					
Adult	0	0			
Juvenile	0.23	0.66	-1.06; 1.52	0.23	0.73
Habitat					
Conifer	0	0			
Deciduous	1.28	1.12	-0.91; 3.48	0.74	0.26
Interactions					
Predator*Visible food	4.39	1.31	1.81; 6.96	1.0	< 0.001
Exploration*Visible food	-0.26	0.12	-0.49; -0.02	1.0	0.03
Exploration*Predator	0.02	0.06	-0.10; 0.14	0.19	0.72

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810   Table 5: Analysis for total choices made by the great tits in four minutes including detour-

811   reaching score as an explanatory variable. The values shown are the average of all the top

812   models within two AICc of the best model. A positive value for the estimate means the visible

813   food is more likely to be selected than the hidden food. 'Age' as a fixed effect and the

814   interaction 'Detour*Predator' have been excluded because they did not appear in any of the top

815   models. The relative importance (averaged weight: sum of Akaike weights) for each parameter

816   is shown.

Inhibitory control Total choices	Estimate	Stan. Error	95% Confidence interval	Averaged weight	P value
Intercept	0.13	0.97	-1.76; 2.02		0.89
Fixed effects					
Predator					
No	0	0			
Yes	-2.41	0.34	-3.07; -1.75	1.0	<0.001
Visible food					
Encased worm	0	0			
Seed	-0.86	0.48	-1.80; 0.08	1.0	0.08
Detour	1.77	1.45	-1.07; 4.61	1.0	0.23
Sex					
Female	0	0			
Male	-0.69	0.75	-2.17; 0.78	0.61	0.36
Habitat					
Coniferous	0	0			
Deciduous	0.43	0.62	-0.79; 1.64	0.47	0.49
Interactions					
Predator*Visible food	2.47	0.50	1.49; 3.45	1.0	<0.001
Detour*Visible food	-2.54	0.96	-4.42; -0.66	1.0	0.009

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819 Table 6. Analysis for total choices made by the great tits in four minutes including exploration

820 score as an explanatory variable. The values shown are the average of all the top models within

821 two AICc of the best model. A positive value for the estimate means the visible food is more

822 likely to be selected than the hidden food. 'Age' as a fixed effect has been excluded because it

823 did not appear in any of the top models. The relative importance (averaged weight: sum of

824 Akaike weights) for each parameter is shown.

Exploration *Total choices*	Estimate	Stan. Error	Confidence interval	Averaged weight	P value
Intercept	0.62	0.51	-0.38; 1.63		0.23
Fixed effects					
Predator					
No	0	0			
Yes	-2.96	0.34	-3.63; -2.29	1.0	<0.001
Visible food					
Encased worm	0	0			
Seed	-1.70	0.31	-2.31; -1.08	1.0	<0.001
Exploration	0.08	0.04	-0.001; 0.17	1.0	0.06
Sex					
Female	0	0			
Male	-1.18	0.45	-2.07; -0.30	1.0	0.009
Habitat					
Conifer	0	0			
Deciduous	0.36	0.51	-0.64; 1.36	0.48	0.48
Interactions					
Predator*Visible food	2.50	0.41	1.70; 3.31	1.0	<0.001
Exploration*Visible food	-0.04	0.05	-0.13; 0.05	0.56	0.41
Exploration*Predator	0.10	0.04	0.03; 0.18	1.0	0.006

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