

1 **Inhibitory control, personality, and manipulated ecological conditions influence foraging**
2 **plasticity in the great tit**

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17 decisions, inhibitory control, great tit, personality, predation

18

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.

50

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.

63

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 breadth, although the direction of this relationship varies; primate
75 species with higher self-control had greater dietary breadth (MacLean *et al.*, 2014), while pheasants
76 with greater dietary breadth had poor performance on inhibitory control tasks (van Horik *et al.*,

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.

79

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 (Grootuis 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-

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 Dingemans *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 Aviary housing

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 Exploration assay and inhibitory control assays

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 Experiment pre-training and training

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

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

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

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.

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 $\Delta\text{AICc} < 2$ 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).

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 Food value and predation risk

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.

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 suppressed: 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-

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

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

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 gathering 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;

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

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

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533 **Data accessibility:** R Code and Data are available as supplementary material, and will be
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535

536

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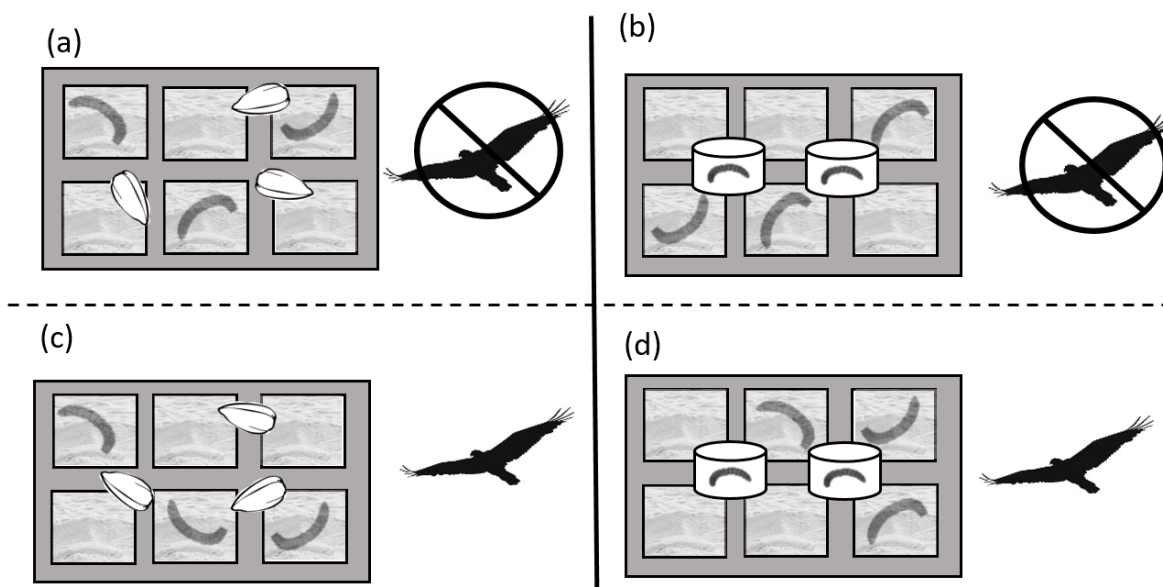
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725 unresponsive personalities', *Proceedings of the National Academy of Sciences of the United*
726 *States of America*, 105(41), 15825–15830. doi: 10.1073/pnas.0805473105.

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729 **Figures and Tables**

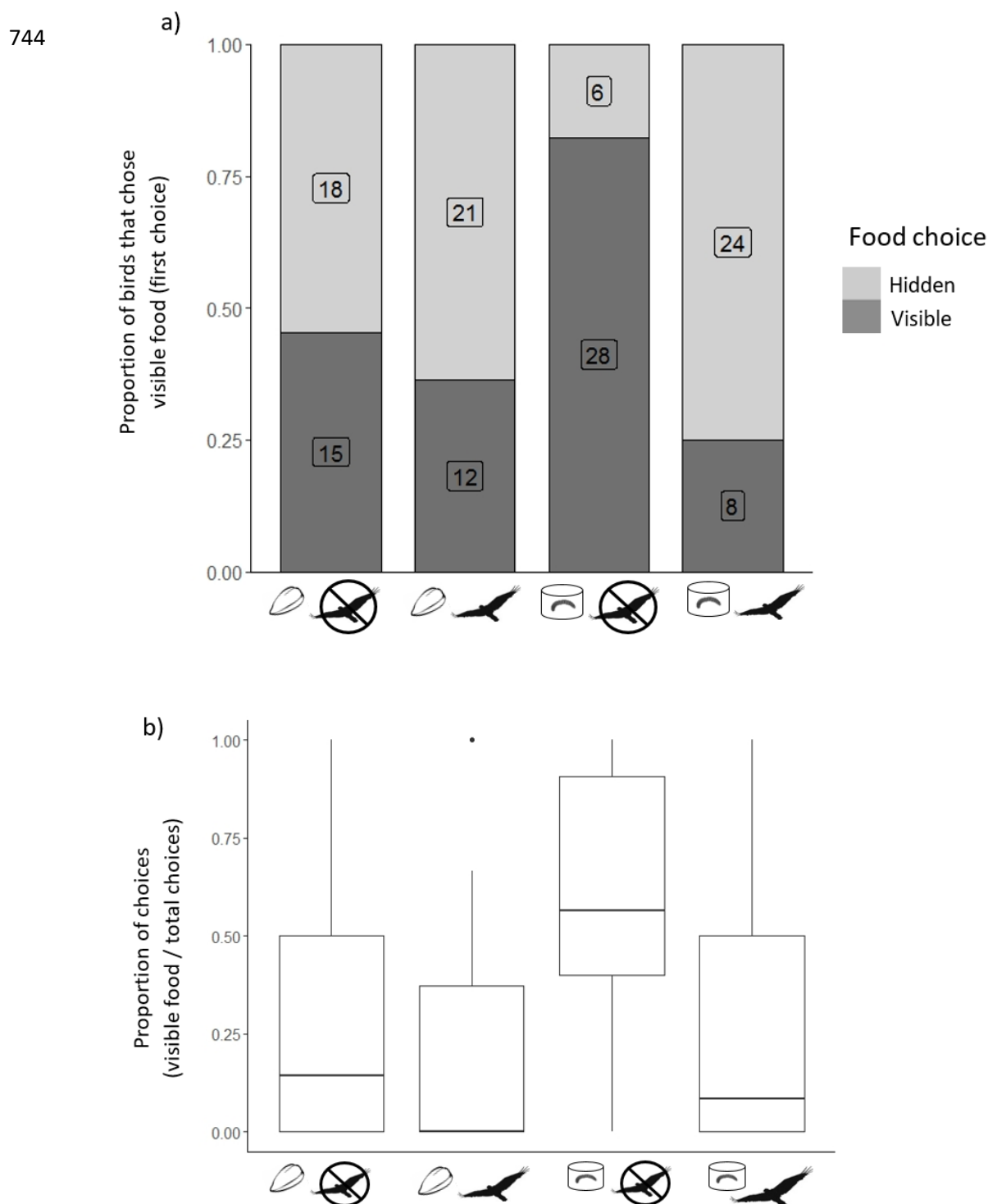
730 Figure 1. The four treatments are illustrated. In each treatment, we presented great tits with a
731 24-well tray filled with sand (six wells are shown here for illustrative purposes) and buried
732 mealworms underneath the sand in ten of the 24 wells. The first treatment (a) had ten
733 sunflower 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.



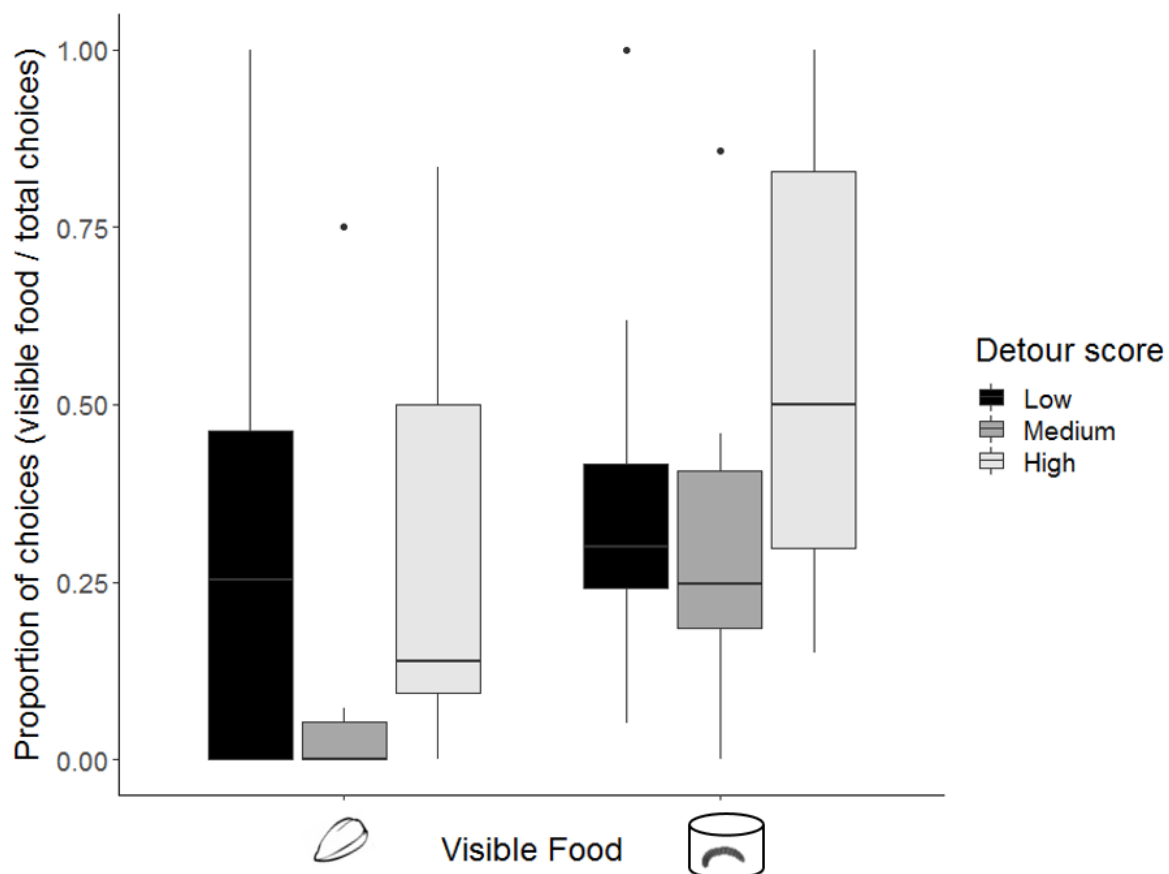
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739 Figure 2. The four treatments with (a) the proportion of birds that chose the visible food and
 740 that chose the hidden food on their first choice and (b), the proportion of choices for the visible
 741 food out of the total number of choices 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 $\pm 1.5 \cdot \text{IQR}$.

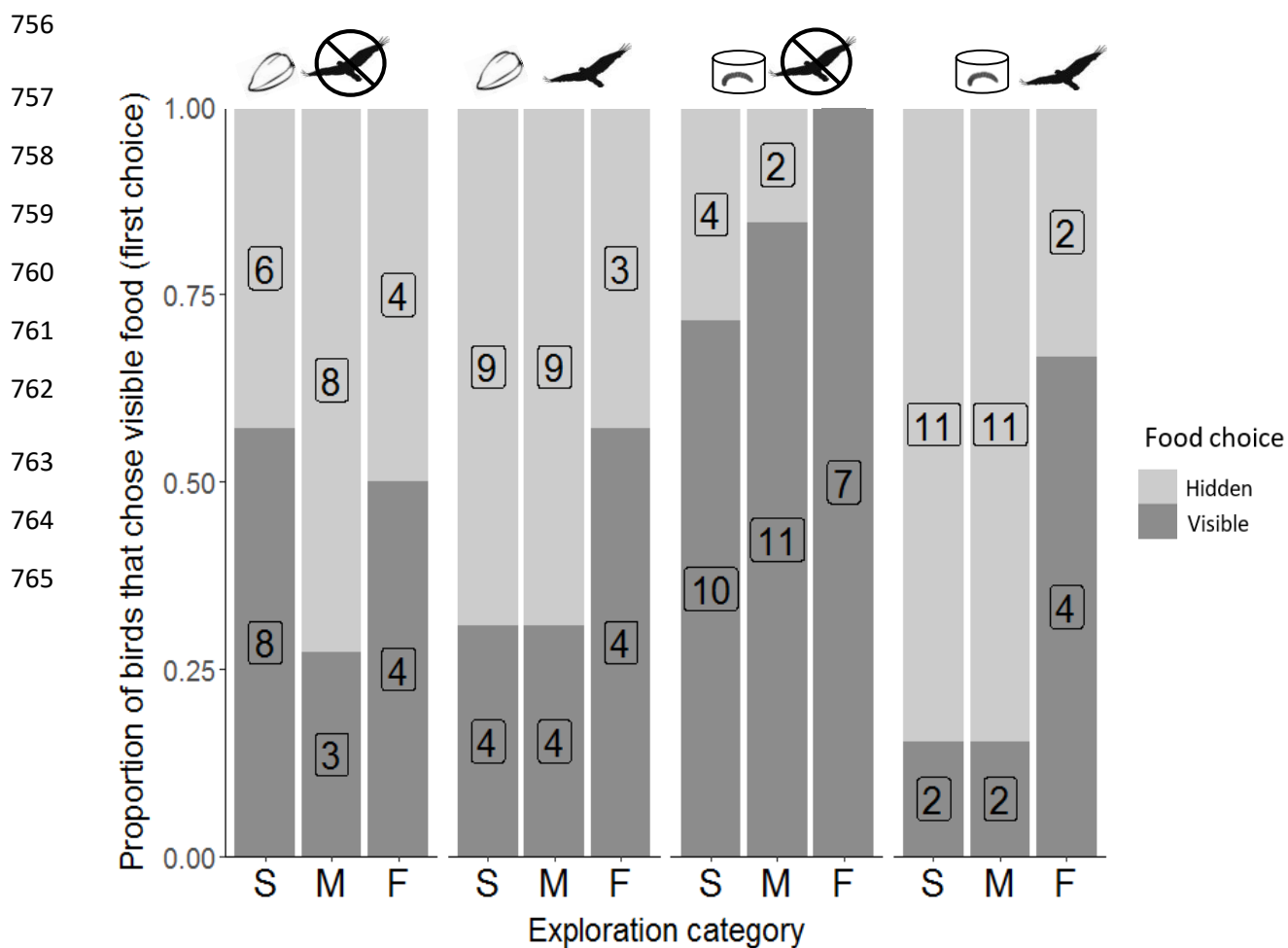


745 Figure 3. Proportion of choices for the visible food out of the total number of choices made in
746 four minutes, against detour-reaching score, for each visible food type (averaged for the two
747 treatments with the same visible food type). For illustrative purposes, the detour-reaching score
748 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).

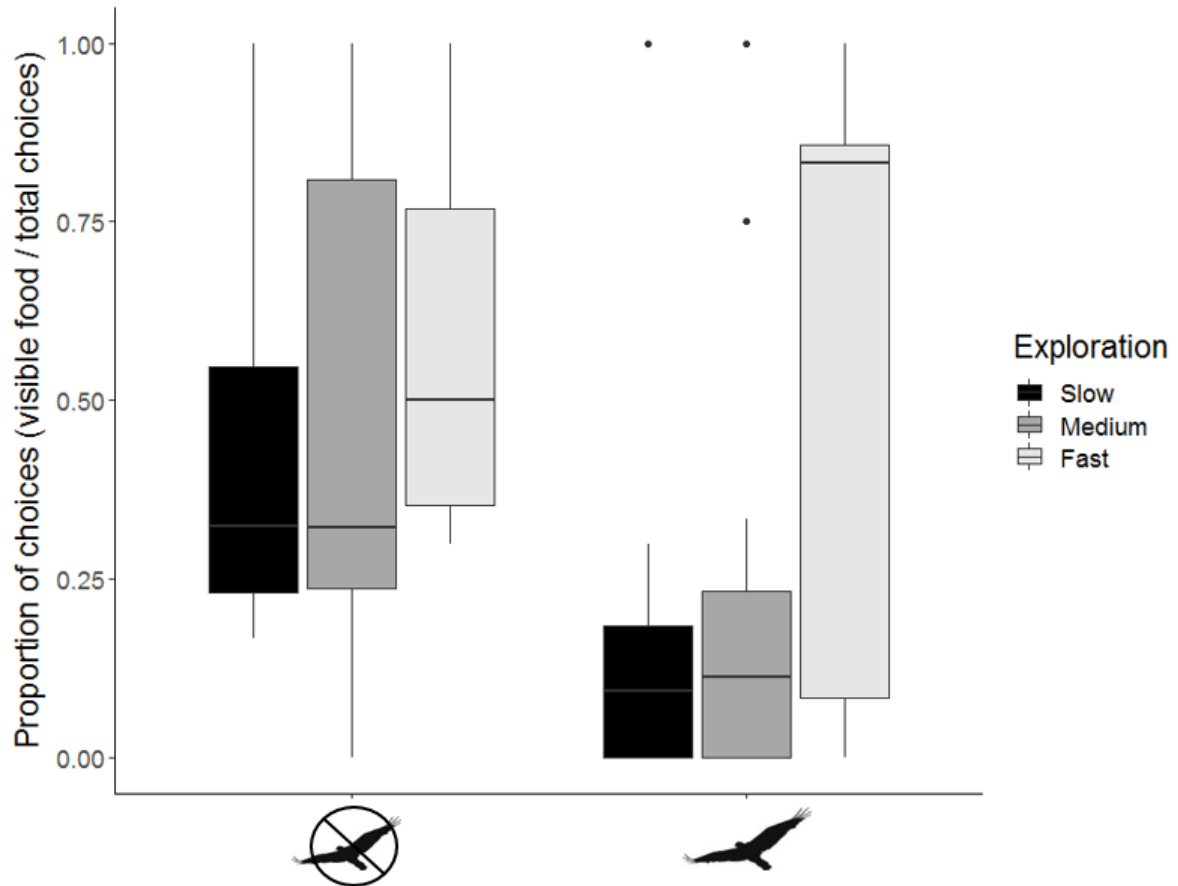


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752 Figure 4. Proportion of birds that chose visible food depending on their exploration score, for
 753 first choice only. For illustrative purposes, the continuous exploration score has been split into
 754 three categories slow, medium and fast (Range, median, mean: Slow: 1-2, 1, 1.43, n = 14;
 755 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.

<i>Inhibitory control First choice</i>	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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797

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.

<i>Exploration First choice</i>	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.

<i>Inhibitory control</i> <i>Total choices</i>	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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818

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.

<i>Exploration</i> <i>Total choices</i>	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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