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Individual differences in foraging decisions : information-gathering strategies or flexibility?

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1 Individual differences in foraging decisions - information
2 gathering strategies or flexibility?

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4 Abbreviated title:

5 Information gathering or behavioral flexibility?

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17 Abstract

18 Information on where to find food patches, their quality and food variance can have implications for
19 fitness and survival when a current food patch fails. Individuals have been found to vary in their
20 response to changes in food availability, and this has been related to several personality traits in
21 animals such as exploration behavior, which measures activity in a novel environment. We examined
22 if personality-related variation in reactions to food availability change could be explained by
23 information gathering strategies, where individuals vary in investing in sampling known patches as a
24 trade-off to seeking new patches. We also examined if these relationships can be explained by an
25 alternative hypothesis where individuals are expected to express variation in behavioral flexibility.
26 The behavioral flexibility hypothesis predicted that individuals rely either more on internal/prior or
27 external/current information. In addition to a standardized exploration behavior test we designed a
28 new 5 day long experiment where individual reactions to changes in food availability were measured
29 using wild great tits (*Parus major*). We found that slow exploring individuals sampled empty food
30 patches more than fast exploring individuals, supporting the information gathering strategy
31 hypothesis. We found no evidence for personality-related differences in feeder choice in response to
32 changes in food availability, nor personality-related differences in flexibility in behavioral responses.

33 *Keywords:* Exploration behavior, information gathering, behavioral flexibility, foraging, animal
34 personality

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40 Lay summary

41 Individual animals differ in their behavioral reactions to changing food availability, and this variation
42 has been linked with innate variation in personality traits. We studied the response of individual
43 Great Tits to changing food situations in an aviary, and examined whether individual responses
44 reflect different information gathering strategies, or overall flexibility of behavior. We found that
45 individuals differ in the way they gather information from feeders and that this was linked with
46 personality.

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59 Introduction

60 In response to challenges in the environment, individuals can display a vast variety of responses as well as
61 variation in the strength of responses that differ consistently between individuals across time and/or context.
62 These consistent between-individual differences are usually defined as animal personality (Gosling, 2001; Sih et
63 al., 2004) which is a widely studied occurrence from evolutionary and ecological perspectives (Sih et al., 2012;
64 Wolf and Weissing, 2012). It is normally considered as a set of underlying personality traits such as exploration
65 (Verbeek et al. 1994), activity (Gosling, 2001) and risk-taking (van Oers et al., 2005). Personality traits have
66 been linked with several different life history traits, such as growth rate (Adriaenssens and Johnsson, 2010),
67 fitness (Nicolaus et al., 2012) and natal dispersal distances (Dingemanse et al., 2003), providing evidence for
68 their role in micro-evolutionary processes (Dochtermann and Dingemanse, 2013; Wolf and Weissing, 2012) and
69 population dynamics (Clobert et al., 2009).

70 Individual differences also appear to exist in dealing with variation in information from the
71 environment, something which has previously been linked with personality (Carter et al., 2013; Marchetti and
72 Drent, 2000; Sih and Del Giudice, 2012). Employing an information gathering strategy can be beneficial in
73 dealing with the unpredictability of information and the costs of time and energy required to gather it,
74 especially if information is clumped (Stephens, 1987). Because of factors such as intrinsic differences between
75 individuals and competition, individuals may employ different information gathering strategies (Mathot et al.,
76 2012). Differences may lie in the resolution of information gathered, for example some individuals may prefer
77 to sample information more shallowly or less often compared to others (Marchetti and Drent, 2000; Sih and
78 Del Giudice, 2012). Differences may also exist in what kind of information is gathered, such as the choice
79 between updating previously gathered information or gathering information in previously unvisited areas.
80 Additionally, individuals may rely more or less on social information instead of, or in addition to, personal
81 information (Kurvers et al., 2010; Marchetti and Drent, 2000; Toelch et al., 2014; Trompf and Brown, 2014).
82 These factors influence the quality and quantity of the information an individual possesses and can
83 consequently affect further behavioral decisions that are crucial for fitness and survival (McNamara and Dall,
84 2010).

85 One specific type of information with strong fitness implications is spatial information about
86 resources, and several studies suggest a link between spatial information gathering and personality. A study by
87 van Overveld et al. (2010) of great tits (*Parus major*) in the wild found a positive relationship between
88 exploration behavior measured in captivity and speed of changing foraging home-range upon removal of food
89 from a feeder. The authors propose a mechanistic link of foraging information use, where fast explorers return
90 more quickly to previously experienced foraging patches whereas slow explorers prefer to seek new
91 information or update old information close to the feeders. A study of blue tits (*Cyanistes caeruleus*) also found
92 a positive correlation between feeder discovery in the wild and a similar measure of exploration behavior in
93 captivity (Herborn et al., 2010), reinforcing the idea that gathering information may be personality-related. A
94 different trait, problem-solving ability, has also been linked with foraging home range sizes (Cole et al., 2012),
95 suggesting that this trait is predictive of information gathering style, where problem-solvers are able to find
96 more detailed information on resources in a specific area than non-problem solvers, who have to move over a
97 larger area to gather the same amount of information. Spatial information gathering strategies for finding
98 resources can therefore be one candidate explanation for the many relationships found between personality
99 traits and between-individual differences in important movement decisions. Examples of such relationships are
100 between exploration behavior and natal dispersal (Dingemanse et al., 2003) or family movements (van
101 Overveld et al., 2011), or between boldness and dispersal (Fraser, 2001) or partial migration (Chapman et al.,
102 2011).

103 There are different hypotheses for how information gathering strategies may explain the observed
104 links between personality and spatial movement decisions. First, individuals may vary in their propensity to
105 invest in information sampling, i.e. updating their information at a source already experienced as empty, as a
106 trade-off to seek information in novel areas. Individuals that gather less detailed information about their
107 proximate environment may cover larger areas to seek information in response to environmental challenges,
108 compared to individuals that gather more detailed information (Kramer and McLaughlin, 2001; Sih and Del
109 Giudice, 2012). Sampling for additional information in areas from which individuals have previous knowledge
110 has the benefit of providing detailed information on variance and quality of resources and saving search time
111 for new unknown resources (Stephens and Krebs, 1986). However, it will also decrease the possibility of
112 encountering better resources and gaining knowledge of resources which can be used as buffers if known

113 resources are failing. Additionally, intrinsic differences between individuals, such as energy state differences,
114 can lead some individuals to search for new resource information instead of returning to known resources, if
115 these are not rewarding enough (Katz and Naug, 2015; Mathot et al., 2012; Sih et al., 2015). Individuals can
116 thus adapt their information gathering strategies to try to optimize energy input according to state. When
117 resources become less rewarding, varying propensities to either sample in known areas or exploring new areas
118 can enhance between-individual differences in distances moved over time. This variation in information
119 gathering strategies could also be expressed in personality testing, as suggested by for example Mathot et al.
120 (2012), Verbeek et al. (1994) and Marchetti and Drent (2000). Individuals investing in sampling information in
121 known areas would be expected to gather more detailed information in known areas, show less risk-taking or
122 slow exploration behavior (Mathot and Dall, 2013). The different strategies would represent choices aimed at
123 maximizing fitness according to the individual's current state and traits. We will refer to this hypothesis as the
124 information gathering strategy (IGS) hypothesis.

125 Second, an alternative hypothesis to the IGS can be derived from the concept of behavioral flexibility
126 (BF). BF involves a suit of reactions based on intrinsic differences between individuals, and is generally defined
127 as the ability to respond to a change in the environment (Coppens et al., 2010). This general definition includes
128 both the speed and strength of a response to a change in the environment, and BF is expected to have its
129 proximate and ultimate underpinning in cognitive neurochemistry and selection pressures on co-evolved
130 behaviors (Coppens et al., 2010; Dingemanse et al., 2010). Individuals with higher or lower BF can be seen as
131 individuals that either rely more on internal (old information; less flexible) or on external stimuli (current
132 information; more flexible). Thus, differences in the use of current versus prior information would reflect
133 behavioral constraints rather than a strategic choice as suggested above (Coppens et al., 2010; Marchetti and
134 Drent, 2000). For example, laboratory studies on exploration behavior and foraging behavior in tits have found
135 that fast explorers prefer returning to previously visited but currently unprofitable food patches for a longer
136 time than slow explorers, and therefore these individuals are interpreted as behaving less flexibly and more
137 routine-like (Herborn et al., 2014; Marchetti and Drent, 2000; Verbeek et al., 1994). Thus, despite having
138 different options, individuals are constrained to either continuing their visits to an unprofitable place or look
139 for new places due to differences in flexibility, themselves linked to personality. Also studies on for example
140 trout (Ruiz-Gomez Mde et al., 2011) and pigs (Bolhuis et al., 2004) have shown that different behavioral types

141 differ in reactions towards changes in the environment. As opposed to the IGS hypothesis, the BF hypothesis
142 does not aim to explain nor predict any direct consequences on individual differences in spatial movements in
143 the wild.

144 The predictions from the BF hypothesis differ from those of the IGS hypothesis. Under the BF
145 hypothesis, fast exploring individuals are expected to return to previously visited resources (i.e. sampling) as an
146 act of routine instead of exploring new resources, as these individuals are more behaviorally constrained,
147 whereas slow explorers are expected to show more flexibility and seek information in more novel areas. We
148 expect fast explorers to sample more than slow explorers, as fast explorers have a propensity to return to
149 known patches and slow explorers continuously look for information and form less routines. Contrary to this, if
150 the IGS hypothesis is true, fast explorers are more active and strategically choose to look for information in
151 novel areas more than slow explorers, who instead prefer to return to already visited patches to sample.
152 Consequently, for the IGS hypothesis we also predict that information gathering and behavioral flexibility are
153 related in an opposite way from the BF hypothesis, with fast explorers moving to new profitable patches
154 sooner than slow explorers. To our knowledge, no published studies have yet attempted to distinguish
155 between these hypotheses.

156 We aim to test these two hypotheses by looking at the relationships between information gathering
157 strategies, BF and personality in a non-social context, using great tits from the wild as a model species. We
158 used the personality trait exploration behavior as it is one of the most commonly measured personality traits in
159 the literature, and it has often been related to individual differences in spatial movements both through
160 phenotypic and genetic correlations, in this species (Dingemanse et al., 2003; Korsten et al., 2013; van Overveld
161 et al., 2011; van Overveld et al., 2014) as well as others (Chapman et al., 2011; Hoset et al., 2010). Exploration
162 behavior is defined as the rate at which an individual moves through a novel space (Dingemanse et al., 2002;
163 Reale et al., 2007; Verbeek et al., 1994). It is commonly measured in a single room containing few or no
164 structures and is expected to reflect an underlying “exploration trait”. This exploration trait is only expressed in
165 an environment novel to the individual (Reale et al., 2007) and laboratory measures of exploration behavior
166 have been found to be heritable within several taxa such as mammals (Careau et al., 2011; Kanda et al., 2012),
167 fish (Dingemanse et al., 2009), and birds (Dingemanse et al., 2002; Korsten et al., 2010; Quinn et al., 2009). In

168 great tit exploration behavior is considered part of a more general proactive/reactive or slow/fast behavioral
169 syndrome (Carere et al., 2005; Coppens et al., 2010).

170 We developed a new experimental test in a foraging context allowing us to collect proxies for
171 information gathering and behavioral flexibility from a single individual at a time. The experiment, from now on
172 referred to as the information experiment, was situated inside an aviary and spanned over 5 days divided into
173 three phases. The aviary was divided into four compartments, each containing a feeder with or without food.
174 The position of the food was manipulated twice in the experiment, forcing the birds to explore new options. On
175 the last day individuals were given a choice between feeders of which they had had positive (food present),
176 negative (no food) or no experiences (feeder not accessible) in the previous days. We used the choice of feeder
177 on the last day as a proxy for the IGSs where birds could choose to either update their prior information, or
178 gather information about a new food patch. We used the absolute number of visits to a newly emptied feeder
179 before a visit to a different feeder as a proxy of BF. In addition we collected data on sampling events to the
180 available empty feeders. We also wanted to see if any of the behaviors in the information experiment were
181 influenced by the current state of individuals, and therefore also tested all behavioral responses against body
182 condition (Peig and Green, 2009). With this, we hoped to capture possible differences in energetic state
183 between individuals as body condition could potentially influence foraging behavior, independently of
184 personality traits (David et al., 2012). Following Dall and Johnstone (2002), we predicted a positive correlation
185 between body condition and sampling as individuals in a good condition can afford to sample uncertain
186 resources more. We also expected individuals in a worse condition to prefer to return to a feeder which had
187 previously contained food when faced with sudden food deprivation in a currently used feeder. Individuals in a
188 better condition can afford to explore novel options instead. We also expected individuals in a bad condition to
189 stop visits to a newly emptied and unrewarding feeder earlier than individuals in a good condition. We
190 collected our measure of exploration behavior, from now on referred to as EB, from a standardized exploration
191 behavior test before the information experiment.

192

193 Methods

194 *Bird handling and study area*

195 Birds originated from the Peerdsbos area north of Antwerp, Belgium, which is an oak-beech forest with a large
196 number of nestboxes (Matthysen et al., 2011). All tests were conducted between 28th October and 28th
197 February during the winters of 2013-2014 and 2014-2015. Individuals were brought to the laboratory during
198 roost checks of nestboxes between 6PM and 12AM and housed individually in cages overnight with ad libitum
199 food and water. The population in Peerdsbos is an ongoing study population and during the breeding season
200 every year all individuals are ringed for identification. Before being brought into the laboratory, new individuals
201 to the population were ringed if needed. Morphological measurements included age and sex based on
202 plumage, tarsus length and body mass. Body mass was obtained in the field, as well as immediately before and
203 following the information experiment. EB tests were performed in the morning just before the start of the
204 information experiment (see details below). Day length across the study period varied with 2h50 between the
205 shortest (8h) and the longest (10h50) day.

206

207 *Information experiment*

208 Individuals chosen for the information experiment were individuals with the highest or lowest EB within their
209 test group, in order to maximize variation in EB scores in the dataset. We excluded 2 individuals that lost
210 considerable body mass (more than ca 12% of the evening-body mass) after the night in captivity, one with a
211 low EB score and one with a high EB score. Individuals who had been EB tested on an earlier occasion were also
212 preferred. Before being put into an aviary, individuals were equipped with Passive Integrated Transponders
213 tags (PIT tags) with individual identification numbers. A total of 25 individuals were tested successfully in the
214 information experiment but due to technical issues, data could not be collected for all individuals on all days.
215 Therefore sample sizes for each variable may differ slightly. 15 individuals were tested in the winter of 2013-
216 2014 and 10 individuals were tested in the winter of 2014-2015, and data for these years were pooled.

217 The information experiment was conducted in 2 outdoor aviaries sheltered from human disturbance.
218 Each aviary consisted of 12 compartments ("rooms") each measuring 2 x 2 x 2m (figure 1) separated by two
219 solid white top panels each 1m wide. Adjacent rooms could be connected by removing the top of a single wall

220 panel , creating a 1x1m window between rooms. The roof consisted of metal net wire of 1x1cm with a layer
221 underneath of “Heavy Duty BirdNet ” of ½ inch polypropylene, permitting natural light conditions, and the
222 walls facing the outside of metal net wire. Flooring was made of bark strips. Rooms were connected by opening
223 one of the two top panels in each wall diagonally towards each other, to provide complexity and increase effort
224 to move between sections. All rooms contained 1-2 large branches without leaves. The four corner rooms each
225 contained a feeder with or without food, as well as unlimited access to water and a nestbox to roost in. Food
226 consisted of ad libitum peanuts, sunflower seeds, mealworms in bowls and also a fatball.

227 The feeders were wooden boxes measuring 30(L) x 24(H) x 19(W)cm, and had an entrance of 10cm
228 diameter on top one of the short sides. Food was only visible from the entrance. In addition, the feeders were
229 put in a position where they were only visible upon entering the room. Every visit to a feeder was monitored by
230 reading of the PIT tags with RFID ring antennas (10cm diameter) around the opening of the feeder, connected
231 to single-channel loggers, and data was stored on memory sticks and retrieved with FMlogger programme
232 (Francis Scientific Instruments, Cambridge, United Kingdom). Infrared mini-cameras facing the feeders and
233 entries to the corner rooms were used to monitor the behavior of the bird and record all entries to the feeders
234 and corner rooms. Recordings were made from sunrise until sunset. To obtain food, individuals had to enter
235 inside a feeder and thereby passing the antenna twice, on the way in and on the way out. To differentiate
236 between a single visit with multiple readings and consecutive visits, we tested 3 different arbitrary cut-off times
237 allowed between two consecutive readings: 15s, 30s and 60s. A visit was defined as all readings connected with
238 a maximum time span of these cut-off times. Visits within individuals were highly correlated (details not
239 shown) and visit length did not differ significantly between the cut-off times, therefore we used a 30s cutoff for
240 defining a visit.

241

242 *General overview of the information experiment procedure*

243 The information experiment was divided into three phases over 5 days; phase 1 lasted 2 days, phase 2 also
244 lasted 2 days and phase 3 was the last day. The aviary was divided into four sections, named A, B, C and D, with
245 feeders of equivalent names (fA, fB, etc.). During the day 1 in phase 1, individuals had access to only sections A
246 and C and only feeder fA contained food. On day 2 in phase 1 they were also allowed access to section B with

247 an empty feeder, without changes in food. In phase 2 (days 3 and 4) the same feeders were available but the
248 food had been switched overnight from fA to fB, forcing individuals to abandon fA and to gather information on
249 the position of the new food patch. At this point we recorded the number of visits to the empty fA before
250 switching to the other feeders, as a proxy for the degree of BF, as this can be interpreted as showing a degree
251 of routine behavior. Before the onset of phase 3 (day 5) we emptied fB and provided food in all other feeders
252 fA, fC and fD. At this stage birds were retained in section B (see details in next section) to make sure they
253 sampled the empty fB before accessing the other sections of the aviary. Birds could then choose from three
254 options: to visit a completely new feeder (fD), to visit a feeder that had never contained food before (fC), or to
255 return to the feeder where there had previously been food (fA). We recorded which of the three feeders was
256 used first, henceforth referred to as "Choice day 5", but also which of the three rooms with a feeder was visited
257 first (in case they did not visit the feeder right away). From day 1 to 4, we collected a proxy for sampling, which
258 was the number of times an individual left a profitable feeder to visits an empty feeder. Per definition no
259 feeder visits used in the BF proxy was used in the sampling variable.

260 Following the IGS hypothesis, we predicted Choice day 5 to be related to EB, with fast explorers
261 choosing the unexplored feeder fD over the previously open feeder fA and empty feeder fC, and slow explorers
262 choosing fA over fC, and the empty feeder fC over fD. We also expected fast explorers to have a lower sampling
263 to empty feeders. According to the BF hypothesis we expected the opposite relationships between Choice day
264 5 and EB, with slow explorers preferring fD over the other two feeders contrary to fast explorers. We expected
265 the behavioral flexibility proxy to be positively related to sampling. For the BF hypothesis, we also expect
266 Choice day 5 to be related to sampling, where individuals with high sampling will choose the novel feeder fD
267 over fA and fC.

268

269 *Details of information experiment procedure*

270 The experiment spanned over 5 days, starting immediately after the EB test between 9:39AM and 12:15PM.
271 See table 1 for a summary of the experimental schedule. The four sections of the aviary, A, B, C and D, each
272 contained 3 rooms (see figure 1) with feeders in the far corners. In between experiments the positions of
273 sections were randomized within the aviaries to control for possible biases due to preference for a certain

274 section in the aviary. The relative positions of the sections to each other never differed however: section A was
275 always next to section C, opposite to section B and diagonal to section D. Day 1 in phase 1 was regarded as a
276 familiarization period, to make sure that all individuals visited a feeder. fA initially had 2-3 peanuts and 2-3
277 sunflower seeds on the top, to guide the individuals to visit the feeders. If fA still had not been visited within 2
278 hours, extra food was provided in trays attached to the outer wall in the same room as the feeder, to avoid
279 starvation. Every day, between 1-2h before sunset, individuals were restricted to the section where food was
280 currently available, enabling observers to access the other parts of the aviary, and providing a similar starting
281 position for the bird on each day. Restriction was done by closing one panel remotely (through pulling a string
282 from the outside of the aviary). After dark, the panel was opened again except on the night before phase 3.
283 Following the food position switch in phase 2 from fA to fB, if an individual had not visited fB after 3 hours from
284 sunrise on day 3, a guiding supplement food of 1-2 peanuts and 1-2 sunflower seeds was put on top of fB when
285 the individual was out of sight to cause minimum disturbance. In phase 2 only fB contained food and no further
286 changes were made between these two days. The panel that restricted individuals to section B was not opened
287 the night before phase 3, to ensure that all individuals had sampled the empty fB in the morning of phase 3 to
288 learn that it was empty. This way we could standardise all individuals' experience with fB. One hour after
289 sunrise on day 5 (phase 3), we checked the data loggers whether birds had sampled any other feeder than fB. If
290 fB was sampled, the panel was opened and individuals could access the entire aviary and all feeders. If it had
291 not been sampled, we waited for 30 minutes at a time to check for sampling of fB, and as soon as sampling had
292 taken place the panel was opened, with a maximum delay of 2h 47min after sunrise. We checked the data
293 loggers whether birds had visited any other feeder than fB 1h after having opened the panel, and continued to
294 check every hour until a visit to fA, fC or fD had been made. This ended the experiment. We then allowed birds
295 at least 30 minutes to feed, after which they were collected from the aviary, weighed and released back into
296 the field before 3 PM.

297

298 *Exploration behavior*

299 The exploration behavior (EB) test followed a standardized procedure described in detail in Dingemanse et al.
300 (2002). In brief, the room is 4m(W)-2m(L)-2.3m(H) and contains 5 artificial trees with 4 branches each. Over 2
301 minutes of testing we counted all landings on each tree and each branch, floor, roof or walls. Movements

302 within a branch were not counted, as well as walking movements shorter than 25cm within a wall or on floor.
303 These movements were added up to a single EB score. All individuals were tested between 8.30-10AM the
304 morning after being brought in from the field the previous night. An excess of individuals were brought into the
305 laboratory to enable us to choose which one or two individuals would be used for the information experiment.
306 Individuals not chosen for the information experiment were brought back to place of capture before 12 PM on
307 the morning after capture. The distribution of used EB scores in the information experiment did not differ
308 noticeably from the distribution of all EB scores. This is because on most days, only up to 8 individuals had been
309 EB tested and therefore choice was limited and sometimes only included intermediate scores. Whenever
310 possible, individuals subjected to the information experiment were tested more than once for EB, which was
311 mostly done within years (20 individuals), but a few were tested in different years (4 individuals). The final EB
312 scores of the birds used in the information experiment were always the first EB scores for each individual
313 taken, and had a span of 1-42.

314 We tested all relationships between body condition and the behavioral variables. Body condition was
315 calculated using the morning mass on day 1 of the information experiment and median tarsus length following
316 Peig et al. (2009).

317

318 *Statistical analyses*

319 EB data was normally distributed with a mean±SD of 18.72±10.08 for 100 tests over 74 individuals. We used a
320 General Linear Mixed Model with a random normal error distribution to test possible fixed effects of season,
321 sequence and interval between two consecutive tests on EB as dependent variable and ID as random effect. EB
322 did not change with interval (days between two consecutive tests; $\beta \pm \text{StE} = -0.011 \pm 0.012$, $p = 0.35$) or July day
323 (number of days from the 1st July) ($\beta \pm \text{StE} = -0.015 \pm 0.024$, $p = 0.53$), but increased with sequence
324 ($\beta \pm \text{StE} = 4.92 \pm 1.31$, $p < 0.001$), which is partly what has been found in other populations (Dingemanse et al.,
325 2012). Therefore adjusted EB scores were calculated by correcting EB for sequence, thus the first EB scores
326 were left uncorrected. This was done with the formula “adjusted EB” = $EB - (\beta_1 \cdot x_1)$, where β_1 is the slope
327 estimate for sequence and x_1 is the sequence, following Dingemanse et al. (2002). Unadjusted repeatability
328 with Gaussian error distribution was then calculated using the adjusted EB scores only for those individuals

329 tested twice, following Nakagawa and Schielzeth (2010) (N=23 individuals). Only one measurement per
330 individual exists for all variables for the information experiment and therefore no repeatability of responses are
331 calculated for those. The relationships between Choice day 5 and all other variables were examined using One-
332 Way-Analysis of Variance models (ANOVA) and we used the post-hoc Tukey Honestly Significant Difference test
333 for pairwise differences between categories of Choice day 5 and each variable. For all variables related to
334 Choice day 5 we used Bartlett test of homogeneity of variances to test for large variations in variances between
335 the three choices but found no significant differences between variances (EB: p-value=0.27, sampling: p-
336 value=0.46, BF: p-value=0.54). However, visual inspection of the data showed a high variance for EB and option
337 fC on day 5 as only 3 out of 22 individuals chose this option. We retained all options and data for the ANOVAs
338 but were cautious on inspection of the results. Relationships between EB, sampling and BF were tested by
339 pairwise Pearson correlations. We also tested if Choice on day 5 was related to the body condition of
340 individuals on the first morning of the information experiment with the same methods as above. All statistics
341 were performed in R version 3.1.1 (RCoreTeam, 2012). We are aware that multiple tests for the same
342 hypothesis might generate Type I-errors, but due to our low sample size and to retain as much power as
343 possible we chose not to proceed with false discovery rate-correction. Instead we are more cautious with
344 interpreting any significant results and couple this with visual inspection of data. All tests were checked for
345 normality of residuals.

346

347 *Ethical note*

348 Researchers involved in experiments were all licensed for bird handling and ringing by the Belgian Ringing
349 Scheme. All behavioral experiments on wild birds were licensed by the Environment, Nature and Energy
350 Department of the Flemish Government (ANB/BL/FF-V14-00426 and ANB/BL/FF-V13-00182). Bird handling was
351 minimized with respect to time and experimental setup.

352

353 Results

354 Original scale repeatability of adjusted EB scores with 95% confidence intervals was $R(CI) = 0.65 (0.31-0.84,$
355 $p < 0.001, N = 23$ individuals), which corresponds to previous estimates for this and other great tit populations
356 (Dingemanse et al., 2012). Sampling events to empty feeders ranged from 0 to 8 ($mean \pm SD = 3.4 \pm 2.2$), which is
357 low compared to the total amount of visits to feeders containing food which was 23-350
358 ($mean \pm SD = 172.5 \pm 76.5$). The proxy for behavioral flexibility (nr visits to newly emptied feeder) ranged from 0-
359 53 ($mean \pm SD = 18.5 \pm 16.1$). Few individuals (3 out of 25) chose to visit the previously empty feeder fC on day 5
360 (figure 2b), 10 individual chose feeder fA and 9 individuals chose feeder fD. Sampling was negatively related
361 with EB ($r = -0.50, p = 0.03$, figure 3). We found no relationship between any behavioral variables and choice day
362 5. We did find that the choice on day 5 was weakly related to body condition, with option fA being preferred by
363 heavier individuals compared to option fC (table 2, figure 2d). We could not find any relationship between any
364 of the other variables (table 3).

365

366 Discussion

367 The existence of different information gathering strategies could serve as an explanation to the between-
368 individual variation in spatial movement decisions often observed in the wild. However, this variation might
369 also be explained by differences in behavioral flexibility, but these two hypotheses have never been explicitly
370 tested. We examined whether foraging movements could be explained by differences in information gathering
371 strategies or variation in behavioral flexibility in relation to a commonly measured personality trait, exploration
372 behavior.

373 Following the prediction of the IGS hypothesis, we found that slow explorers sampled empty feeders
374 more than fast explorers. Slow explorers therefore seem to try to reduce uncertainty around foraging options
375 more than fast explorers. This finding is an important confirmation that despite equal proximity to empty
376 feeders and availability to ad libitum food, the personality trait exploration behavior is related to variation in
377 information gathering in a foraging context. The substantial genetic component in the differences between
378 fast and slow exploring birds (Korsten et al., 2013) implies that this relationship may reflect among-individual
379 rather than state-dependent variation in foraging choices, although repeated tests would have been needed to
380 confirm this. According to the IGS hypothesis, we would then have expected birds with a higher EB score to

381 explore new options instead of sampling previously visited options, thus choose the novel feeder fD on day 5.
382 However, there was no significant relationship between EB and Choice day 5, and from visual inspection of the
383 graph with EB and choice day 5 it appears that birds with a higher EB score seem to be more reliant on prior
384 information by going back to the previously food-filled feeder fA rather than a completely novel feeder fD on
385 day 5. The average score of individuals that chose fC did not differ from either fA or fD. This result is not
386 significant mainly due to a single individual with a high EB score choosing feeder fD. If this result would have
387 shown a clearer pattern, this would have been lending support to the BF hypothesis, but we refrain from any
388 conclusions as there was no significant result from this. However, we did find that the Choice day 5 was
389 influenced by body condition, where option fA was chosen by individuals in better condition, and fC by the
390 ones in worse condition, suggesting that choice day 5 was, at least partly, a state-dependent decision. Since fA
391 was the only feeder where individuals had experienced food before, and feeder fC had always been empty, it
392 could have been expected that individuals in worse condition prefer the option with a positive experience. A
393 possible explanation to this could be that individuals differ in their relative risk-aversion behavior when
394 foraging due to a state-dependent foraging strategy carried over from the field (Mathot et al., 2015).
395 Individuals in a good condition might afford to be risk-averse and therefore return to a more secure option
396 than individuals in a worse condition.

397 The behavioral flexibility measure (number of visits at feeder fA when food had just been removed)
398 was on average higher than sampling to empty feeders on other occasions (18.5 visits compared to 3.2 visits).
399 Therefore, as long as an available resource was known, sampling of empty feeders was not done often, despite
400 the little distance between them. We could not find any relationships between neither sampling nor behavioral
401 flexibility and body condition, and therefore no clear indication that these behaviors were condition
402 dependent. This suggests that there was no exploitation-exploration trade-off where satiated individuals or
403 individuals in a better condition would be expected to spend more time examining other food patches than
404 individuals who are starved or in a worse condition (as opposed to bees: Katz and Naug, 2015). However,
405 opposing trends in within- and between individual variation could mask potential covariation, and our single-
406 measure setup did not allow us to partition these variances. Our proxy of BF was not related with any of the
407 other variables in our study. This is surprising given that other studies on the same species have found
408 significant correlations between for example number of sampling following food removal and exploration score
409 (Marchetti and Drent, 2000; van Overveld and Matthysen, 2013). This could mean that differences in reaction

410 to food removal from a previously rewarding food patch do not reflect variation in BF in our population, or that
411 the reaction to food removal is context- or situation-dependent. Individuals may have been energetically
412 constrained in the morning in our experiment and therefore behavior at this time would not necessarily reflect
413 the same behavior found in other experiments where birds had not been food deprived for a longer period
414 than maximum a couple of hours (e.g. Marchetti and Drent, 2000; Verbeek et al., 1994). As discussed above, we
415 did not find a relationship between body condition and behavioral flexibility, but immediate energy
416 requirements might differ from long-term state. Immediate energy requirements may be influenced by for
417 example basal metabolic rate, whereas state such as body condition could be influenced for longer time by
418 external factors such as competition, temperature and food availability (Gosler, 1996). This point is also
419 relevant for all other measures in the information experiment, as foraging behavior might be influenced by
420 immediate energetic requirements as much as long-term state of individuals. As we do not have any repeated
421 measures in this experiment, we cannot assess the possible influence of long-term body condition on variables.

422 One major point in this experiment is that no social information was available and individuals had to
423 rely on their own information, even if in the wild they might employ a strategy such as scrounging (Webster
424 and Ward, 2011), something which has earlier been linked with personality variation. Fast explorers have been
425 found to use social information more than slow explorers in a laboratory study (Marchetti and Drent, 2000),
426 and other studies have reported on reactive and shy individuals behaving more collectively (Aplin et al., 2014;
427 Kurvers et al., 2010) and responding more to a partner (Kurvers et al., 2010) than proactive and bold
428 individuals. Extrapolating results from single-individual experiments to the wild should be done with care
429 because of the likely (occasional or common) influence of conspecifics, but rather be viewed as a contribution
430 to further investigations. Ideally, experiments like ours where individuals are tested alone should be validated
431 with a social context to measure the influence of conspecifics on each individual's behavior.

432 In addition to the quality of food resources, the unpredictability of food availability has also been
433 hypothesized to influence foraging decisions in a personality-related way (Mathot et al., 2012). However, in this
434 experiment we did not specifically manipulate the degree of predictability of a feeder's food availability, but
435 mainly focused on creating options differing in information value; an unpredictable feeder with varying food
436 availability (fA, first containing food, then empty), a predictably empty feeder (fC) and an unpredictable feeder
437 due to no previous experience with and with no known value (fD). We recommend that experiments
438 manipulating the degree of predictability could elucidate more mechanisms behind for example personality-

439 related variation in foraging movements and to study in detail the influence of resource variability on possible
440 behavioral flexibility constraints or information gathering strategies.

441 Although our results do not allow us to draw firm conclusions we saw indications of only the IGS
442 hypothesis receiving support, with a suggestion that body condition may also influence foraging choices. It is
443 therefore possible that individuals exhibit differences in information gathering strategies, depending on
444 context and/or state-differences. Further studies with repeated measures would provide more clarification into
445 whether or not the observed patterns were governed by the state of individuals or among-individuals
446 differences in behavior. This experiment is to our knowledge the first attempt to explicitly test the BF and the
447 IGS hypotheses and we hope this may be an inspiration for further experimental manipulations of this kind.
448 Experiments in the wild have been recommended to study personality-related variation in foraging (Niemela
449 and Dingemanse, 2014) but the difficulty in controlling the resource options and foraging outside of the
450 experimental setup make these studies more problematic to interpret. We see that this kind of experiment can
451 be increased in complexity, with more manipulated foraging options present, manipulated state of individuals
452 and the inclusion of conspecific- or predator presence.

453

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456

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461 References

- 462 Adriaenssens B, Johnsson JI, 2010. Shy trout grow faster: exploring links between personality and
463 fitness-related traits in the wild. *Behavioral Ecology* 22:135-143. doi:
464 10.1093/beheco/arq185.
- 465 Aplin LM, Farine DR, Mann RP, Sheldon BC, 2014. Individual-level personality influences social
466 foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B*
467 281:20141016. doi: 10.1098/rspb.2014.1016.
- 468 Bolhuis JE, Schouten WG, de Leeuw JA, Schrama JW, Wiegant VM, 2004. Individual coping
469 characteristics, rearing conditions and behavioural flexibility in pigs. *Behav Brain Res*
470 152:351-360. doi: 10.1016/j.bbr.2003.10.024.
- 471 Careau V, Thomas D, Pelletier F, Turki L, Landry F, Garant D, Reale D, 2011. Genetic correlation
472 between resting metabolic rate and exploratory behaviour in deer mice (*Peromyscus*
473 *maniculatus*). *Journal of evolutionary biology* 24:2153-2163. doi: 10.1111/j.1420-
474 9101.2011.02344.x.
- 475 Carere C, Drent PJ, Privitera L, Koolhaas JM, Groothuis TGG, 2005. Personalities in great tits, *Parus*
476 *major*: stability and consistency. *Animal Behaviour* 70:795-805. doi:
477 10.1016/j.anbehav.2005.01.003.
- 478 Carter AJ, Marshall HH, Heinsohn R, Cowlshaw G, 2013. Personality predicts decision making only
479 when information is unreliable. *Animal Behaviour* 86:633-639. doi:
480 10.1016/j.anbehav.2013.07.009.
- 481 Chapman BB, Hulthen K, Blomqvist DR, Hansson LA, Nilsson JA, Brodersen J, Anders Nilsson P, Skov C,
482 Bronmark C, 2011. To boldly go: individual differences in boldness influence migratory
483 tendency. *Ecology letters* 14:871-876. doi: 10.1111/j.1461-0248.2011.01648.x.
- 484 Clobert J, Le Galliard J-F, Cote J, Meylan S, Massot M, 2009. Informed dispersal, heterogeneity in
485 animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology*
486 *letters* 12:197-209. doi: 10.1111/j.1461-0248.2008.01267.x.

- 487 Cole EF, Morand-Ferron J, Hinks AE, Quinn JL, 2012. Cognitive ability influences reproductive life
488 history variation in the wild. *Current biology* : CB 22:1808-1812. doi:
489 10.1016/j.cub.2012.07.051.
- 490 Coppens CM, de Boer SF, Koolhaas JM, 2010. Coping styles and behavioural flexibility: towards
491 underlying mechanisms. *Philos Trans R Soc Lond B Biol Sci* 365:4021-4028. doi:
492 10.1098/rstb.2010.0217.
- 493 Dall SRX, Johnstone RA, 2002. Managing uncertainty information and insurance under the risk of
494 starvation. *Philosophical Transactions of the Royal Society London B* 357:1519–1526.
- 495 David M, Auclair Y, Giraldeau L-A, Cézilly F, 2012. Personality and body condition have additive
496 effects on motivation to feed in Zebra Finches. *IBIS* 154:372-378. doi: 0.1111/j.1474-
497 919X.2012.01216.x.
- 498 Dingemanse NJ, Both C, Drent PJ, Van Oers K, Van Noordwijk AJ, 2002. Repeatability and heritability
499 of exploratory behaviour in great tits from the wild. *Animal Behaviour* 64:929-938. doi: DOI
500 10.1006/anbe.2002.2006.
- 501 Dingemanse NJ, Both C, van Noordwijk AJ, Rutten AL, Drent PJ, 2003. Natal dispersal and
502 personalities in great tits (*Parus major*). *Proceedings of the Royal Society B* 270:741-747. doi:
503 10.1098/rspb.2002.2300.
- 504 Dingemanse NJ, Bouwman KM, van de Pol M, van Overveld T, Patrick SC, Matthysen E, Quinn JL,
505 2012. Variation in personality and behavioural plasticity across four populations of the great
506 tit *Parus major*. *The Journal of animal ecology* 81:116-126. doi: 10.1111/j.1365-
507 2656.2011.01877.x.
- 508 Dingemanse NJ, Kazem AJ, Reale D, Wright J, 2010. Behavioural reaction norms: animal personality
509 meets individual plasticity. *Trends in ecology & evolution* 25:81-89. doi:
510 10.1016/j.tree.2009.07.013.
- 511 Dingemanse NJ, Van der Plas F, Wright J, Reale D, Schrama M, Roff DA, Van der Zee E, Barber I, 2009.
512 Individual experience and evolutionary history of predation affect expression of heritable

- 513 variation in fish personality and morphology. *Proceedings of the Royal Society B* 276:1285-
514 1293. doi: 10.1098/rspb.2008.1555.
- 515 Dochtermann NA, Dingemanse NJ, 2013. Behavioral syndromes as evolutionary constraints.
516 *Behavioral Ecology* 24:806-811. doi: 10.1093/beheco/art002.
- 517 Fraser DF, Gilliam, J.F., Daley, M.J., Le, A.N., Skalski, G.T., 2001. Explaining Leptokurtic Movement
518 Distributions Intrapopulation Variation in Boldness and exploration. *The American Naturalist*
519 158:124-135. doi: 10.1086/321307.
- 520 Gosler AG, 1996. Environmental and social determinants of winter fat storage in the great tit. *Journal*
521 *of Animal Ecology* 65:1-17. doi: 10.2307/5695.
- 522 Gosling SD, 2001. From mice to men: what can we learn about personality from animal research?
523 *Psychological bulletin* 127:45-86. doi: 10.1037//0033-2909.127.1.45.
- 524 Herborn KA, Heidinger BJ, Alexander L, Arnold KE, 2014. Personality predicts behavioral flexibility in a
525 fluctuating, natural environment. *Behavioral Ecology* 25:1374-1379. doi:
526 10.1093/beheco/aru131.
- 527 Herborn Ka, Macleod R, Miles WTS, Schofield ANB, Alexander L, Arnold KE, 2010. Personality in
528 captivity reflects personality in the wild. *Animal Behaviour* 79:835-843. doi:
529 10.1016/j.anbehav.2009.12.026.
- 530 Hoset KS, Ferchaud aL, Dufour F, Mersch D, Cote J, Le Galliard JF, 2010. Natal dispersal correlates
531 with behavioral traits that are not consistent across early life stages. *Behavioral Ecology*
532 22:176-183. doi: 10.1093/beheco/arq188.
- 533 Kanda LL, Louon L, Straley K, 2012. Stability in Activity and Boldness Across Time and Context in
534 Captive Siberian Dwarf Hamsters. *Ethology* 118:518-533. doi: 10.1111/j.1439-
535 0310.2012.02038.x.
- 536 Katz K, Naug D, 2015. Energetic state regulates the exploration–exploitation trade-off in honeybees.
537 *Behavioral Ecology* 26:1045-1050. doi: 10.1093/beheco/arv045.

- 538 Korsten P, Mueller JC, Hermannstädter C, Bouwman KM, Dingemanse NJ, Drent PJ, Liedvogel M,
539 Matthysen E, van Oers K, van Overveld T, Patrick SC, Quinn JL, Sheldon BC, Tinbergen JM,
540 Kempnaers B, 2010. Association between DRD4 gene polymorphism and personality
541 variation in great tits: a test across four wild populations. *Molecular ecology* 19:832-843. doi:
542 10.1111/j.1365-294X.2009.04518.x.
- 543 Korsten P, van Overveld T, Adriaensen F, Matthysen E, 2013. Genetic integration of local dispersal
544 and exploratory behaviour in a wild bird. *Nature communications* 4:2362-2362. doi:
545 10.1038/ncomms3362.
- 546 Kramer DL, McLaughlin RL, 2001. The behavioral ecology of intermittent locomotion. *American*
547 *Zoologist* 41:137–153. doi: 10.1668/0003-1569.
- 548 Kurvers RH, van Oers K, Nolet BA, Jonker RM, van Wieren SE, Prins HH, Ydenberg RC, 2010.
549 Personality predicts the use of social information. *Ecology letters* 13:829-837. doi:
550 10.1111/j.1461-0248.2010.01473.x.
- 551 Marchetti C, Drent PJ, 2000. Individual differences in the use of social information in foraging by
552 captive great tits. *Animal Behaviour* 60:131-140. doi: 10.1006/anbe.2000.1443.
- 553 Mathot KJ, Dall SR, 2013. Metabolic rates can drive individual differences in information and
554 insurance use under the risk of starvation. *Am Nat* 182:611-620. doi: 10.1086/673300.
- 555 Mathot KJ, Nicolaus M, Araya-Ajoy YG, Dingemanse NJ, Kempnaers B, Grémillet D, 2015. Does
556 metabolic rate predict risk-taking behaviour? A field experiment in a wild passerine bird.
557 *Functional Ecology* 29:239-249. doi: 10.1111/1365-2435.12318.
- 558 Mathot KJ, Wright J, Kempnaers B, Dingemanse NJ, 2012. Adaptive strategies for managing
559 uncertainty may explain personality-related differences in behavioural plasticity. *Oikos*
560 121:1009-1020. doi: 10.1111/j.1600-0706.2012.20339.x.
- 561 Matthysen E, Adriaensen F, Dhondt Aa, 2011. Multiple responses to increasing spring temperatures
562 in the breeding cycle of blue and great tits (*Cyanistes caeruleus*, *Parus major*). *Global Change*
563 *Biology* 17:1-16. doi: 10.1111/j.1365-2486.2010.02213.x.

- 564 McNamara JM, Dall SRX, 2010. Information is a fitness enhancing resource. *Oikos* 119:231-236. doi:
565 10.1111/j.1600-0706.2009.17509.x.
- 566 Nakagawa S, Schielzeth H, 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide
567 for biologists. *Biological reviews of the Cambridge Philosophical Society* 85:935-956. doi:
568 10.1111/j.1469-185X.2010.00141.x.
- 569 Nicolaus M, Tinbergen JM, Bouwman KM, Michler SPM, Ubels R, Both C, Kempenaers B, Dingemanse
570 NJ, 2012. Experimental evidence for adaptive personalities in a wild passerine bird.
571 *Proceedings of the Royal Society B*. doi: 10.1098/rspb.2012.1936.
- 572 Niemela PT, Dingemanse NJ, 2014. Artificial environments and the study of 'adaptive' personalities.
573 *Trends in ecology & evolution* 29:245-247. doi: 10.1016/j.tree.2014.02.007.
- 574 Peig J, Green AJ, 2009. New perspectives for estimating body condition from mass/length data: The
575 scaled mass index as an alternative method. *Oikos* 118:1883-1891. doi: 10.1111/j.1600-
576 0706.2009.17643.x.
- 577 Quinn JL, Patrick SC, Bouwhuis S, Wilkin TA, Sheldon BC, 2009. Heterogeneous selection on a
578 heritable temperament trait in a variable environment. *The Journal of animal ecology*
579 78:1203-1215. doi: 10.1111/j.1365-2656.2009.01585.x.
- 580 RCoreTeam, 2012. R: A language and environment for statistical computing. R Foundation for
581 Statistical Computing, Vienna, Austria.
- 582 Reale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ, 2007. Integrating animal temperament
583 within ecology and evolution. *Biological reviews of the Cambridge Philosophical Society*
584 82:291-318. doi: 10.1111/j.1469-185X.2007.00010.x.
- 585 Ruiz-Gomez Mde L, Huntingford FA, Overli O, Thornqvist PO, Hoglund E, 2011. Response to
586 environmental change in rainbow trout selected for divergent stress coping styles. *Physiology
587 & behavior* 102:317-322. doi: 10.1016/j.physbeh.2010.11.023.
- 588 Sih A, Bell A, Johnson JC, 2004. Behavioral syndromes: an ecological and evolutionary overview.
589 *Trends in ecology & evolution* 19:372-378. doi: 10.1016/j.tree.2004.04.009.

- 590 Sih A, Cote J, Evans M, Fogarty S, Pruitt J, 2012. Ecological implications of behavioural syndromes.
591 Ecology letters 15:278-289. doi: 10.1111/j.1461-0248.2011.01731.x.
- 592 Sih A, Del Giudice M, 2012. Linking behavioural syndromes and cognition: a behavioural ecology
593 perspective. Philos Trans R Soc Lond B Biol Sci 367:2762-2772. doi: 10.1098/rstb.2012.0216.
- 594 Sih A, Mathot KJ, Moiron M, Montiglio PO, Wolf M, Dingemanse NJ, 2015. Animal personality and
595 state-behaviour feedbacks: a review and guide for empiricists. Trends in ecology & evolution
596 30:50-60. doi: 10.1016/j.tree.2014.11.004.
- 597 Stephens DW, 1987. On economically tracking a variable environment. Theoretical Population
598 Biology 32:15-25.
- 599 Stephens DW, Krebs JR, 1986. Foraging Theory. Princeton University Press.
- 600 Toelch U, Bruce MJ, Newson L, Richerson PJ, Reader SM, 2014. Individual consistency and flexibility in
601 human social information use. Proceedings Biological sciences / The Royal Society
602 281:20132864. doi: 10.1098/rspb.2013.2864.
- 603 Trompf L, Brown C, 2014. Personality affects learning and trade-offs between private and social
604 information in guppies, *Poecilia reticulata*. Animal Behaviour 88:99-106. doi:
605 10.1016/j.anbehav.2013.11.022.
- 606 van Oers K, Klunder M, Drent PJ, 2005. Context dependence of personalities: risk-taking behavior in a
607 social and a nonsocial situation. Behavioral Ecology 16:716-723. doi: 10.1093/beheco/ari045.
- 608 van Overveld T, Adriaensen F, Matthysen E, 2011. Postfledging family space use in great tits in
609 relation to environmental and parental characteristics. Behavioral Ecology 22:899-907. doi:
610 10.1093/beheco/arr063.
- 611 van Overveld T, Careau V, Adriaensen F, Matthysen E, 2014. Seasonal- and sex-specific correlations
612 between dispersal and exploratory behaviour in the great tit. Oecologia 174:109-120. doi:
613 10.1007/s00442-013-2762-0.
- 614 van Overveld T, Matthysen E, 2013. Personality and Information gathering in free-ranging great tits.
615 PLoS ONE 8. doi: 10.1371/journal.pone.0054199.g001

616 10.1371/journal.pone.0054199.t001.

617 Verbeek M, Drent PJ, Wiepkema PR, 1994. Consistent individual differences in early exploratory
618 behaviour of male great tits. *Animal Behaviour* 44:1113-1121.

619 Webster MM, Ward AJ, 2011. Personality and social context. *Biological reviews of the Cambridge*
620 *Philosophical Society* 86:759-773. doi: 10.1111/j.1469-185X.2010.00169.x.

621 Wolf M, Weissing FJ, 2012. Animal personalities: consequences for ecology and evolution. *Trends in*
622 *ecology & evolution* 27:452-461. doi: 10.1016/j.tree.2012.05.001.

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636 Figures and tables

637 Figure 1. Information experiment setup as seen from above, see table 1 for experimental procedure. Four
638 feeders were placed in four corners of the aviary (boxes A-D), with differential access depending on the day of
639 the experiment. Black lines indicate permanently closed walls, dotted lines indicate open top walls (free
640 passage). Grey lines indicate walls closed during day 1-4 of the experiment, enclosing room D. White wall
641 indicates a wall that was closed during day 1, and on the morning of day 5, but open during the rest of the
642 experiment.

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644 Figure 2. Boxplots with the 25th and 75th percentiles for feeder choice on day 5 related to (a) sampling during
645 days 1-4 of the information experiment, (b) first EB score, (c) behavioural flexibility and (d) body condition
646 calculated from the body mass of the individual at the start of the experiment (day1). Feeder choices are
647 labelled beneath the boxplot together with sample sizes for each choice. Each individual point is plotted.

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649 Figure 3. The relationship between number of sampling events in the information experiment and the EB
650 scores. Each dot represents one individual. A regression line shows the significant relationship.

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659 Table 1. Overview of the information experiment procedure. A to D refer to the four feeders in the aviary (see
 660 Fig. 1) which on a given day may or may not contain food. Entry = food available after the bird enters the
 661 compartment; Sunrise = available from when the bird wakes up; After B sampled = compartments made
 662 accessible after the bird visited empty feeder B.

Phase	Day	Accessible feeders	Food	Access time
1	1	A, C	A	Entry
	2	A, B, C	A	Sunrise
2	3	A, B, C	B	Sunrise
	4	A, B, C	B	Sunrise
3	5	A, B, C, D	A, C & D	After B sampled

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675 Table 2. ANOVA results on behavioral variables and body condition of birds in relation to their choice of feeder
 676 on day 5. Tukey's HSD test results for significant or near-significant ANOVAs are displayed with difference and
 677 95% confidence intervals within brackets between each pair of feeders.

	Choice day 5	Tukey's HSD test
EB first score	F = 1.68, p = 0.21	
Behavioral flexibility	F = 0.18, p = 0.84	
Sampling	F = 0.60, p=0.56	
Body condition	F=3.03, p=0.07	D-A = -0.69 (-1.68-0.30), p = 0.21 C-A = -1.23 (-2.65-0.19), p = 0.10 D-C = 0.54 (-0.89-1.98), p = 0.61

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690 Table 3. Correlation coefficients between all variables except for Choice day 5, with 95% confidence intervals
 691 within brackets.

	Sampling	Behavioral flexibility	Body condition
EB	-0.50 (-0.77- -0.07), p = 0.03	0.006 (-0.41-0.42), p = 0.98	0.16 (-0.25-0.52), p = 0.44
Sampling		0.33 (-0.15-0.68), p = 0.17	-0.15 (-0.56-0.31), p = 0.52
Body condition		0.11, (-0.32-0.49), p = 0.63	

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