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► To cite this version:

Jennifer Morinay, Jukka Forsman, Marion Germain, Blandine Doligez. Behavioural traits modulate the use of heterospecific social information for nest site selection: experimental evidence from a wild bird population. *Proceedings of the Royal Society B: Biological Sciences*, 2020, 287 (1925), pp.20200265. 10.1098/rspb.2020.0265 . hal-02990528

HAL Id: hal-02990528

<https://cnrs.hal.science/hal-02990528>

Submitted on 24 Nov 2020

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1 **Behavioural traits modulate the use of heterospecific social information for nest**
2 **site selection: experimental evidence from a wild bird population**

3

4

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21 **Keywords:** collared flycatcher, copying, personality, boldness, aggressiveness, neophobia

22 **Abstract**

23

24 The use of social information for making decisions is common but can be constrained by
25 behavioural traits via e.g. the ability to gather information. Such constrained information use
26 has been described in foraging habitat selection; yet it remains unexplored in the breeding
27 habitat selection context, despite potentially strong fitness consequences. We experimentally
28 tested whether three behavioural traits (aggressiveness, boldness, neophobia) affected the use
29 of heterospecific social information for nest site selection in wild collared flycatchers
30 *Ficedula albicollis*. Flycatchers have previously been found to copy or reject an artificial
31 apparent preference of tits (their main competitors) for a nest site feature: they preferred nest
32 boxes with the same or a different feature, depending on tit early reproductive investment.
33 Here, we confirmed this result and showed that, shy individuals and less aggressive old males
34 (i.e. 2 years old or older) copied tit apparent preference, while more aggressive old males
35 rejected the tit preference. Aggressiveness and boldness may allow males to access more
36 information sources or affect males' interactions with dominant tits when selecting a nest site.
37 Our study highlights the links between variation in behaviours and social information use for
38 breeding habitat selection and calls for further work to explore underlying mechanisms.

39 **Introduction**

40

41 In spatio-temporally variable environments, individuals can use a great variety of information
42 to make decisions. In particular, they can use personal information (derived from their own
43 knowledge about – or experience with - the environment) and/or social information (derived
44 from observing other individuals' actions in the environment; [1,2]). Depending on the
45 relative reliability and availability of these two types of information, individuals can flexibly
46 use personal and/or social information [e.g. 3,4]. Social information use is known to depend
47 on environmental conditions [e.g. population size, spatio-temporal predictability; 5,6] but also
48 on individual factors, such as age [7] or personality traits [8]. Personality traits may constrain
49 the use of social information by affecting either the propensity to acquire information or the
50 decisions made once information is acquired. Personality traits may in particular shape
51 individual's willingness to prospect in general (activity), and more specifically in new or risky
52 environments (exploration and boldness), or when prospecting involves social interactions
53 (aggressiveness and sociality); thereby, they may affect individuals' overall knowledge of the
54 environment.

55 Thus far, 24 published studies (to our knowledge) have investigated the links between
56 social information use and personality traits, mostly in the context of foraging decisions
57 (Table 1; see Table S1 for full details). Among these studies, the investigation of the
58 exploration / neophobia axis [8] was predominant (19 over 24 studies, i.e. 79%). Higher
59 neophobia level was frequently associated with higher social information use (in 7
60 relationships over 11; Table 1). Conversely, no overall pattern was found for the links
61 between social information use and other personality traits, either because most relationships
62 were non-significant (for exploration and boldness) or very few studies (or even none)
63 investigated these links (for activity, sociality and in particular aggressiveness; Table 1, Table

64 S1). Furthermore, testing the causality of links between personality traits and social
65 information use requires experimentally manipulating information sources. Yet, such
66 manipulations have only been conducted in captivity thus far. Therefore, the extent to which
67 different personality traits, but also more flexible behavioural traits in general may favour or
68 constrain the use of social information for decision-making in the wild remains poorly
69 understood.

70 Social information use for breeding habitat selection and dispersal decisions is well
71 documented [e.g. 5,9,10]. In parallel, dispersal syndromes involving behavioural traits have
72 been well studied [e.g. 11,12]. However, to our knowledge, no study has directly investigated
73 the link between behavioural traits and social information use for breeding site choice (Table
74 S1). Yet, prospecting to gather social information on potential breeding sites can be costly in
75 terms of time, energy and increased agonistic interactions with competitors [13] and only
76 individuals displaying specific behaviours may be able to face these costs. For example, more
77 aggressive, bold and/or explorative individuals may have access to more and/or larger-scale
78 social information sources. Social information use itself may also increase intra- and
79 interspecific competition when individuals spatially aggregate because of con- or hetero-
80 specific attraction or because they use the same information [6,9]. Therefore, the realised
81 breeding site choices may notably depend on aggressiveness allowing individuals to acquire
82 and defend the chosen site/territory against competitors. Assessing to what extent behavioural
83 traits shape social information use for breeding site choice is needed to understand how
84 selective pressures act on behaviour over different decision-making contexts.

85 Here, we tested whether difference in the use of an experimentally manipulated source
86 of social information for nest site selection was related to three main behavioural traits
87 (aggressiveness, boldness and neophobia), previously shown to be partly repeatable [14], in a
88 natural population of a small passerine bird, the collared flycatcher *Ficedula albicollis*.

89 Collared and pied flycatchers *F. hypoleuca* (a sister species) have been repeatedly shown to
90 use social information from con- and heterospecific (titmice) competitors when choosing a
91 nest site [5,10,15–19]. However, this social information use shows high between-individual
92 variability, only partly explained by sex [5], age [20] or dispersal status [15], and depends on
93 years [21] and environmental conditions (e.g. clutch size [20], or titmice density [24]). We
94 tested here whether differences in the three behavioural traits investigated could explain part
95 of the observed variability in social information use. Using an experimental design already
96 successfully implemented in our study species, we created an apparent local preference of
97 dominant tutors (here tits) for a specific nest box feature observable from a distance
98 (geometric symbols) [10,23]. We then recorded whether flycatchers copied or rejected this
99 preference by settling in boxes displaying the same feature. After settlement, we measured
100 levels of aggressiveness, boldness and neophobia of the experimental birds to test the link
101 between these behavioural traits and the probability of copying tit apparent preference. Due to
102 potential risks of collecting information at the vicinity of tit territories, we expected
103 aggressive individuals to be more likely to copy tutors' preference than less aggressive ones.
104 Furthermore, shyness (lack of boldness) and/or neophobia could restrain access to other
105 conspecific or heterospecific information sources besides tit apparent preference (e.g. if they
106 affect the gathering of information available at a large-scale, for neophobia [5], or risky to
107 acquire, for boldness [9]), and thus shy and/or more neophobic individuals could be
108 expected to be more likely to copy tutors' preference than less neophobic and/or bolder ones.

109

110

111 **Methods**

112

113 *Species and study site*

114 The experiment was conducted in spring 2012 and 2013 in a wild breeding population of
115 collared flycatchers on the island of Gotland (Baltic Sea, Sweden). Collared flycatchers are
116 sexually dimorphic migratory hole-nesting passerine birds that readily breed in artificial nest
117 boxes provided in the forest patches of the study area. Breeding flycatchers were captured in
118 boxes (during incubation for females and chick rearing for males) as part of the long-term
119 monitoring of the population. Caught individuals were measured and aged based on plumage
120 criteria (yearling vs. older individuals. In this population, collared flycatchers compete for
121 nest boxes with great tits *Parus major* and blue tits *Cyanistes caeruleus* (Gustafsson 1988),
122 which are resident passerine species, are competitively dominant over flycatchers and
123 typically start laying on average two weeks before flycatchers' arrival (but see Table S2 and
124 [21]).

125

126 *Heterospecific preference copying: experimental design*

127 In 12 (in 2012) and 17 (in 2013) experimental forest patches (2,048 nest boxes in total over
128 the two years), we created an apparent preference of tits for a specific nest box feature to
129 measure flycatchers' subsequent copying behaviour by attaching around the entrance of boxes
130 one of two geometric symbols (white plastic shapes; either a triangle or a circle) depending on
131 the species occupying the box [21]. Before flycatchers' arrival (i.e. in the first two weeks of
132 April), we attached on all boxes occupied by great and blue tits (and the few coal tits
133 *Periparus ater*) in a given forest patch the same symbol (shape alternated between patches,
134 see Figure S1 for more details). At the same time, we randomly attached a triangle on half of
135 the remaining (empty) boxes, i.e. boxes available for newcomers' settlement, and a circle on
136 the other half. We attached no symbol on the few boxes occupied by other species (nuthatches
137 *Sitta europaea*, sparrows *Passer domesticus* and *P. montanus* and wrynecks *Jynx torquilla*; 25
138 boxes in total over the two years). Therefore, when flycatchers arrived from migration (late

139 April to mid-May), they had the choice between copying tit preference by settling in a box
140 with the same symbol as on tit boxes, or rejecting it by settling in a box with the opposite
141 symbol. When a flycatcher pair had settled in a box, as shown by the presence of new nest
142 material in the box, we removed the symbol on this box. This avoided providing conspecific
143 information via the symbol chosen to later arriving flycatchers. We checked empty boxes
144 every other day to detect newly started nest building and removed (for new flycatcher nests)
145 or changed if needed (for new tit nests) the symbol accordingly. At the same time, we
146 adjusted the number of triangles and circles on empty boxes within a forest patch to keep an
147 equal proportion of available boxes displaying each symbol, and thus an equal probability for
148 newcomers to choose a symbol at random. Because this equal proportion of both symbols
149 could not always be met (e.g. when an odd number of empty boxes remained in a patch), we
150 controlled for the deviation from random (0.5) of the proportion of empty boxes matching the
151 tit apparent preference within a plot on the day of choice for each flycatcher pair [see 21 for
152 more details]. Because we can assume that flycatchers naïve to the experimental design have
153 no previous experience with geometric symbols, this design minimises genetic and ecological
154 effects on nest site choice and is a powerful method to reveal factors affecting individuals'
155 choices [10].

156

157 *Measuring behavioural traits*

158 The three behavioural traits of interest here, namely aggressiveness, boldness and neophobia,
159 were measured as described in a former study on the same population (see [14] for detailed
160 methods). In this former study based on a larger sample [14], all three traits were found to be
161 weakly repeatable between years ($R=0.2$, 0.1 and 0.4 for aggressiveness, boldness and
162 neophobia respectively) and weakly phenotypically correlated (-0.2 for aggressiveness-
163 neophobia, -0.3 for boldness-neophobia) but they did not associate in behavioural syndromes

164 (i.e. no between-individual covariance between them [14]). In the present study, we refer to
165 these traits as behavioural rather than personality traits, because we could not separate the
166 effect of the repeatable vs. flexible part of the traits on the use of social information; indeed
167 the copying behaviour was measured only once (i.e. in naïve birds).

168 We measured aggressiveness through the agonistic response of a focal pair to a
169 simulated intrusion by competitors on the nest box during nest building stage, i.e. when the
170 risk of losing a nest site is highest [as in 14]. We used both conspecific and heterospecific
171 (great tit) decoys (in successive tests) because flycatchers respond aggressively to both
172 species [24,25]. A total of 2 to 4 tests were conducted for each focal pair (1 or 2 tests per
173 stimuli species, depending on field constraints), with one test maximum per day and 2 days
174 maximum in a row to avoid habituation. The decoy species was randomized for the first test
175 and alternated between subsequent tests. At the start of a test, an observer attached on the box
176 decoys of either a flycatcher pair or a male great tit, randomly chosen among 10 different sets
177 for each species, as well as a loudspeaker broadcasting songs of the same species as the
178 decoy(s), randomly chosen among 5 different song tracks per species. The observer then hid
179 under a camouflage net approximately 8-10 meters away from the box and recorded all
180 behaviours performed by each member of the focal pair during 15 minutes on average (mean
181 15.12 minutes \pm 0.96 SD): movements around- and distance from- the box, flights and attacks
182 towards a decoy or live birds attracted by the stimulus. To account for differences in the
183 latency to respond between individuals, each behavioural variable recorded was converted
184 into frequency per minute using the time interval between the first observation of the
185 individual during the test and the end of the test. We then estimated an aggressiveness score
186 for each individual and for each test as the sum of the frequencies of (i) movements within 2
187 meters from the box, (ii) attacks or stationary flights towards a decoy and (iii) chases towards
188 live intruders [similarly to 14]. We excluded from the datasets individuals that were observed

189 less than 5 minutes. In total, we used 1168 behavioural responses of both sexes, performed
190 during 790 aggressiveness tests on 224 males and 271 females and 313 reproductive events
191 over the two years of the experiment. The final individual aggressiveness score was calculated
192 as the average of the scores measured for each individual within one season.

193 We measured boldness through the reaction to the presence of a human observer near
194 the box and neophobia through the reaction to the presence of a novel object attached on the
195 box (i.e. in a familiar environment) [as in 14]. We conducted one combined boldness /
196 neophobia test per breeding pair per year, when chicks were 5 or 6 days old. The test
197 consisted of two consecutive periods lasting one hour each, during which the provisioning
198 behaviour of both parents was video-recorded from a distance (6-8m). In the first period, an
199 observer settled a recorder and opened the box to check chick satiety before leaving the area.
200 In the second period, the observer came back to the box, checked chick satiety again, attached
201 a novel object (here a coloured figurine approximately 7 cm high) near the entrance of the box
202 and left again for one hour. Chick satiety was checked in order to avoid performing
203 behavioural tests if chicks' condition was too poor. We estimated a boldness score for each
204 parent based on the latency to enter the box after the observer's departure in the first period of
205 the test, i.e. without the novel object. To obtain meaningful boldness scores (i.e. increasing
206 boldness for decreasing latency), we subtracted this latency from the maximum latency
207 observed in our data set [as in 14]. We estimated a neophobia score for each parent based on
208 the latency to enter the box after the departure of the observer in the second period of the test,
209 i.e. in the presence of the novel object. Among the 318 individuals that entered the box in the
210 first period, 38% did not enter in the second period and thus had no latency available. To take
211 into account those highly neophobic individuals, we discretized neophobia as a 5-level score,
212 with the first four levels corresponding to latency quartiles and the last level assigned to these
213 non-returning individuals [as in 14]. Results however remained quantitatively unchanged (not

214 detailed here) when considering neophobia as a continuous latency instead of a score by
215 attributing a maximum latency to non-returning individuals (here 4,000 seconds, the
216 maximum observed latency plus one minute).

217

218 *Statistical analyses*

219 We analysed the probability for flycatchers to copy the apparent preference of tits (binary
220 response variable: copy vs. reject) in the two years of the experiment (2012 and 2013). In the
221 second year, we retained only individuals naïve to the symbol experiment, i.e. which had not
222 been caught as breeders in the first year. The overall lower number of males in the sample and
223 differences in sample sizes between models were mostly due to early breeding failures (before
224 the boldness/neophobia test and/or male capture). Because aggressiveness, boldness and
225 neophobia are slightly phenotypically correlated within individuals [14], we fitted separate
226 models for each trait. Furthermore, because nest site choice is a joint decision by both pair
227 members, the most appropriate model to estimate the effect of individual behavioural traits on
228 the joint copying decision would include both male and female trait estimates simultaneously.
229 However, retaining only nests where both pair members have been captured and aged, are
230 naïve to the symbols and have responded to behavioural tests strongly reduced sample size
231 (by up to 33%). Therefore, we first fitted sex-specific models. Second, we fitted models with
232 both male and female estimates of the behavioural trait and age, the same other main effects
233 as above, the two-way interaction between male and female behavioural trait estimates, and
234 the interactions that were significant in the sex-specific models. In total, we fitted 6 sex- and
235 behaviour- specific models (see Table S3 for the full models) and 3 behaviour-specific models
236 with both male and female trait estimates simultaneously (see Table S4 for the full and final
237 models).

238 Models included as fixed effects the individual's behavioural trait estimate considered
239 (aggressiveness, boldness or neophobia score), individual's age (yearling vs. older), tit density
240 and tit early reproductive investment within the forest patch on the day of flycatcher
241 settlement, and the potential bias in the proportion of empty boxes with each symbol in the
242 patch on the same day. These latter variables have indeed been found to influence the
243 probability of copying tit apparent symbol preference in this and other populations
244 [9,16,21,23]. Tit density was estimated as the proportion of boxes occupied by great tits (i.e.
245 with tit nest material) within the forest patch on the day of flycatcher choice. Tit early
246 investment was measured as the average great tit clutch (or possibly brood for the earliest
247 great tit nests) size within the forest patch on the day of flycatcher choice. The bias in the
248 proportion of empty boxes with each symbol was calculated as the proportion of boxes
249 bearing the symbol associated to the tit preference on the day of flycatcher choice minus 0.5.
250 To account for age-specific behavioural effects, we included in the models the two-way
251 interaction between age and the behavioural trait estimate considered. We also included the
252 two-way interactions of age or the behavioural trait estimate with tit density and tit early
253 reproductive investment. This gave a total of 5 main effects and 5 two-way interactions for
254 each sex- and behaviour-specific model; the maximum number of fixed effects for the models
255 with both male and female trait estimates was 7 main effects and 3 two-way interactions (see
256 full models output in Tables S3-S4). Prior to analyses, all continuous fixed effects were
257 scaled. Finally, we included forest patch and year as random factors to control for potential
258 spatio-temporal effects on social information use.

259 We fitted generalized linear mixed-effects models (GLMM) in R [26] with the *glmer*
260 function (*lme4* R package [27]) and 'binomial' family and selected our fixed effects using a
261 stepwise backward selection procedure. Because the stepwise approach can increase the risk
262 of type-I error [28,29], we checked that the significant effects retained in the final models

263 were significant in the full models too (see Tables S3-S4 for the full models output). Overall,
264 results remained similar when using a model averaging approach (AIC-based selection of
265 subset models with $\Delta AIC < 2$ using the ‘*MuMIn*’ R package [30]; results not detailed). The fit
266 of final models was assessed based on ROC curves, and Areas Under the Curves (AUC),
267 estimated using *pROC* R package [31].

268

269

270 **Results**

271

272 The probability for flycatchers to copy tit preference was affected by male aggressiveness
273 score differently between yearlings and older males (interaction aggressiveness by age; Table
274 2). Among older males, less aggressive ones significantly copied tit preference, whereas more
275 aggressive ones rejected it (Figure 1a); conversely, there was no relation between the
276 probability of copying tit preference and aggressiveness in yearling males (Figure 1a). Female
277 aggressiveness did not affect the probability of copying tit preference (z-value= -0.47, p-
278 value= 0.64; Table S3).

279 In addition, the probability of copying tit preference was affected by boldness score,
280 again differently between yearlings and older individuals, but this time both in males and
281 females (interaction boldness by age; Table 2). Among older individuals of both sexes, shyer
282 ones were more likely to copy tit preference than bolder ones, while the reverse was observed
283 in yearlings, even though in females, 95% Confidence Intervals largely overlapped a random
284 choice, i.e. a probability of copying of 0.5; Figure 1b&c).

285 Finally, in females, the interaction between neophobia score and tit clutch/brood size
286 seemed to affect the probability of copying tit preference (N= 173, z-value= -2.33, p-value=
287 0.020; Table 2): for the most neophobic females (neophobia score of 5, i.e. non-returning

288 females in the presence of the novel object), tit clutch/brood size had no effect on copying,
289 while high tit clutch/brood size was associated with higher probability of copying in other
290 females (neophobia category 1 to 4; Figure S2). However, this interaction was not strongly
291 supported in a model averaging approach (relative importance= 0.78) and when the most
292 neophobic females were excluded, no effect of neophobia remained among females with score
293 1 to 4 (z-value= 0.154, p-value= 0.877 for the interaction between female neophobia and tit
294 clutch/brood size; z-value= 0.268, p-value= 0.788 for the simple neophobia effect). This
295 suggests that the effect of neophobia was not strong. Male neophobia did not affect the
296 probability of copying tit preference (z-value= 1.34, p-value= 0.18; Table S3).

297 As found previously, both male and female flycatchers were more likely to copy (resp.
298 reject) tit apparent preference when tit clutch / brood size was high (resp. low) in the forest
299 patch on the day of settlement (z-value > 2.73 and p-value ≤ 0.01 over all models; Tables 2, S3;
300 Figure S3). The probability of copying tit preference also increased with the bias in the
301 proportion of empty boxes with the symbol associated to tits in the model with female
302 aggressiveness (z-value= 2.59, p-value= 0.01 in the final model; see Table S3) but not in other
303 models (Table S3). Tit density did not affect the probability of copying tit preference (Table
304 S3).

305 Variances associated to forest patch and year were negligible in all models (not
306 detailed here). Including both male and female behavioural trait estimates simultaneously in
307 models led to similar results (Table S4).

308

309

310 **Discussion**

311

312 We have experimentally shown in our wild bird population that the use of heterospecific
313 social information for nest site selection depended not only on external factors (here, the early
314 reproductive investment of the heterospecific tutors) but also on individual factors, and more
315 particularly on behavioural traits (here, male aggressiveness and both parents' boldness).
316 Among old males, the probability of copying heterospecific competitors' preference
317 decreased with increasing male aggressiveness. In addition, both parents' boldness score
318 modulated the probability of copying tit apparent preference depending on age: pairs with old
319 and shy individuals, on the one hand, and young and bold individuals, on the other hand, were
320 more likely to copy tit preference compared to other pairs. Finally, we found no strong effect
321 of female or male neophobia, even though increased exploration and decreased neophobia [8]
322 could be expected to favour prospecting and thereby large-scale (social and non-social)
323 information gathering and use. This was in contrast with former studies in the foraging
324 context, which usually found neophobia to promote conspecific attraction or scrounging
325 strategies, i.e. foraging strategies based on social information (e.g. [32–38], but see [39]). The
326 joint copying behaviour of the pair was therefore affected by different behavioural traits that
327 may in particular impact information access and thus availability but also the ability to cope
328 with the consequences of information use. Flycatcher pairs were besides also more likely to
329 copy apparent preference of tits when average tit clutch / brood size in the patch was high at
330 the time of nest site choice. This is in line with previous results [9,16,17,21,23] and suggests
331 that flycatchers adjusted the use of this heterospecific social information source depending on
332 the quality and/or decisions of tit tutors, on top of their own behavioural traits.

333

334 *Social information use and male aggressiveness*

335 Our results provide clear evidence that aggressiveness, i.e. the agonistic reaction towards
336 competitors, can shape the use of heterospecific social information, with different effects

337 depending on age. Aggressive individuals (especially those high in the dominance hierarchy,
338 e.g. older individuals) could be more likely to acquire social information than less aggressive
339 ones when this involves engaging in agonistic interactions with others, including
340 heterospecifics. Here, however, less aggressive old males copied tit apparent preference and
341 more aggressive ones rejected it, suggesting that all old males could have access to
342 information about tit preference independently from their aggressiveness level.

343 More aggressive individuals could be expected to be more prone to copy competitors'
344 decisions because they would benefit from competitors' experience [40] while at the same
345 time being able to cope with potentially increased competitive costs. Contrary to this
346 expectation, aggressive males avoided competitors' apparent preference. One possible
347 explanation may be that more aggressive individuals pay a greater cost from competition with
348 tits compared to less aggressive ones, because they engage more in territorial defence. More
349 aggressive males may thus reject tit apparent preference to avoid costs of heterospecific
350 agonistic interactions with dominant competitors. Conversely, less aggressive flycatchers may
351 engage less in agonistic interactions with tits and thus benefit more from using information
352 from tits. Indeed, even though tits are dominant over flycatchers, they tolerate flycatchers'
353 settlement in the vicinity of their nest (Doligez, pers. obs.). In line with this prediction, house
354 crickets *Acheta domesticus* with a high Resource Holding Potential were more likely to win
355 contests, but if losing, they ended the contest sooner [41]. Assessing whether increased
356 aggressiveness increases the risk of heterospecific agonistic interactions and thus potential
357 costs for flycatchers would be needed to confirm this explanation.

358

359 *Social information use and boldness*

360 Boldness also affected the probability of copying tit preference: especially in males, copying
361 probability was higher for old and shy individuals, as well as young and bold ones, compared

362 to old and bold, and young and shy ones, respectively (Figure 1). Former studies reported
363 highly contrasting results regarding the link between boldness and social information use
364 (Tables 1 and S1). In some studies, shy individuals were more likely to shoal and follow
365 others [42–44], as a result of higher attention paid to, and higher probability to rely on, others’
366 decisions. Other studies however found that bold individuals paid more attention to others
367 [45], or even no support for boldness to affect the propensity to use three different types of
368 social information [46]. The effect of boldness on social information use may thus be strongly
369 dependent on the context and in particular on social organisation and individual’s experience.
370 Here, the link between boldness and social information use depended on age, which likely
371 shapes both competitive ability and experience [47,48] and thereby information access and
372 use. Yearlings may have a restrained access to information, but this effect may be
373 compensated for by boldness. Furthermore, old and bold individuals may have access to
374 additional information sources such that only old and shy individuals may rely on tit apparent
375 preference (that can be obtained from a distance with limited risks) over other sources.
376 Constraints on the access to social information imposed by the behavioural trait considered
377 may shape the link between this trait and information use.

378

379 *Modulation of social information use or of the response to our behavioural tests?*

380 The three behavioural traits considered here are only weakly repeatable [14] and thus mostly
381 plastic. Therefore, we cannot exclude that flycatchers adjusted their behavioural responses to
382 our behavioural tests depending on whether they copied tit apparent preference for nest box
383 choice rather than adjusting their copying behaviour depending on their behavioural traits.
384 Yet, our experiment was designed so that choosing a given symbol had no subsequent
385 reproductive consequence for flycatchers, because symbols were randomized in space and
386 thus independent from intrinsic site quality [21]. Post-settlement adjustment of behavioural

387 responses to our tests would require different levels (or expectance) of competition level or
388 predation risk depending on the symbol chosen. For example, for this mechanism to explain
389 the observed patterns in aggressiveness, old males that rejected tit preference would have had
390 to expect, or to be exposed to, higher competition level by settling in a box displaying the
391 opposite symbol than the one associated with tits, and thus increased their aggressiveness
392 response to defend their nest box. We consider as unlikely such age-specific difference in
393 competition level due to the presence of an artificial nest feature that was removed days (for
394 aggressiveness tests) or weeks (for boldness and neophobia tests) before. Many social factors
395 after settlement are likely to affect flycatchers' behaviour, making the alternative explanation
396 of a post-settlement adjustment of behavioural responses unlikely.

397

398 *Modulation of heterospecific social information use based on tutors' investment*

399 The increase in the probability of copying tit apparent preference with increasing tit clutch /
400 brood size in the patch on the day of choice implies that flycatchers can estimate average tit
401 reproductive investment at the patch scale when they settle and use it for modulating nest site
402 choice according to tit preference. This is in line with former experimental results at a smaller
403 scale, showing that pied flycatchers use tit clutch size as social information (i) to choose
404 between two close-by boxes according to the feature (symbol) associated to tit nest [9,16,23]
405 but also (ii) to adjust breeding investment later on ([49], see also [17] for an experimental test
406 of patch choice according to tit phenology). Overall, our results provide clear evidence that
407 flycatchers modulated their use of heterospecific social information obtained from tit apparent
408 preference for nest site features based on other information sources (here, tit early
409 reproductive investment). This modulation did not depend on their behavioural traits, but
410 more work is needed to investigate whether behavioural traits can in general affect the relative
411 use of different social information sources.

412

413 Our study extends the importance of behavioural traits in shaping the use of social
414 information reported in previous studies to the context of breeding habitat selection in the
415 wild, using a powerful experimental manipulation of social information. The joint copying
416 behaviour of the pair for nest site selection was likely constrained both by access to social
417 information, explaining the age-dependent link with boldness, and by competitive costs
418 related to the use of social information after gathering it, explaining the link with age-
419 dependent male aggressiveness. More generally, how behavioural traits affect access to social
420 information and resulting decision-making based on this information may be a prevalent issue
421 in explaining among-individual variation in social information use over contexts. Such
422 constraints may have evolutionary consequences through the costs / benefits balance of the
423 use of social information, which may favour functional integration between certain types of
424 personality traits and social information use depending on the relative availability and
425 reliability of these and other information sources. The evolution of such trait associations
426 however relies on genetic bases for both social information use and behavioural traits, which
427 was not the case in our system [14,21,50]. Yet, whether the same behavioural traits may be
428 expected to shape social information use in different contexts and/or the use of different types
429 of social information remains to be explored. Theoretical approaches could prove useful in
430 this respect to explore whether features of the decisions to be made (e.g. spatio-temporal
431 scales) may lead to associations between certain behavioural traits and social information use
432 across contexts.

433

434

435 **Acknowledgements**

436 We thank Lars Gustafsson for providing access to the field site, the landowners from Gotland
437 to allow us collecting data on their properties, all fieldworkers who collected the data,
438 especially Laure Cauchard, Gregory Daniel, Sami M. Kivelä, Uéline Courcoux-Caro and
439 Louise Riotte-Lambert. We are grateful to all the students who contributed to extracting
440 behaviours from the recordings. We also thank Jelmer Samplonius, an anonymous reviewer
441 and the associate editor Sarah Brosnan for constructive comments on a previous version of the
442 manuscript.

443

444 **Funding**

445 This work was funded by the Ministère de l'Enseignement Supérieur et de la Recherche and
446 the Department of Ecology and Genetics from Uppsala University (PhD grants to JM and
447 MG), by research grants from Uppsala University (Stiftelsen för Zoologisk Forskning to JM
448 and MG), by the Région Auvergne Rhone-Alpes (Explora'Doc grants to JM) and by the
449 University of Lyon (IDEX mobility grant to JM). JTF was funded by the Kone Foundation,
450 and BD by the Centre National pour la Recherche Scientifique and the Région Auvergne
451 Rhone-Alpes (CIBLÉ programme).

452

453 **Ethics**

454 Permission for catching and ringing adult and young birds was granted every year by the
455 Ringing Centre from the Museum of Natural History in Stockholm (licence nb. 471: M015 to
456 B.D.). Personality tests only required observing individuals from a distance from below a
457 camouflage net or video-recording their behaviour, without catching them, and special care
458 was taken to avoid any detrimental effect of behavioural test on the health of the nestlings
459 (see the Methods section).

460

461 **Data, code and materials**

462 The datasets supporting this article have been uploaded as part of the supplementary material
463 (Table S5).

464 **Competing interests**

465 The authors declare no competing interests.

466 **Authors' contributions**

467 BD designed the study; MG, BD, JTF and many assistants carried out the fieldwork; JM
468 analysed the data, and drafted the manuscript. JM, JTF, MG, and BD critically revised the
469 manuscript. All authors gave approval for publication and agree to be held accountable for the
470 work performed therein.

471

472

473 **References**

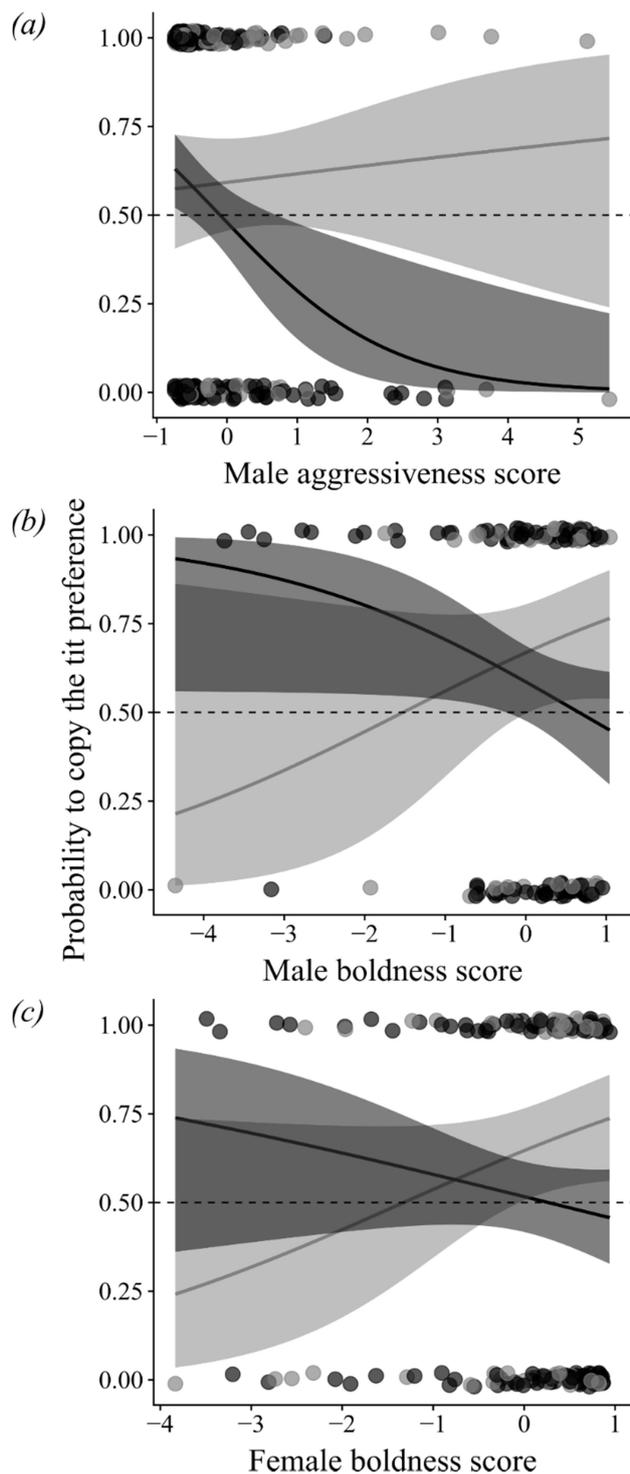
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652

653 **Figure 1. Probability for flycatchers to copy tit apparent preference depending on (a)**
 654 **male aggressiveness and age, (b) male boldness and age, and (c) female boldness and age**
 655 **(yearlings: light grey; older: dark grey). Data points show actual choices (copy = 1 / reject =**
 656 **0). The predicted means (lines) and corresponding 95%CI (shaded areas) were derived from**
 657 **the final model for an averaged value of tit clutch / brood size.**

658 **Table 1. Summary of the results of studies investigating relations between personality**
659 **traits and social information use:** for each personality trait, number of studies that found a
660 positive (+), negative (-), or non-significant (NS) relation. Full details on each study and
661 measured traits are given in Table S1. Note that neophobia and exploration were often
662 referred to as ‘boldness’ in articles, but we follow here the definitions from [8] and refer to
663 boldness as the reaction in a risky situation (presence of potential predators, including
664 humans).

Definitions	Nb. and signs of the links with social information use			References
	-	0	+	
Reaction in a known environment	0	1	1	[49]
Agonistic reaction towards others	0	0	0	
Reaction in a risky situation	2	5	1	[34, 40, 41, 43, 44]
Reaction in a novel environment	3	4	2	[36, 50-57]
Reaction towards a novel object	2	2	7	[30-35, 37, 43, 57,58]
Non-agonistic reaction towards others	1	1	2	[35, 56, 59, 60]

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666 [1] Budaev and Zworykin [51]; [2] Ward et al. [42]; [3] Dyer et al. [43]; [4] Carter et al. [36];
667 [5] Carter et al. [45]; [6] Harcourt et al. [46]; [7] Marchetti and Drent [52]; [8] Webster et al.
668 [53]; [9] Nomakuchi et al. [54], [10] Sibbald et al. [55]; [11] David et al. [56]; [12] Aplin et
669 al. [57]; [13] Webster and Laland [58]; [14] Snijders et al. [38]; [15] Smit and van Oers [59];
670 [16] Michelena et al. [32]; [17] Kurvers et al. [34]; [18] Kurvers et al. [33]; [19] Kurvers et al.
671 [35]; [20] Jolles et al. [39]; [21] Trompf and Brown [37]; [22] Carter et al. [60]; [23] Aplin et
672 al. [61]; [24] Evans et al. [62].

673 **Table 2. Influence of male aggressiveness and boldness scores, female neophobia score**
674 **and tit clutch / brood ‘c/b’ size on the probability of copying tit apparent preference of**
675 **nest box artificial features.** Aggressiveness has been log-transformed and all continuous
676 traits have been standardized prior analysis. Age estimates are given for yearling individuals
677 (older individuals being the reference). P-values below the risk α of 0.05 are highlighted in bold.

	Estimate \pm SE	z-value	p-value
<i>Final model with male aggressiveness score, N=224</i>			
Intercept	-0.37 \pm 0.19	-1.95	0.05
Age δ	0.46 \pm 0.33	1.36	0.17
Aggressiveness δ	-0.83 \pm 0.30	-2.79	0.01
Tit clutch / brood (c/b) size	0.68 \pm 0.15	4.48	< 10⁻⁵
Aggressiveness δ : Age δ	0.93 \pm 0.36	2.59	0.01
<i>Final model with male boldness score, N=142</i>			
Intercept	0.05 \pm 0.22	0.22	0.83
Age δ	0.35 \pm 0.41	0.85	0.39
Boldness δ	-0.53 \pm 0.27	-1.95	0.05
Tit c/b size	0.75 \pm 0.20	3.77	< 10⁻³
Boldness δ : Age δ	0.98 \pm 0.45	2.21	0.03
<i>Final model with female boldness score, N=173</i>			
Intercept	-0.20 \pm 0.20	-1.01	0.31
Age δ	0.54 \pm 0.35	1.54	0.12
Boldness δ	-0.25 \pm 0.21	-1.23	0.22
Tit c/b size	0.64 \pm 0.17	3.78	< 10⁻³
Boldness δ : Age δ	0.71 \pm 0.35	2.03	0.04
<i>Final model with female neophobia score, N=173</i>			
Intercept	0.00 \pm 0.16	-0.01	0.99
Neophobia δ	-0.02 \pm 0.17	-0.10	0.92
Tit c/b size	0.68 \pm 0.17	3.92	< 10⁻⁴
Neophobia δ : Tit c/b size	-0.47 \pm 0.20	-2.33	0.02

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