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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

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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

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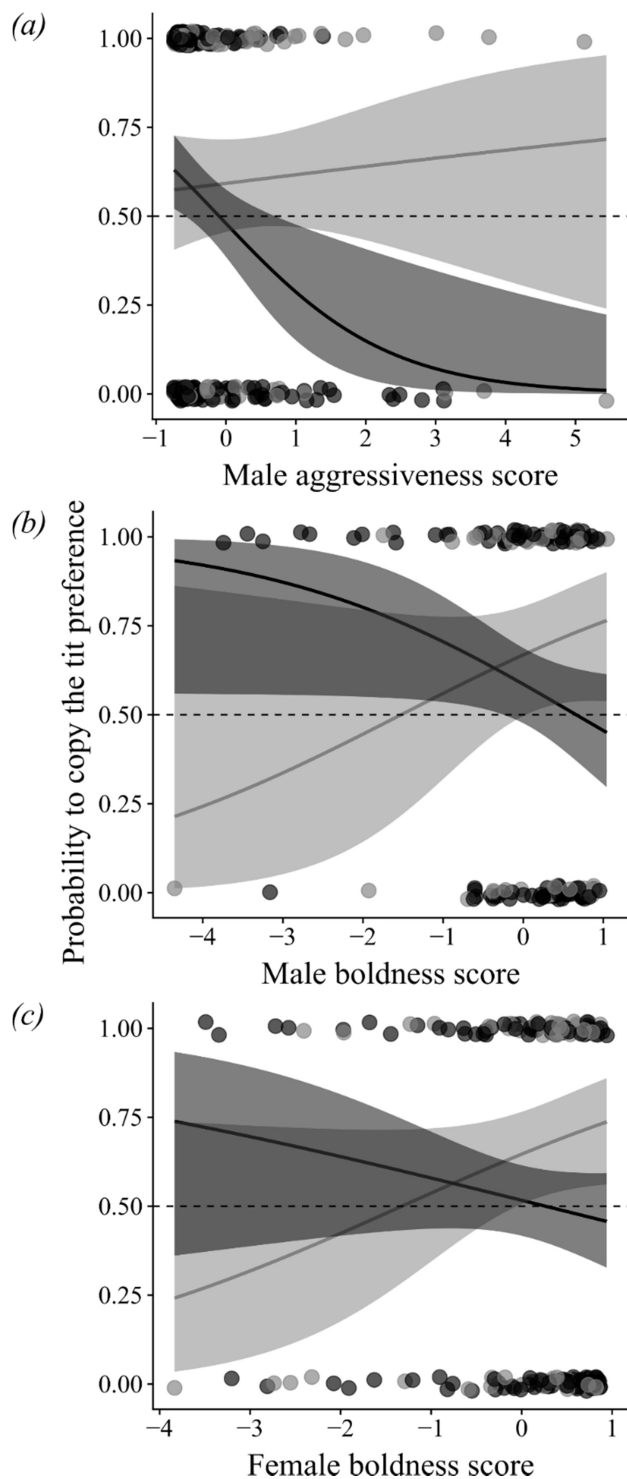
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652

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]

665

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  $\alpha$  of 0.05 are highlighted in bold.

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

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