

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

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19

20 **Abstract**

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

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37

## 39 **Introduction**

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

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

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

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

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

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

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109

## 110 **Methods**

111

112 *Species and study site*

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

124

125 *Heterospecific preference copying: experimental design*

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

136 *Sitta europaea*, sparrows *Passer domesticus* and *P. montanus* and wrynecks *Jynx torquilla*; 25  
137 boxes in total over the two years). Therefore, when flycatchers arrived from migration (late  
138 April to mid-May), they had the choice between copying tit preference by settling in a box  
139 with the same symbol as on tit boxes, or rejecting it by settling in a box with the opposite  
140 symbol. When a flycatcher pair had settled in a box, as shown by the presence of new nest  
141 material in the box, we removed the symbol on this box. This avoided providing conspecific  
142 information via the symbol chosen to later arriving flycatchers. We checked empty boxes  
143 every other day to detect newly started nest building and removed (for new flycatcher nests)  
144 or changed if needed (for new tit nests) the symbol accordingly. At the same time, we  
145 adjusted the number of triangles and circles on empty boxes within a forest patch to keep an  
146 equal proportion of available boxes displaying each symbol, and thus an equal probability for  
147 newcomers to choose a symbol at random. Because this equal proportion of both symbols  
148 could not always be met (e.g. when an odd number of empty boxes remained in a patch), we  
149 controlled for the deviation from random (0.5) of the proportion of empty boxes matching the  
150 tit apparent preference within a plot on the day of choice for each flycatcher pair [see 21 for  
151 more details]. Because we can assume that flycatchers naïve to the experimental design have  
152 no previous experience with geometric symbols, this design minimises genetic and ecological  
153 effects on nest site choice and is a powerful method to reveal factors affecting individuals'  
154 choices [10].

155

### 156 *Measuring behavioural traits*

157 The three behavioural traits of interest here, namely aggressiveness, boldness and neophobia,  
158 were measured as described in a former study on the same population (see [14] for detailed  
159 methods). In this former study based on a larger sample [14], all three traits were found to be  
160 weakly repeatable between years ( $R=0.2$ ,  $0.1$  and  $0.4$  for aggressiveness, boldness and

161 neophobia respectively) and weakly phenotypically correlated (-0.2 for aggressiveness-  
162 neophobia, -0.3 for boldness-neophobia) but they did not associate in behavioural syndromes  
163 (i.e. no between-individual covariance between them [14]). In the present study, we refer to  
164 these traits as behavioural rather than personality traits, because we could not separate the  
165 effect of the repeatable vs. flexible part of the traits on the use of social information; indeed  
166 the copying behaviour was measured only once (i.e. in naïve birds).

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



186 meters from the box, (ii) attacks or stationary flights towards a decoy and (iii) chases towards  
187 live intruders [similarly to 14]. We excluded from the datasets individuals that were observed  
188 less than 5 minutes. In total, we used 1168 behavioural responses of both sexes, performed  
189 during 790 aggressiveness tests on 224 males and 271 females and 313 reproductive events  
190 over the two years of the experiment. The final individual aggressiveness score was calculated  
191 as the average of the scores measured for each individual within one season.

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

211 with the first four levels corresponding to latency quartiles and the last level assigned to these  
212 non-returning individuals [as in 14]. Results however remained quantitatively unchanged (not  
213 detailed here) when considering neophobia as a continuous latency instead of a score by  
214 attributing a maximum latency to non-returning individuals (here 4,000 seconds, the  
215 maximum observed latency plus one minute).

216

### 217 *Statistical analyses*

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

235 with both male and female trait estimates simultaneously (see Table S4 for the full and final  
236 models).

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

258 We fitted generalized linear mixed-effects models (GLMM) in R [26] with the *glmer*  
259 function (*lme4* R package [27]) and 'binomial' family and selected our fixed effects using a

260 stepwise backward selection procedure. Because the stepwise approach can increase the risk  
261 of type-I error [28,29], we checked that the significant effects retained in the final models  
262 were significant in the full models too (see Tables S3-S4 for the full models output). Overall,  
263 results remained similar when using a model averaging approach (AIC-based selection of  
264 subset models with  $\Delta AIC < 2$  using the ‘*MuMIn*’ R package [30]; results not detailed). The fit  
265 of final models was assessed based on ROC curves, and Areas Under the Curves (AUC),  
266 estimated using *pROC* R package [31].

267

## 268 **Results**

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

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

282 Finally, in females, the interaction between neophobia score and tit clutch/brood size  
283 seemed to affect the probability of copying tit preference (N= 173, z-value= -2.33, p-value=

284 0.020; Table 2): for the most neophobic females (neophobia score of 5, i.e. non-returning  
285 females in the presence of the novel object), tit clutch/brood size had no effect on copying,  
286 while high tit clutch/brood size was associated with higher probability of copying in other  
287 females (neophobia category 1 to 4; Figure S2). However, this interaction was not strongly  
288 supported in a model averaging approach (relative importance= 0.78) and when the most  
289 neophobic females were excluded, no effect of neophobia remained among females with score  
290 1 to 4 (z-value= 0.154, p-value= 0.877 for the interaction between female neophobia and tit  
291 clutch/brood size; z-value= 0.268, p-value= 0.788 for the simple neophobia effect). This  
292 suggests that the effect of neophobia was not strong. Male neophobia did not affect the  
293 probability of copying tit preference (z-value= 1.34, p-value= 0.18; Table S3).

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

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

305

## 306 **Discussion**

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

328

### 329 *Social information use and male aggressiveness*

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

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

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

353

354 *Social information use and boldness*

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

373

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

375 The three behavioural traits considered here are only weakly repeatable [14] and thus mostly  
376 plastic. Therefore, we cannot exclude that flycatchers adjusted their behavioural responses to  
377 our behavioural tests depending on whether they copied tit apparent preference for nest box  
378 choice rather than adjusting their copying behaviour depending on their behavioural traits.  
379 Yet, our experiment was designed so that choosing a given symbol had no subsequent



380 reproductive consequence for flycatchers, because symbols were randomized in space and  
381 thus independent from intrinsic site quality [21]. Post-settlement adjustment of behavioural  
382 responses to our tests would require different levels (or expectance) of competition level or  
383 predation risk depending on the symbol chosen. For example, for this mechanism to explain  
384 the observed patterns in aggressiveness, old males that rejected tit preference would have had  
385 to expect, or to be exposed to, higher competition level by settling in a box displaying the  
386 opposite symbol than the one associated with tits, and thus increased their aggressiveness  
387 response to defend their nest box. We consider as unlikely such age-specific difference in  
388 competition level due to the presence of an artificial nest feature that was removed days (for  
389 aggressiveness tests) or weeks (for boldness and neophobia tests) before. Many social factors  
390 after settlement are likely to affect flycatchers' behaviour, making the alternative explanation  
391 of a post-settlement adjustment of behavioural responses unlikely.

392

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

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

405 more work is needed to investigate whether behavioural traits can in general affect the relative  
406 use of different social information sources.

407

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

428

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446

447 **Ethics**

448 Permission for catching and ringing adult and young birds was granted every year by the  
449 Ringing Centre from the Museum of Natural History in Stockholm (licence nb. 471: M015 to  
450 B.D.). Personality tests only required observing individuals from a distance from below a  
451 camouflage net or video-recording their behaviour, without catching them, and special care

452 was taken to avoid any detrimental effect of behavioural test on the health of the nestlings  
453 (see the Methods section).

454

#### 455 **Data, code and materials**

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

#### 458 **Competing interests**

459 The authors declare no competing interests.

#### 460 **Authors' contributions**

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

465

466

#### 467 **References**

- 468 1. Danchin E, Giraldeau L-A, Valone TJ, Wagner RH. 2004 Public information: from  
469 nosy neighbors to cultural evolution. *Science*. **305**, 487–491.  
470 (doi:10.1126/science.1098254)
- 471 2. Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW. 2005 Information  
472 and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 187–193.  
473 (doi:http://dx.doi.org/10.1016/j.tree.2005.01.010)
- 474 3. van Bergen Y, Coolen I, Laland KN. 2004 Nine-spined sticklebacks exploit the most  
475 reliable source when public and private information conflict. *Proc. Biol. Sci.* **271**, 957–  
476 62. (doi:10.1098/rspb.2004.2684)
- 477 4. Templeton JJ, Giraldeau L-A. 1996 Vicarious sampling: the use of personal and public

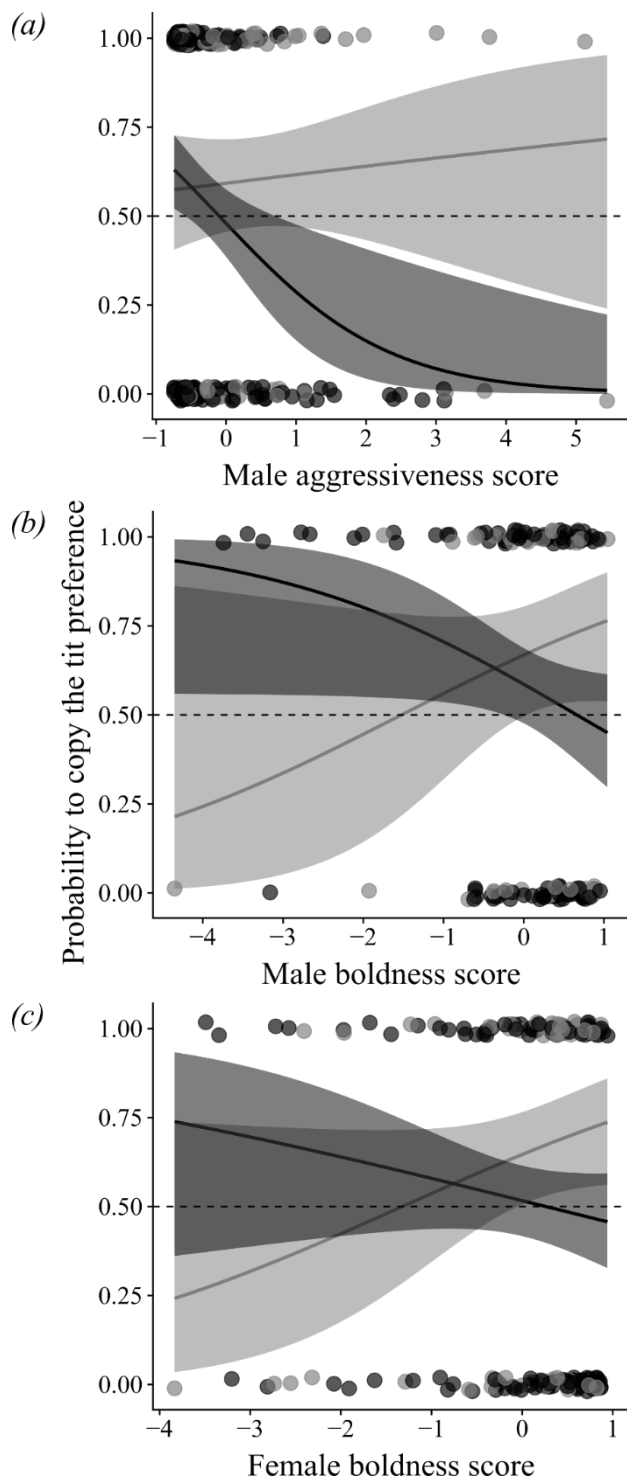
- 478 information by starlings foraging in a simple patchy environment. *Behav. Ecol.*  
479 *Sociobiol.* **38**, 105–114. (doi:10.1007/s002650050223)
- 480 5. Doligez B, Danchin E, Clobert J, Gustafsson L. 1999 The use of conspecific  
481 reproductive success for breeding habitat selection in a non-colonial, hole-nesting  
482 species, the collared flycatcher. *J. Anim. Ecol.* **68**, 1193–1206. (doi:10.1046/j.1365-  
483 2656.1999.00362.x)
- 484 6. Doligez B, Cadet C, Danchin E, Boulinier T. 2003 When to use public information for  
485 breeding habitat selection? The role of environmental predictability and density  
486 dependence. *Anim. Behav.* **66**, 973–988. (doi:10.1006/anbe.2002.2270)
- 487 7. Dugatkin LA, Godin JGJ. 1993 Female mate copying in the guppy (*Poecilia*  
488 *reticulata*): Age-dependent effects. *Behav. Ecol.* **4**, 289–292.  
489 (doi:10.1093/beheco/4.4.289)
- 490 8. Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007 Integrating animal  
491 temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318.  
492 (doi:10.1111/j.1469-185X.2007.00010.x)
- 493 9. Loukola OJ, Seppänen J-T, Krams I, Torvinen SS, Forsman JT. 2013 Observed fitness  
494 may affect niche overlap in competing species via selective social information use. *Am.*  
495 *Nat.* **182**, 474–483. (doi:10.1086/671815)
- 496 10. Seppänen J-T, Forsman JT. 2007 Interspecific social learning: novel preference can be  
497 acquired from a competing species. *Curr. Biol.* **17**, 1248–1252.  
498 (doi:10.1016/j.cub.2007.06.034)
- 499 11. Dingemanse NJ, Both C, van Noordwijk AJ, Rutten AL, Drent PJ. 2003 Natal dispersal  
500 and personalities in great tits (*Parus major*). *Proceedings. Biol. Sci.* **270**, 741–7.  
501 (doi:10.1098/rspb.2002.2300)
- 502 12. Cote J, Clobert J, Brodin T, Fogarty S, Sih A. 2010 Personality-dependent dispersal:  
503 characterization, ontogeny and consequences for spatially structured populations.  
504 *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **365**, 4065–4076.  
505 (doi:10.1098/rstb.2010.0176)
- 506 13. Forsman JT, Thomson RL. 2008 Evidence of information collection from  
507 heterospecifics in cavity-nesting birds. *Ibis (Lond. 1859)*. **150**, 409–412.  
508 (doi:10.1111/j.1474-919X.2007.00773.x)
- 509 14. Morinay J, Daniel G, Gustafsson L, Doligez B. 2019 No evidence for behavioural  
510 syndrome and genetic basis for three personality traits in a wild bird population. *Anim.*  
511 *Behav.* **153**, 69–82. (doi:10.1016/j.anbehav.2019.05.001)
- 512 15. Kivelä SM, Seppänen J-T, Ovaskainen O, Doligez B, Gustafsson L, Mönkkönen M,  
513 Forsman JT. 2014 The past and the present in decision-making: the use of conspecific  
514 and heterospecific cues in nest site selection. *Ecology* **95**, 3428–3439. (doi:10.1890/13-  
515 2103.1)
- 516 16. Forsman JT, Seppänen J-T. 2011 Learning what (not) to do: testing rejection and  
517 copying of simulated heterospecific behavioural traits. *Anim. Behav.* **81**, 879–883.  
518 (doi:10.1016/j.anbehav.2011.01.029)
- 519 17. Samplonius JM, Both C. 2017 Competitor phenology as a social cue in breeding site  
520 selection. *J. Anim. Ecol.* **86**, 615–623. (doi:10.1111/1365-2656.12640)
- 521 18. Jaakkonen T, Kivelä SM, Meier CM, Forsman JT. 2015 The use and relative  
522 importance of intraspecific and interspecific social information in a bird community.  
523 *Behav. Ecol.* **26**, 55–64. (doi:10.1093/beheco/aru144)
- 524 19. Samplonius JM, Kromhout Van Der Meer IM, Both C. 2017 Nest site preference  
525 depends on the relative density of conspecifics and heterospecifics in wild birds. *Front.*  
526 *Zool.* **14**. (doi:10.1186/s12983-017-0246-5)
- 527 20. Doligez B, Pärt T, Danchin E, Clobert J, Gustafsson L. 2004 Availability and use of

- 528 public information and conspecific density for settlement decisions in the collared  
529 flycatcher. *J. Anim. Ecol.* **73**, 75–87. (doi:10.1111/j.1365-2656.2004.00782.x)
- 530 21. Morinay J, Forsman JT, Kivelä SM, Gustafsson L, Doligez B. 2018 Heterospecific nest  
531 site copying behavior in a wild bird: assessing the influence of genetics and past  
532 experience on a joint breeding phenotype. *Front. Ecol. Evol.* **5**, 167.  
533 (doi:10.3389/fevo.2017.00167)
- 534 22. Forsman JT, Hjernquist MB, Taipale J, Gustafsson L. 2008 Competitor density cues for  
535 habitat quality facilitating habitat selection and investment decisions. *Behav. Ecol.* **19**,  
536 539–545. (doi:10.1093/beheco/arn005)
- 537 23. Seppänen J-T, Forsman JT, Mönkkönen M, Krams I, Salmi T. 2011 New behavioural  
538 trait adopted or rejected by observing heterospecific tutor fitness. *Proc. R. Soc. B Biol.*  
539 *Sci.* **278**, 1736–1741. (doi:10.1098/rspb.2010.1610)
- 540 24. Gustafsson L. 1988 Interspecific and intraspecific competition for nest holes in a  
541 population of the collared flycatcher *Ficedula albicollis*. *Ibis (Lond. 1859)*. **130**, 11–16.  
542 (doi:10.1111/j.1474-919X.1988.tb00951.x)
- 543 25. Král M, Bícík V. 1992 Nest defence by the collared flycatcher (*Ficedula albicollis*)  
544 against the great tit (*Parus major*). *Folia zoologica* **41**, 263–269.
- 545 26. R Core Team. 2016 R: a language and environment for statistical computing.
- 546 27. Bates D, Maechler M, Bolker BM, Walker S. 2015 Fitting linear mixed-effects models  
547 using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01.)
- 548 28. Mundry R, Nunn CL. 2009 Stepwise model fitting and statistical inference: turning  
549 noise into signal pollution. *Am. Nat.* **173**, 119–123. (doi:10.1086/593303)
- 550 29. Forstmeier W, Wagenmakers E, Parker TH. 2017 Detecting and avoiding likely false-  
551 positive findings – a practical guide. *Biol. Rev.* **92**, 1941–1968.  
552 (doi:10.1111/brv.12315)
- 553 30. Barton K. 2016 MuMIn: Multi-Model Inference. R package version 1.15.6.
- 554 31. Robin X, Turck N, Hainard A, Tiberti N, Lisacek F, Sanchez J-C, Müller M. 2011  
555 pROC: an open-source package for R and S+ to analyze and compare ROC curves.  
556 *BMC Bioinformatics* **12**, 77. (doi:10.1186/1471-2105-12-77)
- 557 32. Michelena P, Sibbald AM, Erhard HW, McLeod JE. 2009 Effects of group size and  
558 personality on social foraging: the distribution of sheep across patches. *Behav. Ecol.*  
559 **20**, 145–152. (doi:10.1093/beheco/arn126)
- 560 33. Kurvers RHJM, Van Oers K, Nolet BA, Jonker RM, Van Wieren SE, Prins HHT,  
561 Ydenberg RC. 2010 Personality predicts the use of social information. *Ecol. Lett.* **13**,  
562 829–837. (doi:10.1111/j.1461-0248.2010.01473.x)
- 563 34. Kurvers RHJM, Prins HHT, van Wieren SE, van Oers K, Nolet BA, Ydenberg RC.  
564 2010 The effect of personality on social foraging: shy barnacle geese scrounge more.  
565 *Proc. R. Soc. B Biol. Sci.* **277**, 601–608. (doi:10.1098/rspb.2009.1474)
- 566 35. Kurvers RHJM, Adamczyk VMAP, van Wieren SE, Prins HHT. 2011 The effect of  
567 boldness on decision-making in barnacle geese is group-size-dependent. *Proc. R. Soc.*  
568 *B Biol. Sci.* **278**, 2018–2024. (doi:10.1098/rspb.2010.2266)
- 569 36. Carter AJ, Marshall HH, Heinsohn R, Cowlshaw G. 2013 Personality predicts decision  
570 making only when information is unreliable. *Anim. Behav.* **86**, 633–639.  
571 (doi:10.1016/J.ANBEHAV.2013.07.009)
- 572 37. Trompf L, Brown C. 2014 Personality affects learning and trade-offs between private  
573 and social information in guppies, *Poecilia reticulata*. *Anim. Behav.* **88**, 99–106.  
574 (doi:10.1016/j.anbehav.2013.11.022)
- 575 38. Snijders L, Naguib M, van Oers K. 2017 Dominance rank and boldness predict social  
576 attraction in great tits. *Behav. Ecol.* **28**, 398–406. (doi:10.1093/beheco/arw158)
- 577 39. Jolles JW, Ostojčić L, Clayton NS. 2013 Dominance, pair bonds and boldness determine

- 578 social-foraging tactics in rooks, *Corvus frugilegus*. *Anim. Behav.* **85**, 1261–1269.  
579 (doi:10.1016/j.anbehav.2013.03.013)
- 580 40. Forsman JT, Seppänen J-T, Mönkkönen M. 2002 Positive fitness consequences of  
581 interspecific interaction with a potential competitor. *Proc. R. Soc. B* **269**, 1619–1623.  
582 (doi:10.1098/rspb.2002.2065)
- 583 41. Briffa M. 2008 Decisions during fights in the house cricket, *Acheta domesticus*: mutual  
584 or self assessment of energy, weapons and size? *Anim. Behav.* **75**, 1053–1062.  
585 (doi:10.1016/j.anbehav.2007.08.016)
- 586 42. Ward AJW, Thomas P, Hart PJB, Krause J. 2004 Correlates of boldness in three-spined  
587 sticklebacks (*Gasterosteus aculeatus*). *Behav. Ecol. Sociobiol.* **55**, 561–568.  
588 (doi:10.1007/s00265-003-0751-8)
- 589 43. Dyer JRG, Croft DP, Morrell LJ, Krause J. 2008 Shoal composition determines  
590 foraging success in the guppy. *Behav. Ecol.* **20**, 165–171. (doi:10.1093/beheco/arn129)
- 591 44. Croft DP, Krause J, Darden SK, Ramnarine IW, Faria JJ, James R. 2009 Behavioural  
592 trait assortment in a social network: patterns and implications. *Behav. Ecol. Sociobiol.*  
593 **63**, 1495–1503. (doi:10.1007/s00265-009-0802-x)
- 594 45. Carter AJ, Marshall HH, Heinsohn R, Cowlshaw G. 2014 Personality predicts the  
595 propensity for social learning in a wild primate. *PeerJ* **2**, e283. (doi:10.7717/peerj.283)
- 596 46. Harcourt JL, Biau S, Johnstone R, Manica A. 2010 Boldness and information use in  
597 three-spined sticklebacks. *Ethology* **116**, 440–447. (doi:10.1111/j.1439-  
598 0310.2010.01757.x)
- 599 47. Qvarnström A. 1997 Experimentally increased badge size increases male competition  
600 and reduces male parental care in the collared flycatcher. *Proc. R. Soc. B Biol. Sci.* **264**,  
601 1225–1231. (doi:10.1098/rspb.1997.0169)
- 602 48. Pärt T. 1995 The importance of local familiarity and search costs for age- and sex-  
603 biased philopatry in the collared flycatcher. *Anim. Behav.* **49**, 1029–1038.  
604 (doi:10.1006/anbe.1995.0132)
- 605 49. Forsman JT, Seppänen J-T, Nykänen IL. 2012 Observed heterospecific clutch size can  
606 affect offspring investment decisions. *Biol. Lett.* **8**, 341–343.  
607 (doi:10.1098/rsbl.2011.0970)
- 608 50. Tolvanen J, Kivelä SM, Doligez B, Morinay J, Gustafsson L, Bijma P, Pakanen V,  
609 Forsman JT. In press. Quantitative genetics of the use of conspecific and heterospecific  
610 social cues for breeding site choice. *Submitted*
- 611 51. Budaev SV, Zworykin DD. 1998 Difference in shoaling behaviour between ocellated  
612 (*Symphodus ocellatus*) and long-striped (*S. tinca*) wrasses and its relation with other  
613 behavioural patterns. *Mar. Freshw. Behav. Physiol.* **31**, 115–121.  
614 (doi:10.1080/10236249809387067)
- 615 52. Marchetti C, Drent P. 2000 Individual differences in the use of social information in  
616 foraging by captive great tits. *Anim. Behav.* **60**, 131–140.  
617 (doi:10.1006/anbe.2000.1443)
- 618 53. Webster MM, Hart AJW, Ward PJB. 2007 Boldness is influenced by social context in  
619 threespine sticklebacks (*Gasterosteus aculeatus*). *Behaviour* **144**, 351–371.  
620 (doi:10.1163/156853907780425721)
- 621 54. Nomakuchi S, Park PJ, Bell MA. 2009 Correlation between exploration activity and  
622 use of social information in three-spined sticklebacks. *Behav. Ecol.* **20**, 340–345.  
623 (doi:10.1093/beheco/arp001)
- 624 55. Sibbald AM, Erhard HW, McLeod JE, Hooper RJ. 2009 Individual personality and the  
625 spatial distribution of groups of grazing animals: An example with sheep. *Behav.*  
626 *Processes* **82**, 319–326. (doi:10.1016/j.beproc.2009.07.011)
- 627 56. David M, Cézilly F, Giraldeau LA. 2011 Personality affects zebra finch feeding

- 628 success in a producer-scrounger game. *Anim. Behav.* **82**, 61–67.  
629 (doi:10.1016/j.anbehav.2011.03.025)
- 630 57. Aplin LM, Farine DR, Mann RP, Sheldon BC. 2014 Individual-level personality  
631 influences social foraging and collective behaviour in wild birds. *Proc. R. Soc. B Biol.*  
632 *Sci.* **281**, 20141016–20141016. (doi:10.1098/rspb.2014.1016)
- 633 58. Webster MM, Laland KN. 2015 Space-use and sociability are not related to public-  
634 information use in ninespine sticklebacks. *Behav. Ecol. Sociobiol.*  
635 (doi:10.1007/s00265-015-1901-5)
- 636 59. Smit JAH, Oers K Van. 2019 Personality types vary in their personal and social  
637 information use. *Anim. Behav.* , 3–11. (doi:10.1016/j.anbehav.2019.02.002)
- 638 60. Carter AJ, Ticó MT, Cowlshaw G. 2016 Sequential phenotypic constraints on social  
639 information use in wild baboons. *Elife* **5**, 1–21. (doi:10.7554/eLife.13125)
- 640 61. Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC. 2012 Social networks predict  
641 patch discovery in a wild population of songbirds. *Proc. R. Soc. B Biol. Sci.* **279**, 4199–  
642 4205. (doi:10.1098/rspb.2012.1591)
- 643 62. Evans JC, Jones TB, Morand-ferron J. 2018 Dominance and the initiation of group  
644 feeding events : the modifying effect of sociality. *Behav. Ecol.* **29**, 448–458.  
645 (doi:10.1093/beheco/ax194)
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648

649 **Figure 1. Probability for flycatchers to copy tit apparent preference depending on (a)**

650 **male aggressiveness and age, (b) male boldness and age, and (c) female boldness and age**

651 (yearlings: light grey; older: dark grey). Data points show actual choices (copy = 1 / reject =

652 0). The predicted means (lines) and corresponding 95%CI (shaded areas) were derived from

653 the final model for an averaged value of tit clutch / brood size.

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

661

662 [1] Budaev and Zworykin [51]; [2] Ward et al. [42]; [3] Dyer et al. [43]; [4] Carter et al. [36];  
663 [5] Carter et al. [45]; [6] Harcourt et al. [46];

664 [7] Marchetti and Drent [52]; [8] Webster et al. [53]; [9] Nomakuchi et al. [54], [10] Sibbald  
665 et al. [55]; [11] David et al. [56]; [12] Aplin et al. [57]; [13] Webster and Laland [58]; [14]  
666 Snijders et al. [38]; [15] Smit and van Oers [59]

667 ; [16] Michelena et al. [32]; [17] Kurvers et al. [34]; [18] Kurvers et al. [33]; [19] Kurvers et  
668 al. [35]; [20] Jolles et al. [39]; [21] Trompf and Brown [37]; [22] Carter et al. [60];

669 [23] Aplin et al. [61]; [24] Evans et al. [62].

670

671

672 **Table 2. Influence of male aggressiveness and boldness scores, female neophobia score**  
 673 **and tit clutch / brood ‘c/b’ size on the probability of copying tit apparent preference of**  
 674 **nest box artificial features.** Aggressiveness has been log-transformed and all continuous  
 675 traits have been standardized prior analysis. Age estimates are given for yearling individuals  
 676 (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
<b><i>Final model with male aggressiveness score, N=224</i></b>			
Intercept	-0.37 $\pm$ 0.19	-1.95	0.05
Age $\text{\textcircled{M}}$	0.46 $\pm$ 0.33	1.36	0.17
Aggressiveness $\text{\textcircled{M}}$	-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 $\text{\textcircled{M}}$ : Age $\text{\textcircled{M}}$	0.93 $\pm$ 0.36	2.59	<b>0.01</b>
<b><i>Final model with male boldness score, N=142</i></b>			
Intercept	0.05 $\pm$ 0.22	0.22	0.83
Age $\text{\textcircled{M}}$	0.35 $\pm$ 0.41	0.85	0.39
Boldness $\text{\textcircled{M}}$	-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 $\text{\textcircled{M}}$ : Age $\text{\textcircled{M}}$	0.98 $\pm$ 0.45	2.21	<b>0.03</b>
<b><i>Final model with female boldness score, N=173</i></b>			
Intercept	-0.20 $\pm$ 0.20	-1.01	0.31
Age $\text{\textcircled{F}}$	0.54 $\pm$ 0.35	1.54	0.12
Boldness $\text{\textcircled{F}}$	-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 $\text{\textcircled{F}}$ : Age $\text{\textcircled{F}}$	0.71 $\pm$ 0.35	2.03	<b>0.04</b>
<b><i>Final model with female neophobia score, N=173</i></b>			
Intercept	0.00 $\pm$ 0.16	-0.01	0.99
Neophobia $\text{\textcircled{F}}$	-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 $\text{\textcircled{F}}$ : Tit c/b size	-0.47 $\pm$ 0.20	-2.33	<b>0.02</b>

677

## Supplementary Material for

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

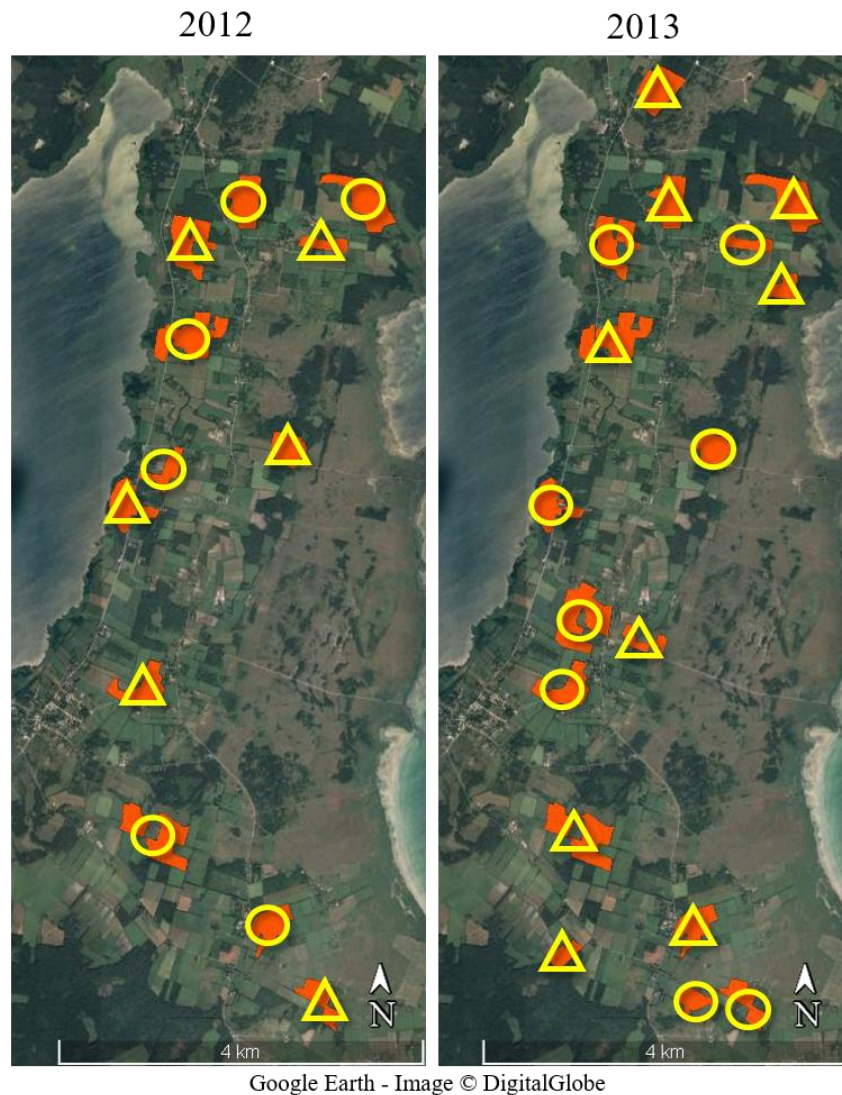
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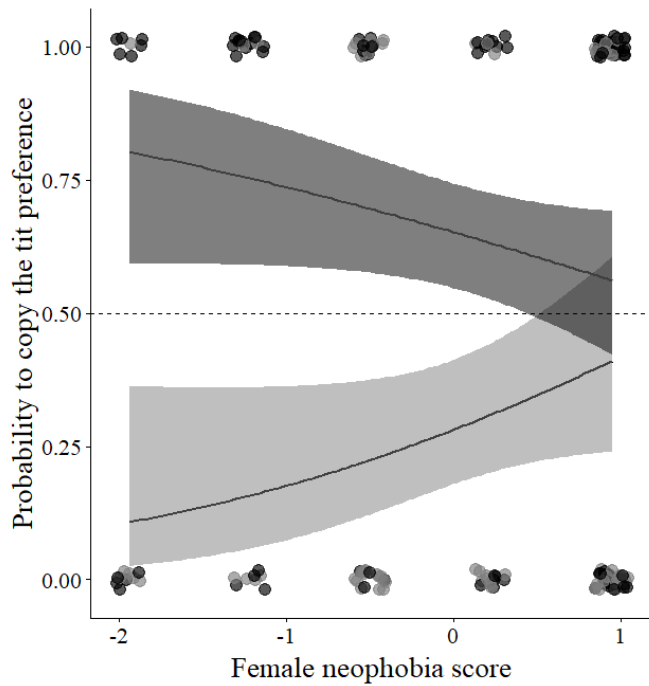
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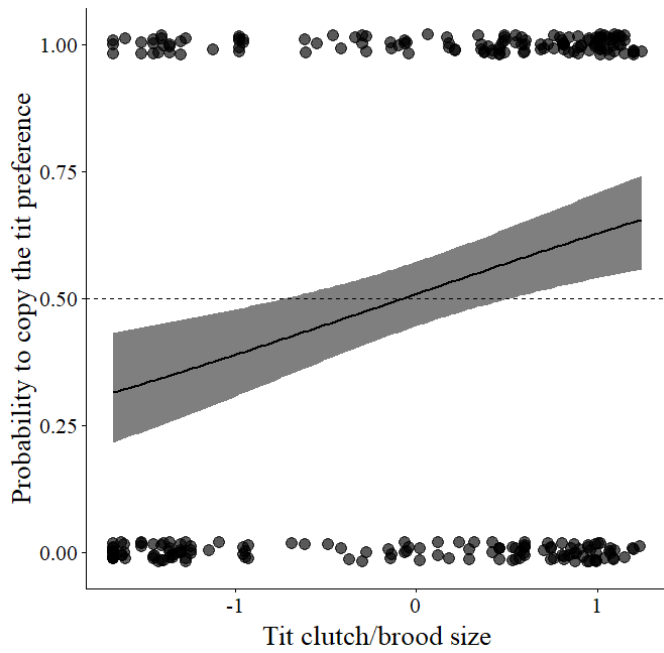


**Figure S1. Symbols associated with nest boxes occupied by tits in 2012 and 2013**

The symbol associated with tits was randomised among experimental forest patches (12 patches in 2012, 17 in 2013), and alternated between 2012 and 2013 in each patch. Switching the symbol associated with tits between years for a given patch allowed us to control for potential across-year experience effects. Indeed, even though we retained only individuals whose symbol choice was naïve (i.e. first choice) in 2013 (see text), we could not exclude a potential influence of individuals' experience with symbols if they were not captured in the first year of the study (2012), e.g. if they failed breeding before capture. Details on the average copying behaviour as well as great tit densities, breeding phenology, reproductive investment and morphology in 2012 and 2013 are provided in Table S2.



**Figure S2. Probability for flycatchers to copy tit apparent preference depending on female neophobia score (5 levels) and tit early reproductive investment** (low clutch/brood size: light grey; high clutch brood size; dark grey). Tit early reproductive investment, considered as a continuous variable in the model, was here categorized for illustration into two equivalent groups (values below or above the median). Data points show actual choices (copy = 1 / reject = 0). The predicted means (lines) and corresponding 95%CI (shaded areas) were derived from the final model for the mean value of the bias in the proportion of empty nest boxes with the symbol associated to tits.



**Figure S3. Probability for flycatchers to copy tit apparent preference depending on tit early reproductive investment** (clutch/brood size, scaled). Data points show the actual choices (copy = 1 / reject = 0). The predicted mean (line) and corresponding 95%CI (shaded area) were derived from the model including only tit clutch/brood size and the bias in the proportion of empty nest boxes with the symbol associated to tits (mean value taken here).

**Table S2. Differences between the two years of the study (2012 and 2013) in flycatcher heterospecific copying behaviour, flycatcher settlement date and tit breeding variables. Estimates are means  $\pm$  SD.**

	<b>2012</b>	<b>2013</b>
% of flycatcher pairs copying tit apparent preference	59.1 %	39.3 %
Flycatcher settlement day	May 10 <sup>th</sup> $\pm$ 4.0 days	May 14 <sup>th</sup> $\pm$ 4.4 days
Great tit laying date	May 2 <sup>nd</sup> $\pm$ 9.1 days	May 13 <sup>th</sup> $\pm$ 5.5 days
Overall great tit density in the forest patch (proportion of boxes where great tits laid eggs, even if they subsequently deserted or failed)	0.44 $\pm$ 0.11	0.27 $\pm$ 0.06
Great tit density in the forest patch at the time of flycatcher settlement	0.35 $\pm$ 0.10	0.24 $\pm$ 0.06
Average great tit clutch size in the forest patch when complete	8.5 $\pm$ 2.2	8.1 $\pm$ 2.0
Great tit clutch/brood size in the forest patch at the time of flycatcher settlement	7.1 $\pm$ 1.5	2.9 $\pm$ 2.8
Great tit adult body mass	18.2 $\pm$ 0.99 g	18.3 $\pm$ 1.03 g
Great tit adult body condition (body mass / tarsus length)	0.80 $\pm$ 0.04 g. mm <sup>-1</sup>	0.80 $\pm$ 0.04 g. mm <sup>-1</sup>



**Table S3. Output of the full models for each behavioural trait and sex.** For age, the estimate is given for yearling individuals (older individuals being the reference). Dev.symbol corresponds to the deviation from 0.5 of the actual proportion of empty boxes matching the tit apparent preference within a patch on the day of choice (see text). P-values below the risk  $\alpha$  of 0.05 are shown in bold.

	<b>Models with male age and behavioural trait</b>				<b>Models with female age and behavioural trait</b>			
	Estimate $\pm$ SE	z-value	p-value		Estimate $\pm$ SE	z-value	p-value	
<i><b>Full model with aggressiveness score</b></i>	<i><b>N=224</b></i>				<i><b>N=271</b></i>			
Intercept	-0.42 $\pm$ 0.20	-2.10	0.04		0.00 $\pm$ 0.17	0.02	0.98	
Age	0.51 $\pm$ 0.33	1.54	0.12		0.06 $\pm$ 0.27	0.24	0.81	
Aggressiveness	-0.88 $\pm$ 0.32	-2.80	<b>0.01</b>		-0.07 $\pm$ 0.16	-0.47	0.64	
Tit clutch/brood (c/b) size	0.90 $\pm$ 0.23	3.84	<b>&lt; 10<sup>-3</sup></b>		0.69 $\pm$ 0.20	3.45	<b>&lt; 10<sup>-3</sup></b>	
Tit density	0.00 $\pm$ 0.21	0.02	0.98		-0.22 $\pm$ 0.19	-1.16	0.25	
Dev.symbol	0.19 $\pm$ 0.17	1.13	0.26		0.41 $\pm$ 0.15	2.67	<b>0.01</b>	
Aggressiveness : Age	1.01 $\pm$ 0.42	2.44	<b>0.01</b>		0.29 $\pm$ 0.29	1.01	0.31	
Aggressiveness : Tit c/b size	0.31 $\pm$ 0.23	1.37	0.17		-0.13 $\pm$ 0.17	-0.74	0.46	
Aggressiveness : Tit density	-0.09 $\pm$ 0.23	-0.37	0.71		-0.24 $\pm$ 0.17	-1.35	0.18	
Age : Tit c/b size	-0.60 $\pm$ 0.40	-1.48	0.14		-0.53 $\pm$ 0.30	-1.77	0.08	
Age : Tit density	0.02 $\pm$ 0.43	0.05	0.96		0.59 $\pm$ 0.31	1.89	0.06	
<i><b>Full model with boldness score</b></i>	<i><b>N=142</b></i>				<i><b>N=173</b></i>			
Intercept	0.09 $\pm$ 0.23	0.37	0.71		-0.22 $\pm$ 0.21	-1.06	0.29	
Age	0.44 $\pm$ 0.43	1.02	0.31		0.59 $\pm$ 0.36	1.65	0.10	
Boldness	-0.62 $\pm$ 0.32	-1.92	0.05		-0.26 $\pm$ 0.21	-1.22	0.22	
Tit c/b size	0.81 $\pm$ 0.30	2.73	<b>0.01</b>		0.78 $\pm$ 0.25	3.10	<b>&lt; 10<sup>-2</sup></b>	
Tit density	-0.12 $\pm$ 0.27	-0.46	0.65		0.06 $\pm$ 0.23	0.25	0.80	
Dev.symbol	0.12 $\pm$ 0.20	0.62	0.53		0.24 $\pm$ 0.18	1.29	0.20	
Boldness : Age	1.04 $\pm$ 0.51	2.06	<b>0.04</b>		0.73 $\pm$ 0.36	2.04	<b>0.04</b>	
Boldness : Tit c/b size	-0.22 $\pm$ 0.37	-0.61	0.55		0.05 $\pm$ 0.19	0.24	0.81	
Boldness : Tit density	0.33 $\pm$ 0.31	1.06	0.29		-0.04 $\pm$ 0.19	-0.21	0.84	
Age : Tit c/b size	-0.28 $\pm$ 0.51	-0.55	0.58		-0.40 $\pm$ 0.39	-1.04	0.30	
Age : Tit density	0.64 $\pm$ 0.64	1.01	0.31		0.23 $\pm$ 0.39	0.58	0.56	
<i><b>Full model with neophobia score</b></i>	<i><b>N=142</b></i>				<i><b>N=173</b></i>			
Intercept	-0.11 $\pm$ 0.24	-0.46	0.65		-0.19 $\pm$ 0.21	-0.91	0.36	
Age	0.34 $\pm$ 0.45	0.76	0.45		0.52 $\pm$ 0.36	1.45	0.15	
Neophobia	0.34 $\pm$ 0.25	1.34	0.18		-0.03 $\pm$ 0.21	-0.16	0.88	
Tit c/b size	1.04 $\pm$ 0.32	3.21	<b>&lt; 10<sup>-2</sup></b>		0.86 $\pm$ 0.26	3.28	<b>&lt; 10<sup>-2</sup></b>	
Tit density	-0.09 $\pm$ 0.26	-0.34	0.74		-0.04 $\pm$ 0.24	-0.15	0.88	
Dev.symbol	0.12 $\pm$ 0.20	0.58	0.56		0.22 $\pm$ 0.18	1.19	0.23	
Neophobia : Age	-0.76 $\pm$ 0.48	-1.57	0.12		0.17 $\pm$ 0.38	0.45	0.66	
Neophobia : Tit c/b size	-0.28 $\pm$ 0.28	-1.01	0.31		-0.55 $\pm$ 0.23	-2.39	<b>0.02</b>	
Neophobia : Tit density	0.03 $\pm$ 0.24	0.12	0.91		0.33 $\pm$ 0.22	1.49	0.14	
Age : Tit c/b size	-0.82 $\pm$ 0.60	-1.37	0.17		-0.37 $\pm$ 0.39	-0.95	0.34	
Age : Tit density	0.55 $\pm$ 0.62	0.89	0.37		0.27 $\pm$ 0.41	0.68	0.50	

**Table S4. Outputs of the full and final behaviour-specific models with both male and female behavioural trait and age combined.** For age, the estimates are given for yearling individuals (older individuals being the reference). Dev.symbol corresponds to the deviation from 0.5 of the actual proportion of empty boxes matching the tit apparent preference within a patch on the day of choice (see text). P-values below the risk  $\alpha$  of 0.05 are shown in bold. We only tested interactions that were significant in the sex-specific models.

	Full model output			Final model output		
	Estimate $\pm$ SE	z-value	p-value	Estimate $\pm$ SE	z-value	p-value
<i>Model with female and male aggressiveness scores, N=182</i>						
Intercept	-0.42 $\pm$ 0.28	-1.53	0.13	-0.41 $\pm$ 0.22	-1.85	0.06
Age <sub>♀</sub>	-0.11 $\pm$ 0.36	-0.30	0.76			
Aggressiveness <sub>♀</sub>	-0.14 $\pm$ 0.22	-0.61	0.54			
Age <sub>♂</sub>	0.70 $\pm$ 0.40	1.74	0.08	0.65 $\pm$ 0.38	1.69	0.09
Aggressiveness <sub>♂</sub>	-1.00 $\pm$ 0.37	-2.69	<b>0.01</b>	-0.99 $\pm$ 0.35	-2.83	<b>&lt; 10<sup>-2</sup></b>
Tit clutch / brood (c/b) size	0.65 $\pm$ 0.22	3.00	<b>&lt; 10<sup>-2</sup></b>	0.66 $\pm$ 0.18	3.78	<b>&lt; 10<sup>-3</sup></b>
Tit density	0.04 $\pm$ 0.23	0.18	0.86			
Dev.symbol	0.49 $\pm$ 0.26	1.88	0.06	0.46 $\pm$ 0.22	2.13	<b>0.03</b>
Aggressiveness <sub>♀</sub> : Aggressiveness <sub>♂</sub>	0.15 $\pm$ 0.21	0.72	0.47			
Aggressiveness <sub>♂</sub> : Age <sub>♂</sub>	0.89 $\pm$ 0.47	1.89	0.06	0.94 $\pm$ 0.42	2.22	<b>0.03</b>
<i>Model with female and male boldness scores, N=116</i>						
Intercept	-0.08 $\pm$ 0.32	-0.24	0.81	-0.20 $\pm$ 0.28	-0.70	0.48
Age <sub>♀</sub>	1.16 $\pm$ 0.57	2.03	<b>0.04</b>	1.15 $\pm$ 0.56	2.07	<b>0.04</b>
Boldness <sub>♀</sub>	0.09 $\pm$ 0.35	0.27	0.79	0.10 $\pm$ 0.35	0.30	0.77
Age <sub>♂</sub>	-0.45 $\pm$ 0.59	-0.77	0.44	-0.28 $\pm$ 0.55	-0.51	0.61
Boldness <sub>♂</sub>	-0.89 $\pm$ 0.47	-1.87	0.06	-0.67 $\pm$ 0.34	-1.94	0.05
Tit c/b size	1.02 $\pm$ 0.30	3.41	<b>&lt; 10<sup>-3</sup></b>	0.88 $\pm$ 0.25	3.59	<b>&lt; 10<sup>-3</sup></b>
Tit density	-0.19 $\pm$ 0.30	-0.64	0.52			
Dev.symbol	0.36 $\pm$ 0.26	1.36	0.17			
Boldness <sub>♀</sub> : Boldness <sub>♂</sub>	-0.16 $\pm$ 0.22	-0.72	0.47			
Boldness <sub>♀</sub> : Age <sub>♀</sub>	1.24 $\pm$ 0.53	2.34	<b>0.02</b>	1.26 $\pm$ 0.56	2.24	<b>0.03</b>
Boldness <sub>♂</sub> : Age <sub>♂</sub>	1.50 $\pm$ 0.73	2.05	<b>0.04</b>	1.28 $\pm$ 0.63	2.02	<b>0.04</b>
<i>Model with female and male neophobia scores, N=116</i>						
Intercept	-0.33 $\pm$ 0.30	-1.11	0.27	0.01 $\pm$ 0.21	0.05	0.96
Age <sub>♀</sub>	0.86 $\pm$ 0.48	1.77	0.08			
Neophobia <sub>♀</sub>	0.13 $\pm$ 0.27	0.50	0.62	0.13 $\pm$ 0.23	0.56	0.57
Age <sub>♂</sub>	-0.04 $\pm$ 0.54	-0.07	0.94			
Neophobia <sub>♂</sub>	0.09 $\pm$ 0.25	0.35	0.73			
Tit c/b size	0.94 $\pm$ 0.30	3.14	<b>&lt; 10<sup>-2</sup></b>	0.88 $\pm$ 0.24	3.67	<b>&lt; 10<sup>-3</sup></b>
Tit density	0.00 $\pm$ 0.26	0.00	1.00			
Dev.symbol	0.31 $\pm$ 0.25	1.22	0.22			
Neophobia <sub>♀</sub> : Neophobia <sub>♂</sub>	0.18 $\pm$ 0.24	0.75	0.45			
Neophobia <sub>♀</sub> : Tit c/b size	-0.58 $\pm$ 0.32	-1.83	0.07	-0.63 $\pm$ 0.31	-2.07	<b>0.04</b>