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

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

1. Introduction

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

Thus far, 24 published studies (to our knowledge) have investigated the links between social information use and personality traits, mostly in the context of foraging decisions (table 1; see the electronic supplementary material, table S1 for full details). Among these studies, the investigation of the exploration/neophobia axis [8] was predominant (19 over 24 studies, i.e. 79%). A higher neophobia level was frequently associated with higher social information use (in 7 relationships over 11; table 1). Conversely, no overall pattern was found for the links between social information use and other personality traits, either because most relationships were non-significant (for exploration and boldness) or very few studies (or even none) investigated these links (for activity, sociability and in particular aggressiveness; table 1, electronic supplementary material, table S1). Furthermore, testing the causality of links between personality traits and social information use requires experimentally manipulating information sources. Yet, such manipulations have only been conducted in captivity thus far. Therefore, the extent to which different personality traits, but also more flexible behavioural traits in general, may favour or constrain the use of social information for decision-making in the wild remains poorly understood.

Social information use for breeding habitat selection and dispersal decisions is well documented (e.g. [5,33,34]). In parallel, dispersal syndromes involving behavioural traits have been well studied (e.g. [35,36]). However, to our knowledge, no study has directly investigated the link between behavioural traits and social information use for breeding site choice (electronic supplementary material, table S1). However, prospecting to gather social information on potential breeding sites can be costly in terms of time, energy and increased agonistic interactions with competitors [37], and only individuals displaying specific behaviours may be able to face these costs. For example, more aggressive, bold and/or explorative individuals may have access to more and/or larger-scale social information sources. Social information use itself may also increase intra- and interspecific competition when individuals spatially aggregate because of con- or heterospecific attraction or because they use the same information [6,33]. Therefore, the realized breeding site choices may notably depend on aggressiveness allowing individuals to acquire and defend the chosen site/territory against competitors. Assessing to what extent behavioural traits shape social information use for breeding site choice is needed to understand how selective pressures act on behaviour over different decision-making contexts.

Here, we tested whether difference in the use of an experimentally manipulated source of social information for nest site selection was related to three main behavioural traits (aggressiveness, boldness and neophobia), previously shown to be partly repeatable [38], in a natural population of a small passerine bird, the collared flycatcher *Ficedula albicollis*. Collared and pied flycatchers *Ficedula hypoleuca* (a sister species) have been repeatedly shown to use social information from con- and heterospecific (titmice) competitors when choosing a nest site [5,34,39–43]. However, this social information use shows high between-individual variability, only partly explained by sex [5], age [44] or dispersal status [39], and depends on years [45] and environmental conditions (e.g. clutch size [44] or titmice density [46]). We tested here whether differences in the three behavioural traits investigated could explain part of the observed variability in social information use. Using an experimental design already successfully implemented in our study species, we created an apparent local preference of dominant tutors (here tits) for a

Table 1. Summary of the results of studies investigating relationships between personality traits and social information use: for each personality trait, number of studies that found a positive (+), negative (−) or non-significant (0) relationship. (Full details on each study and measured traits are given in the electronic supplementary material, table S1. Note that neophobia and exploration were often referred to as 'boldness' in articles, but we follow here the definitions from [8] and refer to boldness as the reaction in a risky situation (presence of potential predators, including humans).)

definitions	no. and signs of the links with social information use			
	−	0	+	references
activity: reaction in a known environment	0	1	1	[9]
aggressiveness: agonistic reaction towards others	0	0	0	
boldness: reaction in a risky situation	2	5	1	[10–14]
exploration: reaction in a novel environment	3	4	2	[15–23]
neophobia: reaction towards a novel object	2	2	7	[10,13,23–30]
sociability: non-agonistic reaction towards others	1	1	2	[22,28,31,32]

specific nest-box feature observable from a distance (geometric symbols) [34,47]. We then recorded whether flycatchers copied or rejected this preference by settling in boxes displaying the same feature. After settlement, we measured levels of aggressiveness, boldness and neophobia of the experimental birds to test the link between these behavioural traits and the probability of copying tit apparent preference. Owing to potential risks of collecting information at the vicinity of tit territories, we expected aggressive individuals to be more likely to copy tutors' preference than less aggressive ones. Furthermore, shyness (lack of boldness) and/or neophobia could restrain access to other conspecific or heterospecific information sources besides tit apparent preference (e.g. if they affect the gathering of information available at a large scale, for neophobia [5], or risky to acquire, for boldness [33]), and thus, shyer and/or more neophobic individuals could be expected to be more likely to copy tutors' preference than less neophobic and/or bolder ones.

2. Material and methods

(a) Species and study site

The experiment was conducted in spring 2012 and 2013 in a wild breeding population of collared flycatchers on the island of Gotland (Baltic Sea, Sweden). Collared flycatchers are sexually dimorphic migratory hole-nesting passerine birds that readily breed in artificial nest-boxes provided in the forest patches of the study area. Breeding flycatchers were captured in boxes (during incubation for females and chick rearing for males) as part of the long-term monitoring of the population. Caught individuals were measured and aged based on plumage criteria (yearling versus older individuals). In this population, collared flycatchers compete for nest-boxes with great tits *Parus major* and blue tits *Cyanistes caeruleus*

[48], which are resident passerine species, are competitively dominant over flycatchers and typically start laying on average two weeks before flycatchers' arrival (but see the electronic supplementary material, table S2 and [45]).

(b) Heterospecific preference copying: experimental design

In 12 (in 2012) and 17 (in 2013) experimental forest patches (2048 nest-boxes in total over the 2 years), we created an apparent preference of tits for a specific nest-box feature to measure flycatchers' subsequent copying behaviour by attaching around the entrance of boxes one of two geometric symbols (white plastic shapes; either a triangle or a circle) depending on the species occupying the box [45]. Before flycatchers' arrival (i.e. in the first two weeks of April), we attached on all boxes occupied by great and blue tits (and the few coal tits *Periparus ater*) in a given forest patch the same symbol (shape alternated between patches; see the electronic supplementary material, figure S1 for more details). At the same time, we randomly attached a triangle on half of the remaining (empty) boxes, i.e. boxes available for newcomers' settlement, and a circle on the other half. We attached no symbol on the few boxes occupied by other species (nuthatches *Sitta europaea*, sparrows *Passer domesticus* and *Passer montanus*, and wrynecks *Jynx torquilla*; 25 boxes in total over the 2 years). Therefore, when flycatchers arrived from migration (late April to mid-May), they had the choice between copying tit preference by settling in a box with the same symbol as on tit boxes and rejecting it by settling in a box with the opposite symbol. When a flycatcher pair had settled in a box, as shown by the presence of new nest material in the box, we removed the symbol on this box. This avoided providing conspecific information via the symbol chosen to later arriving flycatchers. We checked empty boxes every other day to detect newly started nest building and removed (for new flycatcher nests) or changed if needed (for new tit nests) the symbol accordingly. At the same time, we adjusted the number of triangles and circles on empty boxes within a forest patch to keep an equal proportion of available boxes displaying each symbol and thus an equal probability for newcomers to choose a symbol at random. Because this equal proportion of both symbols could not always be met (e.g. when an odd number of empty boxes remained in a patch), we controlled for the deviation from random (0.5) of the proportion of empty boxes matching the tit apparent preference within a plot on the day of choice for each flycatcher pair (see [45] for more details). Because we can assume that flycatchers naive to the experimental design have no previous experience with geometric symbols, this design minimizes genetic and ecological effects on nest site choice and is a powerful method to reveal factors affecting individuals' choices [34].

(c) Measuring behavioural traits

The three behavioural traits of interest here, namely aggressiveness, boldness and neophobia, were measured as described in a former study on the same population (see [38] for detailed methods). In this former study based on a larger sample [38], all three traits were found to be weakly repeatable between years ($R = 0.2$, 0.1 and 0.4 for aggressiveness, boldness and neophobia, respectively) and weakly phenotypically correlated (−0.2 for aggressiveness neophobia and −0.3 for boldness neophobia), but they did not associate in behavioural syndromes (i.e. no between-individual covariance between them [38]). In the present study, we refer to these traits as behavioural rather than personality traits, because we could not separate the effect of the repeatable versus flexible part of the traits on the use of social information; indeed, the copying behaviour was measured only once (i.e. in naive birds).

We measured aggressiveness through the agonistic response of a focal pair to a simulated intrusion by competitors on the nest-box during nest building stage, i.e. when the risk of losing a nest site is highest (as in [38]). We used both conspecific and heterospecific (great tit) decoys (in successive tests) because flycatchers respond aggressively to both species [46,49]. A total of two to four tests were conducted for each focal pair (one or two tests per stimuli species, depending on field constraints), with one test maximum per day and 2 days maximum in a row to avoid habituation. The decoy species was randomized for the first test and alternated between subsequent tests. At the start of a test, an observer attached on the box decoys of either a flycatcher pair or a male great tit, randomly chosen among 10 different sets for each species, as well as a loudspeaker broadcasting songs of the same species as the decoy(s), randomly chosen among five different song tracks per species. The observer then hid under a camouflage net approximately 8–10 m away from the box and recorded all behaviours performed by each member of the focal pair during 15 min on average (mean 15.12 min ± 0.96 s.d.): movements around—and distance from—the box, flights and attacks towards a decoy or live birds attracted by the stimulus. To account for differences in the latency to respond between individuals, each behavioural variable recorded was converted into frequency per minute using the time interval between the first observation of the individual during the test and the end of the test. We then estimated an aggressiveness score for each individual and for each test as the sum of the frequencies of (i) movements within 2 m from the box, (ii) attacks or stationary flights towards a decoy and (iii) chases towards live intruders (similarly to [38]). We excluded from the datasets individuals that were observed less than 5 min. In total, we used 1168 behavioural responses of both sexes, obtained during 790 aggressiveness tests on 224 males and 271 females and 313 reproductive events over the 2 years of the experiment. The final individual aggressiveness score was calculated as the average of the scores measured for each individual within one season.

We measured boldness through the reaction to the presence of a human observer near the box and neophobia through the reaction to the presence of a novel object attached on the box (i.e. in a familiar environment) (as in [38]). We conducted one combined boldness/neophobia test per breeding pair per year when chicks were 5 or 6 days old. The test consisted of two consecutive periods lasting 1 h each, during which the provisioning behaviour of both parents was video-recorded from a distance (6–8 m). In the first period, an observer settled a recorder and opened the box to check chick satiety before leaving the area. In the second period, the observer came back to the box, checked chick satiety again, attached a novel object (here a coloured figurine approximately 7 cm high) near the entrance of the box and left again for 1 h. Chick satiety was checked in order to avoid performing behavioural tests if chicks' condition was too poor. We estimated a boldness score for each parent based on the latency to enter the box after the observer's departure in the first period of the test, i.e. without the novel object. To obtain meaningful boldness scores (i.e. increasing boldness for decreasing latency), we subtracted this latency from the maximum latency observed in our dataset (as in [38]). We estimated a neophobia score for each parent based on the latency to enter the box after the departure of the observer in the second period of the test, i.e. in the presence of the novel object. Among the 318 individuals that entered the box in the first period, 38% did not enter in the second period and thus had no latency available. To take into account those highly neophobic individuals, we discretized neophobia as a 5-level score, with the first four levels corresponding to latency quartiles and the last level assigned to these non-returning individuals (as in [38]). Results, however, remained quantitatively unchanged (not detailed here) when considering neophobia as a continuous latency instead of a score by attributing a maximum latency to non-returning individuals (here 4000 s, the maximum observed latency plus 1 min).

(d) Statistical analyses

We analysed the probability for flycatchers to copy the apparent preference of tits (binary response variable: copy versus reject) in the 2 years of the experiment (2012 and 2013). In the second year, we retained only individuals naive to the symbol experiment, i.e. which had not been caught as breeders in the first year. The overall lower number of males in the sample and differences in sample sizes between models were mostly due to early breeding failures (before the boldness/neophobia test and/or male capture). Because aggressiveness, boldness and neophobia are slightly phenotypically correlated within individuals [38], we fitted separate models for each trait. Furthermore, because nest site choice is a joint decision by both pair members, the most appropriate model to estimate the effect of individual behavioural traits on the joint copying decision would include both male and female trait estimates simultaneously. However, retaining only nests where both pair members have been captured and aged, are naive to the symbols and have responded to behavioural tests strongly reduced sample size (by up to 33%). Therefore, we first fitted sex-specific models. Second, we fitted models with both male and female estimates of the behavioural trait and age, the same other main effects as above, the two-way interaction between male and female behavioural trait estimates and the interactions that were significant in the sex-specific models. In total, we fitted six sex- and behaviour-specific models (see the electronic supplementary material, table S3 for the full models) and three behaviour-specific models with both male and female trait estimates simultaneously (see the electronic supplementary material, table S4 for the full and final models).

Models included as fixed effects the individual's behavioural trait estimate considered (aggressiveness, boldness or neophobia score), individual's age (yearling versus older), tit density and tit early reproductive investment within the forest patch on the day of flycatcher settlement and the potential bias in the proportion of empty boxes with each symbol in the patch on the same day. These latter variables have indeed been found to influence the probability of copying tit apparent symbol preference in this and other populations [33,40,45,47]. Tit density was estimated as the proportion of boxes occupied by great tits (i.e. with tit nest material) within the forest patch on the day of flycatcher choice. Tit early investment was measured as the average great tit clutch (or possibly brood for the earliest great tit nests) size within the forest patch on the day of flycatcher choice. The bias in the proportion of empty boxes with each symbol was calculated as the proportion of boxes bearing the symbol associated with the tit preference on the day of flycatcher choice minus 0.5. To account for age-specific behavioural effects, we included in the models the two-way interaction between age and the behavioural trait estimate considered. We also included the two-way interactions of age or the behavioural trait estimate with tit density and tit early reproductive investment. This gave a total of five main effects and five two-way interactions for each sex- and behaviour-specific model; the maximum number of fixed effects for the models with both male and female trait estimates was seven main effects and three two-way interactions (see full models output in the electronic supplementary material, tables S3–S4). Prior to analyses, all continuous fixed effects were scaled. Finally, we included forest patch and year as random factors to control for potential spatio-temporal effects on social information use.

We fitted generalized linear mixed-effects models in R [50] with the *glmer* function (*lme4* R package [51]) and 'binomial' family and selected our fixed effects using a stepwise backward selection procedure. Because the stepwise approach can increase the risk of type I error [52,53], we checked that the significant effects retained in the final models were significant in the full models too (see the electronic supplementary material, tables S3–S4 for the full models output). Overall, results remained similar when using a model averaging approach (selection of subset models based on Akaike information criterion (AIC) with ΔAIC < 2 using the '*MuMIn*' R package [54]; results not detailed). The fit of final models was assessed based on receiver operating characteristic (ROC) curves, and areas under the curves, estimated using *pROC* R package [55].

3. Results

The probability for flycatchers to copy tit preference was affected by male aggressiveness score differently between yearlings and older males (interaction aggressiveness by age; table 2). Among older males, less aggressive ones significantly copied tit preference, whereas more aggressive ones rejected it (figure 1a); conversely, there was no relationship between the probability of copying tit preference and aggressiveness in yearling males (figure 1a). Female aggressiveness did not affect the probability of copying tit preference (z-value = −0.47, p-value = 0.64; electronic supplementary material, table S3).

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

Finally, in females, the interaction between the neophobia score and tit clutch/brood size seemed to affect the probability of copying tit preference (n = 176, z-value = −2.33, p-value = 0.020; table 2): for the most neophobic females (neophobia score of 5, i.e. non-returning females in the presence of the novel object), tit clutch/brood size had no effect on copying, while high tit clutch/brood size was associated with higher probability of copying in other females (neophobia category 1–4; electronic supplementary material, figure S2). However, this interaction was not strongly supported in a model averaging approach (relative importance = 0.78) and when the most neophobic females were excluded, no effect of neophobia remained among females with scores 1–4 (z-value = 0.154, p-value = 0.877 for the interaction between female neophobia and tit clutch/brood size; z-value = 0.268, p-value = 0.788 for the simple neophobia effect). This suggests that the effect of neophobia was not strong. Male neophobia did not affect the probability of copying tit preference (z-value = 1.34, p-value = 0.18; electronic supplementary material, table S3).

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

Variances associated with forest patch and year were negligible in all models (not detailed here). Including both male and female behavioural trait estimates simultaneously in
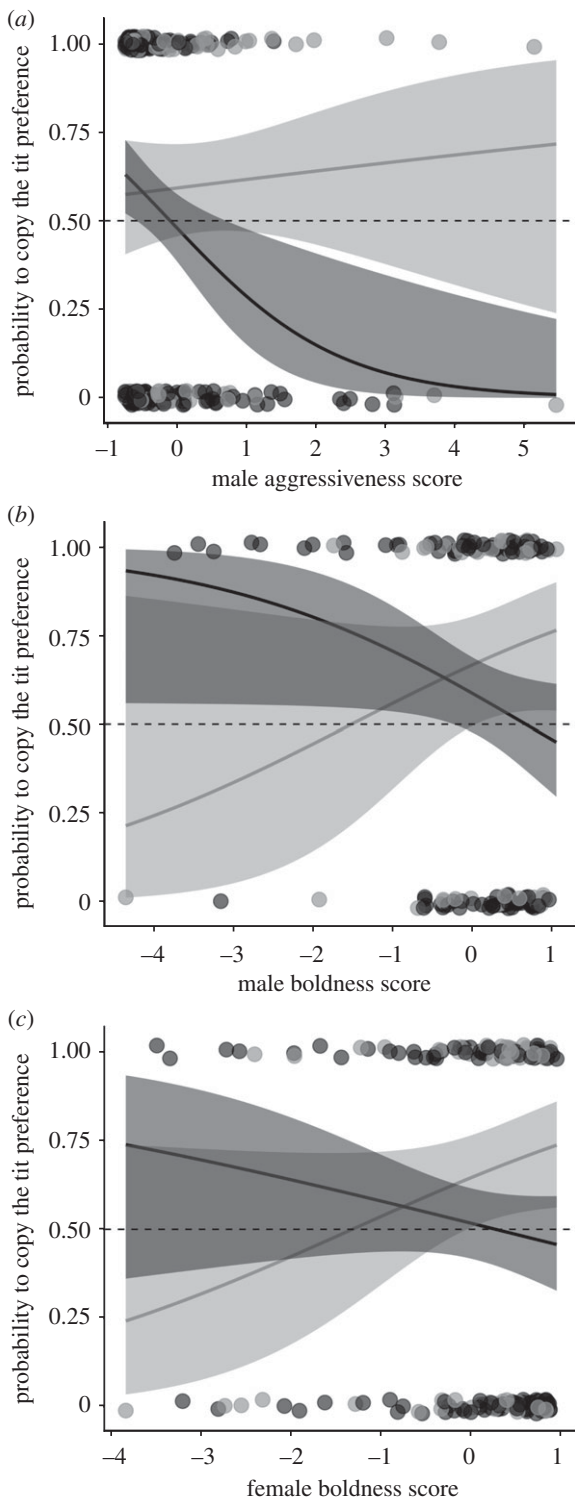
Figure 1. Probability for flycatchers to copy tit apparent preference depending on (*a*) male aggressiveness and age, (*b*) male boldness and age and (*c*) female boldness and age (yearlings: light grey; older: dark grey). Data points show actual choices (copy = 1/reject = 0). The predicted means (lines) and corresponding 95% confidence interval (shaded areas) were derived from the final model for an averaged value of tit clutch/brood size.

models led to similar results (electronic supplementary material, table S4).

4. Discussion

We have experimentally shown in our wild bird population that the use of heterospecific social information for nest

Table 2. Influence of male aggressiveness and boldness scores, female boldness and neophobia scores and tit clutch/brood 'c/b' size on the probability of copying tit apparent preference of nest-box artificial features. (All continuous traits have been scaled prior analysis. Age estimates are given for yearling individuals (older individuals being the reference). *p*-values below the risk α of 0.05 are highlighted in bold)

	estimate ± s.e.	z-value	p-value
final model with male aggressiveness score, n = 224			
intercept	−0.37 ± 0.19	−1.95	0.05
age$_\male$	0.46 ± 0.33	1.36	0.17
aggressiveness$_\male$	−0.83 ± 0.30	−2.79	**0.01**
tit clutch/brood (c/b) size	0.68 ± 0.15	4.48	**$<10^{-5}$**
aggressiveness$_\male$: age$_\male$	0.93 ± 0.36	2.59	**0.01**
final model with male boldness score, n = 142			
intercept	0.05 ± 0.22	0.22	0.83
age$_\male$	0.35 ± 0.41	0.85	0.39
boldness$_\male$	−0.53 ± 0.27	−1.95	0.05
tit c/b size	0.75 ± 0.20	3.77	**$<10^{-3}$**
boldness$_\male$: age$_\male$	0.98 ± 0.45	2.21	**0.03**
final model with female boldness score, n = 173			
intercept	−0.20 ± 0.20	−1.01	0.31
age$_\female$	0.54 ± 0.35	1.54	0.12
boldness$_\female$	−0.25 ± 0.21	−1.23	0.22
tit c/b size	0.64 ± 0.17	3.78	**$<10^{-3}$**
boldness$_\female$: age$_\female$	0.71 ± 0.35	2.03	**0.04**
final model with female neophobia score, n = 176			
intercept	0.00 ± 0.16	−0.01	0.99
neophobia$_\female$	−0.02 ± 0.17	−0.10	0.92
tit c/b size	0.68 ± 0.17	3.92	**$<10^{-4}$**
neophobia$_\female$: tit c/b size	−0.47 ± 0.20	−2.33	**0.02**

site selection depended not only on external factors (here, the early reproductive investment of the heterospecific tutors) but also on individual factors, and more particularly on behavioural traits (here, male aggressiveness and both parents' boldness). Among old males, the probability of copying heterospecific competitors' preference decreased with increasing male aggressiveness. In addition, both parents' boldness score modulated the probability of copying tit apparent preference depending on age: pairs with old and shy individuals, on the one hand, and young and bold individuals, on the other hand, were more likely to copy tit preference compared to other pairs. Finally, we found no strong effect of female or male neophobia, even though increased exploration and decreased neophobia [8] could be expected to favour prospecting and thereby large-scale (social and non-social) information gathering and use. This was in contrast with former studies in the foraging context, which usually found neophobia to promote conspecific attraction or scrounging strategies, i.e. foraging strategies based on social information (e.g. [10,15,24–28], but see [29]). The joint copying behaviour of the pair was therefore affected by different behavioural traits that may, in particular, impact

information access and thus availability but also the ability to cope with the consequences of information use. Flycatcher pairs were besides also more likely to copy apparent preference of tits when average tit clutch/brood size in the patch was high at the time of nest site choice. This is in line with previous results [33,40,41,45,47] and suggests that flycatchers adjusted the use of this heterospecific social information source depending on the quality and/or decisions of tit tutors on top of their own behavioural traits.

(a) Social information use and male aggressiveness

Our results provide clear evidence that aggressiveness, i.e. the agonistic reaction towards competitors, can shape the use of heterospecific social information, with different effects depending on age. Aggressive individuals (especially those high in the dominance hierarchy, e.g. older individuals) could be more likely to acquire social information than less aggressive ones when this involves engaging in agonistic interactions with others, including heterospecifics. Here, however, less aggressive old males copied tit apparent preference and more aggressive ones rejected it, suggesting that all old males could have access to information about tit preference independently from their aggressiveness level.

More aggressive individuals could be expected to be more prone to copy competitors' decisions because they would benefit from competitors' experience [56] while at the same time being able to cope with potentially increased competitive costs. Contrary to this expectation, aggressive males avoided competitors' apparent preference. One possible explanation may be that more aggressive individuals pay a greater cost from competition with tits compared to less aggressive ones, because they engage more in territorial defence. More aggressive males may thus reject tit apparent preference to avoid costs of heterospecific agonistic interactions with dominant competitors. Conversely, less aggressive flycatchers may engage less in agonistic interactions with tits and thus benefit more from using information from tits. Indeed, even though tits are dominant over flycatchers, they tolerate flycatchers' settlement in the vicinity of their nest (B. Doligez 2004–2016, personal observation). In line with this prediction, house crickets *Acheta domesticus* with a high resource holding potential were more likely to win contests, but if losing, they ended the contest sooner [57]. Assessing whether increased aggressiveness increases the risk of heterospecific agonistic interactions and thus potential costs for flycatchers would be needed to confirm this explanation.

(b) Social information use and boldness

Boldness also affected the probability of copying tit preference: especially in males, copying probability was higher for old and shy individuals, as well as young and bold ones, compared to old and bold, and young and shy ones, respectively (figure 1). Former studies reported highly contrasting results regarding the link between boldness and social information use (table 1; electronic supplementary material, table S1). In some studies, shy individuals were more likely to shoal and follow others [11,12,58], as a result of higher attention paid to, and higher probability to rely on, others' decisions. Other studies, however, found that bold individuals paid more attention to others [13], or even no support for boldness to affect the propensity to use three different types of social information [14]. The effect of boldness on social information use may thus be strongly dependent on the context and in particular on social organization and

individual's experience. Here, the link between boldness and social information use depended on age, which probably shapes both competitive ability and experience [59,60] and thereby information access and use. Yearlings may have a restrained access to information, but this effect may be compensated for by boldness. Furthermore, old and bold individuals may have access to additional information sources such that only old and shy individuals may rely on tit apparent preference (that can be obtained from a distance with limited risks) over other sources. Constraints on the access to social information imposed by the behavioural trait considered may shape the link between this trait and information use.

(c) Modulation of social information use or of the response to our behavioural tests?

The three behavioural traits considered here are only weakly repeatable [38] and thus mostly plastic. Therefore, we cannot exclude that flycatchers adjusted their behavioural responses to our behavioural tests depending on whether they copied tit apparent preference for nest-box choice rather than adjusting their copying behaviour depending on their behavioural traits. Yet, our experiment was designed so that choosing a given symbol had no subsequent reproductive consequence for flycatchers, because symbols were randomized in space and thus independent from intrinsic site quality [45]. Post-settlement adjustment of behavioural responses to our tests would require different levels (or expectance) of competition level or predation risk depending on the symbol chosen. For example, for this mechanism to explain the observed patterns in aggressiveness, old males that rejected tit preference would have had to expect, or to be exposed to, a higher competition level by settling in a box displaying the opposite symbol than the one associated with tits and thus increased their aggressiveness response to defend their nest-box. We consider as unlikely such age-specific difference in the competition level owing to the presence of an artificial nest feature that was removed days (for aggressiveness tests) or weeks (for boldness and neophobia tests) before. Many social factors after settlement are likely to affect flycatchers' behaviour, making the alternative explanation of a post-settlement adjustment of behavioural responses unlikely.

(d) Modulation of heterospecific social information use based on tutors' investment

The increase in the probability of copying tit apparent preference with increasing tit clutch/brood size in the patch on the day of choice implies that flycatchers can estimate average tit reproductive investment at the patch scale when they settle and use it for modulating nest site choice according to tit preference. This is in line with former experimental results at a smaller scale, showing that pied flycatchers use tit clutch size as social information (i) to choose between two close-by boxes according to the feature (symbol) associated with tit nest [33,40,47] and also (ii) to adjust breeding investment later on ([61], see also [41] for an experimental test of the patch choice according to tit phenology). Overall, our results provide clear evidence that flycatchers modulated their use of heterospecific social information obtained from tit apparent preference for nest site features based on other information sources (here, tit early reproductive investment). This modulation did not depend on their behavioural traits, but more work is needed to investigate

whether behavioural traits can in general affect the relative use of different social information sources.

Our study extends the importance of behavioural traits in shaping the use of social information reported in previous studies to the context of breeding habitat selection in the wild, using a powerful experimental manipulation of social information. The joint copying behaviour of the pair for nest site selection was probably constrained both by access to social information, explaining the age-dependent link with boldness, and by competitive costs related to the use of social information after gathering it, explaining the link with age-dependent male aggressiveness. More generally, how behavioural traits affect access to social information and resulting decision-making based on this information may be a prevalent issue in explaining among-individual variation in social information use over contexts. Such constraints may have evolutionary consequences through the costs/benefits balance of the use of social information, which may favour functional integration between certain types of personality traits and social information use depending on the relative availability and reliability of these and other information sources. The evolution of such trait associations, however, relies on genetic bases for both social information use and behavioural traits, which was not the case in our system [38,45,62]. Yet, whether the same behavioural traits may be expected to shape social information use in different contexts and/or the use of different types of social information remains to be explored. Theoretical approaches could prove useful in this respect to explore whether features of the decisions to be made (e.g. spatio-temporal scales) may lead to associations between certain behavioural traits and social information use across contexts.

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