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1     **Heterospecific song quality as social information for settlement**  
2             **decisions: an experimental approach in a wild bird**

3

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17

18    **Keywords:** aggressiveness, bird song, breeding site choice, eavesdropping, *Ficedula*  
19    *albicollis*, heterospecific competition, individual quality, *Parus major*, signal, social  
20    information

21 **Abstract**

22 Assessing local habitat quality via social cues provided by con- or heterospecific individuals  
23 sharing the same needs is a widespread strategy of social information use for breeding habitat  
24 selection. However, gathering information about putative competitors may involve agonistic  
25 costs. The use of social cues reflecting local habitat quality acquired from a distance, such as  
26 acoustic cues, could therefore be favoured. Bird songs are conspicuous signals commonly  
27 assumed to reliably reflect producer quality, and thereby local site quality. Birds of different  
28 species have been shown to be attracted to breeding sites by con- and heterospecific songs,  
29 and to use conspecific song features as information on producer (and by extension habitat)  
30 quality. Whether they can do the same with heterospecific song features, possibly differently  
31 depending on individuals' own phenotype and in particular competitive ability, remains  
32 unknown. We used a playback experiment in a wild population of collared flycatchers  
33 (*Ficedula albicollis*), a species known to eavesdrop on dominant great tits' (*Parus major*)  
34 presence and performance. We tested whether flycatchers, whose aggressiveness was  
35 experimentally assessed, preferred to settle near broadcasts of a high quality great tit song (i.e.  
36 song with large repertoire size, long strophes, high song rate), a low quality great tit song or a  
37 chaffinch song (control). Among old females, aggressive ones preferred to settle near  
38 broadcasts of high quality tit song and avoided broadcasts of low quality tit song, while less  
39 aggressive females preferred to settle near broadcasts of low quality tit song. Male personality  
40 or age did not influence settlement decisions. This shows that collared flycatcher females use  
41 great tit song quality features as information for settlement decisions, though differently  
42 depending on their own competitive ability and/or previous experience with great tit songs.  
43 Our study therefore further illustrates the complex condition-dependent use of heterospecific  
44 social information for breeding habitat selection.

45 **Introduction**

46 When habitat quality varies in time and space, choosing where to breed can have crucial  
47 consequences for individual fitness. Hence, strong selective pressures can be expected to  
48 promote behavioural strategies allowing individuals to optimize habitat selection decisions. In  
49 particular, individuals can collect and use information about habitat quality to choose among  
50 alternative breeding sites or patches (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005;  
51 Danchin, Giraldeau, Valone, & Wagner, 2004). Such information can be acquired from the  
52 individual's own interactions with its environment, i.e. its personal experience ('personal  
53 information', e.g. its own reproductive success, Switzer, 1997). Alternatively, information can  
54 be acquired from observing the interactions of other individuals sharing similar needs (either  
55 con- or heterospecific putative competitors) with the environment and the result of these  
56 interactions, either inadvertently or when they intentionally communicate with others ("social  
57 information", Danchin et al. 2004, Dall et al. 2005).

58 When cueing on others, individuals can rely on the mere presence of con- or  
59 heterospecifics (through site occupancy and/or breeding density, e.g. Jaakkonen, Kivelä,  
60 Meier, & Forsman, 2015; Samplonius, Kromhout Van Der Meer, & Both, 2017; Thiebault,  
61 Mullers, Pistorius, & Tremblay, 2014); this information can be easily accessible but does not  
62 directly inform on the fitness consequences of others' decisions. Individuals can also use the  
63 performance of others, i.e. the success obtained after making a decision, an information that  
64 can be more difficult to access but better informs about the fitness consequences of the  
65 decision. In the context of breeding habitat selection, information about others' performance  
66 (when available) can often be used only after a delay, up to a whole breeding season  
67 (Boulinier, Mariette, Doligez, & Danchin, 2008). When breeding synchrony with individuals  
68 sharing similar needs is low, as might be the case for heterospecific competitors in particular,

69 eavesdropping on the reproductive investment of early competitors could inform on habitat  
70 quality for decisions later in the same season (e.g. Forsman & Seppänen, 2011; Loukola,  
71 Seppänen, Krams, Torvinen, & Forsman, 2013; Seppänen, Forsman, Mönkkönen, Krams, &  
72 Salmi, 2011). However, assessing competitors' performance can involve proximity to their  
73 breeding sites and therefore increase the risk of agonistic interactions (e.g. Ahola, Laaksonen,  
74 Eeva, & Lehikoinen, 2007; Forsman et al., 2018; Merilä & Wiggins, 1995; Samplonius &  
75 Both, 2019; Slagsvold, 1975). In this case, balancing the trade-off between information  
76 accuracy and reliability, on the one hand, and information availability and costs associated to  
77 information gathering, on the other hand, may require reducing such costs. This should favour  
78 the use of cues reflecting others' performance obtained to a low cost, such as cues obtained  
79 from a distance.

80         Among such cues, acoustic signals have been shown to be an information source  
81 easily eavesdropped on, even from a long distance (e.g. anti-predatory strategies involving  
82 eavesdropping on conspecific and heterospecific alarm calls; reviewed in Magrath et al.  
83 2015). Experimental studies have clearly shown that calls and songs can, on their own, induce  
84 conspecific (Hahn & Silverman, 2006) and heterospecific attraction (Fletcher, 2008;  
85 Szymkowiak, Thomson, & Kuczyński, 2017) to otherwise empty breeding sites, a property  
86 sometimes used in reintroduction programmes to enhance local settlement of released animals  
87 (e.g. Ward and Schlossberg 2004). Importantly, signals used in sexual communication, which  
88 include acoustic signals, are selected (1) to be conspicuous, allowing emitters to be detected  
89 by the highest possible number of potential partners (in intersexual communication) and/or  
90 competitors (in intrasexual communication), and (2) to reliably reflect individual quality (e.g.  
91 in terms of health, competitive ability, etc.; Andersson, 1994; Catchpole & Slater, 2008).  
92 Female birds have for example been shown to eavesdrop on males singing contests and adjust

93 mate choice and reproductive behaviour accordingly (Mennill, Ratcliffe, & Boag, 2002; Otter  
94 et al., 1999). Therefore, acoustic signals can provide social information on individual quality  
95 (e.g. Bischoff, Tschirren, & Richner, 2009; Buchanan & Catchpole, 2000; Møller, 1991), and  
96 thereby indirectly on habitat / territory quality. Song features reflecting individual quality or  
97 competitive ability have indeed been shown to affect breeding settlement decisions of  
98 conspecifics in migratory passerine birds (e.g. song repetition and frequency variation in  
99 yellow warblers, Kelly & Ward, 2017; song rate in wood warblers, Szymkowiak, Thomson, &  
100 Kuczyński, 2016). Such refined acoustic information use could occur not only within, but also  
101 between species; however this has not been explored yet even though it would have important  
102 implications for our understanding of interactions and information sharing within  
103 communities.

104         Using a playback experiment in a wild population of collared flycatchers *Ficedula*  
105 *albicollis*, we experimentally tested whether individuals use songs from heterospecific  
106 competitors as a source of information for nest site selection and whether they modulate the  
107 use of this cue depending on song features reflecting the singer's quality. Migratory  
108 flycatchers are known to use different heterospecific social information from their main  
109 competitor, the resident great tit *Parus major*, for nest site selection (tit presence: Kivelä et al.  
110 2014; tit density: Forsman et al. 2008; tit early reproductive investment: Seppänen et al. 2011,  
111 Loukola et al. 2013; tit breeding phenology: Samplonius & Both, 2017). Flycatchers and tits  
112 indeed largely share the same niche during breeding in terms of breeding sites, food resources  
113 to nestlings and predators, and tits start breeding only a couple of weeks before flycatchers'  
114 arrival from migration, thus providing flycatchers with valuable information for their own  
115 breeding habitat choice decisions. Flycatchers have been shown to gain fitness benefits from  
116 using these heterospecific information for settlement decisions and invest more in their

117 reproduction when copying great tits' choice (Forsman, Seppänen, & Mönkkönen, 2002;  
118 Forsman, Thomson, & Seppänen, 2007). Prospecting tit nests to gather information on tit  
119 presence or reproductive investment may nevertheless be risky (Ahola et al., 2007; Forsman  
120 et al., 2018; Forsman & Thomson, 2008; Merilä & Wiggins, 1995; Samplonius & Both, 2019;  
121 Slagsvold, 1975). Therefore, flycatchers could be expected to rely also on less costly cues,  
122 such as great tit songs, which can be heard from a distance and whose characteristics  
123 (repertoire size and strophe length) have been shown to correlate with great tit quality  
124 (Lambrechts & Dhondt, 1986; McGregor, Krebs, & Perrins, 1981). The use of heterospecific  
125 song features by flycatchers may nevertheless be expected to be sex-, personality-, and/or age-  
126 dependent, as found for other heterospecific social cues (e.g. Forsman, Seppänen, & Nykänen,  
127 2012; Morinay, Forsman, Germain, Daniel, & Doligez, in revision; Samplonius & Both,  
128 2017).

129         Upon flycatchers' arrival from migration, we broadcasted artificially created great tit  
130 songs of either high quality (large repertoire, long strophes, high song rate) or low quality  
131 (small repertoire, short strophes, lower song rate) and monitored flycatchers' settlement in  
132 experimental zones. If flycatchers are attracted by great tits songs when choosing where to  
133 breed, they should settle preferentially in zones with broadcasted tit songs; in addition, if  
134 flycatchers use information about great tit quality as reflected by song features, they should  
135 settle preferentially in zones with broadcasted high quality tit songs, i.e. presumably  
136 indicating high quality habitat. We also tested whether the choice of a zone with high vs. low  
137 quality tit song depended on flycatchers' age, which may affect previous experience with  
138 great tit songs, and aggressiveness, which may affect the ability to face competitive costs with  
139 great tits. Finally, we tested whether flycatchers adjusted early reproductive investment, as

140 previously found in this population (in response to tit density; Forsman et al. 2008), here  
141 according to the experimental song treatment.

142

143

## 144 **Materials and methods**

### 145 *Animal welfare note*

146 To minimize disturbance during aggressiveness tests, we approached nest boxes as quietly as  
147 possible and hid below a camouflage net. The Ringing Centre from the Museum of Natural  
148 History in Stockholm granted permission for catching and ringing adults (here 77 females and  
149 60 males) with individually numbered aluminium rings (licences nb. 471:M025 to JM and  
150 471:M043 to Cécile Vansteenberghé). We captured male and female adults in the nest, either  
151 directly (females during incubation) or using swinging-door traps (both parents during chick  
152 rearing). We set up traps for 30-60 minutes maximum depending on nestling age (30 min  
153 when nestlings were 5 days old or younger), to avoid nestling starvation if parents did not  
154 resume feeding during the catching period; we checked upon the traps every 5-10 minutes,  
155 and removed them as soon as the adults had been caught. We started catching sessions after  
156 6:00 am to let birds feed and provision nestlings undisturbed for at least two hours after the  
157 night period (sunrise occurs approx. at 4:00 am during spring). We handled adults during 5 to  
158 10 minutes and released them straight after manipulation or (when catching both parents  
159 during nestling feeding) kept them until capturing the partner (up to 40 min maximum). All  
160 manipulations were done in accordance with the Swedish legislation applying at the time.

161

### 162 *Study area and population monitoring*



163           The experiment was conducted in spring 2017, in a patchy population of collared  
164 flycatchers breeding on the island of Gotland (Sweden, Baltic Sea). In this population,  
165 collared flycatchers and dominant great and blue tits (*Cyanistes caeruleus*) largely share the  
166 same ecological niche during breeding: all three are hole-nesting species breeding in tree  
167 cavities and readily accept nest boxes provided in excess in the study area (Doligez, Pärt,  
168 Danchin, Clobert, & Gustafsson, 2004; Gustafsson, 1988); they also partly feed the same food  
169 resources to nestlings (in particular caterpillars) and share predators (Lundberg & Alatalo,  
170 1992). Collared flycatchers start arriving from migration on the breeding grounds late April-  
171 early May, i.e. 2 weeks on average after the beginning of tit breeding season. Over the period  
172 2012-2017, 33.5% of the nest boxes available in the population were occupied by collared  
173 flycatchers, 25.7% by great tits, 9.4% by blue tits, 2.7% by other species (e.g. nuthatches,  
174 sparrows, coal tits) or by tits that abandoned their nest before identification, and 28.7%  
175 remain empty. In all nest boxes occupied by flycatchers, we captured females during  
176 incubation and males during the chick rearing period (for nests reaching this stage). All  
177 captured individuals were identified (or ringed if previously unringed), measured, weighed  
178 and aged based on plumage criteria (yearlings vs. older adults; Svensson 1992). Nest boxes  
179 were then visited regularly throughout the breeding season to record the main breeding  
180 variables for each breeding pair (laying and hatching date, clutch size, number and condition  
181 of nestlings, final fledging success).

182

### 183 *Playback experimental design*

184           In the 13 forest patches chosen for the study on the basis of a sufficiently high number  
185 of nest boxes (> 30, and up to 180), we established experimental zones composed of five

186 neighbouring nest boxes (except for one zone, which had four), with four boxes (three for the  
187 four-box zone) spread around a central nest box (at approximately 20 m distance);  
188 experimental zones were separated from each other by at least 40 m (i.e. each zone was  
189 surrounded by at least one row of non-experimental nest boxes). Each selected forest patch  
190 contained 3 to 9 experimental zones, for a total of 57 experimental zones (19 of each  
191 broadcast treatment; 4 patches with 3 zones, 7 patches with 4 or 5 zones and 2 patches with 8  
192 or 9 zones). We conducted the playback experiment between the 29<sup>th</sup> of April and the 27<sup>th</sup> of  
193 May, i.e. during the whole period of flycatcher settlement. During these 29 days, we  
194 broadcasted at the centre of each experimental zone either (i) a great tit song track with high  
195 quality song features, i.e. mimicking singing activity of high quality individuals (i.e. large  
196 repertoire, long strophes, high song rate, Lambrechts & Dhondt, 1986; McGregor et al., 1981;  
197 Rivera-Gutierrez, Pinxten, & Eens, 2010), (ii) a great tit song track with song features of low  
198 quality individuals (i.e. with a small repertoire size, short strophes, low song rate) or (iii) a  
199 song track from a generalist and widespread forest-dwelling bird species with no previously  
200 shown influence on flycatcher settlement decisions, the common chaffinch, *Fringilla coelebs*,  
201 as a control. Common chaffinches are migrant (on Gotland), are open-cup nesters and are  
202 larger than collared flycatchers just like great tits. Even though chaffinches and flycatchers  
203 partly share the same food resource to nestlings (insect larva), chaffinches are habitat  
204 generalists and their presence should not reflect a particular resource. Furthermore, there is  
205 currently no direct evidence about resource or interference competition, or about interspecific  
206 information use, between chaffinches and flycatchers. Consequently, chaffinches appear a  
207 good control species for the song playback experiment. We ensured that each patch contained  
208 at least one experimental zone of each treatment. The distance between experimental zones  
209 reliably reflected the natural density of great tit breeding pairs in our forest patches (average

210 minimal distance between breeding great tits in our experimental forest patches in the  
211 preceding year, i.e. 2016: 59.8 m  $\pm$  9.3 SD; N=403). Because great tit and chaffinch songs can  
212 be heard from a long distance ( $>$  100 m in our forest patches), a prospecting flycatcher should  
213 thus have been able to simultaneously hear several experimental broadcasts and choose  
214 among treatments.

215         Song tracks were broadcasted from dawn (1 hour before sunrise) for a duration of 17  
216 hours, corresponding to dusk at the beginning of the broadcasting period and up to 1h30  
217 before dusk at the end of the broadcasting period. Along the broadcasting period, the starting  
218 hour of the broadcast was adjusted (15 minutes earlier every 10 days) to match the seasonal  
219 change of dawn hour, but the length of the track remained unchanged. To match the natural  
220 singing activity of great tits, we broadcasted 10 minute-long song periods every 30 minutes  
221 from dawn to 3 hours after dawn, and then every hour till the end of the sequence (see Figure  
222 A1), similarly to Krebs et al. (1978). Tracks were broadcasted at  $\sim$ 85-95dB, i.e. close to the  
223 natural sound amplitude of great tit songs (McGregor and Horn 1992; sound amplitude  
224 checked at 1 m distance with a sound level meter “Dr. Meter MS10”). In each experimental  
225 zone, song track was broadcasted from a camouflaged loudspeaker (Zealot S1) attached 1.5-2  
226 m above ground on a tree next to the central nest box of each experimental zone.

227

### 228 *Playback song structure*

229 To create the broadcasted sound tracks while limiting pseudoreplication risk, we used songs  
230 from 4 different great tits to mimic songs of high quality tits, from 4 others to mimic songs of  
231 low quality tits and from 4 different chaffinches for controls. Great tit songs were recorded in  
232 the same population in 2016, at dawn chorus, with a Sennheiser MKH70 microphone and a

233 Zoom H4N recorder. Chaffinch songs were recorded either on Gotland in 2016 (1 individual)  
234 or on the Swedish mainland (3 individuals) and available on-line (Xeno Canto on-line  
235 database, [www.xeno-canto.org](http://www.xeno-canto.org), accessed in April 2017; recordings ID: XC84011, XC196974,  
236 and XC27602). Each sound track was composed of songs originating from only one  
237 individual to mimic the presence of a single singing individual in each experimental zone, and  
238 in each zone, the song track broadcasted remained unchanged during the whole broadcasting  
239 period, to avoid mixing signals from different individuals in case flycatchers were able to  
240 individually recognize singers. All recordings were in .wav format to ensure sufficient sound  
241 quality and had a sample frequency of 44.1 kHz and a resolution of 16 bit. Using Audacity  
242 software (v. 2.1.0, <http://audacity.sourceforge.net/>), original recordings were high-pass  
243 filtered with a threshold below the song minimum frequency (2 kHz), modified to create the  
244 song bouts (see Figure A1) and amplified. We amplified whole song bouts (see Figure A1)  
245 but kept natural variations in amplitude within bouts, to mimic singing bird movements to a  
246 flycatcher listening from a fixed point.

247

#### 248 *Controlling for neighbouring live great tits*

249 To keep nest boxes in the experimental zones available to flycatchers and avoid songs from  
250 live great tits to strongly interfere with our broadcasted great tit songs, we prevented great tits  
251 (but not blue tits) to settle in our experimental zones from early April by narrowing the  
252 entrance hole of all experimental nest boxes to 28 mm diameter with drilled chipboards  
253 attached around the nest box hole. At the beginning of the broadcasting period, i.e. on the 29<sup>th</sup>  
254 of April, we removed the chipboards to expand again the nest box entrance hole to 32 mm  
255 diameter (recommended size for both great tits and flycatchers, L. Gustafsson pers. comm.).

256 As a consequence, late blue and great tits could also settle in the experimental zones during  
257 the broadcasting period. When this happened before the first flycatcher pair had settled in the  
258 experimental zone and the nest box density was sufficiently low (for 3 of the 57 zones), we  
259 slightly relocated the experimental zone by adding one nest box on the edge of the zone and  
260 excluding the box occupied by the tit pair, in order to provide the same number of available  
261 nest boxes (5) to the first flycatcher pair to settle in all zones. Out of the 57 experimental  
262 zones, 30 (52%) remained free from great tits during the whole playback experiment.

263 The singing performance of great tits in the vicinity of our experimental zones might  
264 locally affect our treatment. Therefore, we controlled for the singing activity of tits within or  
265 in close vicinity of each experimental zone. We counted the number of different songs that  
266 could be heard close-by from the tree where the loudspeaker was placed, during 10 minutes  
267 picked at random before 10:00 am and in between two broadcasted songs. We recorded this  
268 measure of singing activity by alive great tits for each zone during 4 to 7 days a week  
269 depending on the experimental zone and field time constraints, obtaining between 16 and 27  
270 measures per zone, and we averaged it over the whole broadcasting period to obtain a  
271 measure of mean song ‘bias’ in each zone.

272

### 273 *Aggressiveness test*

274 We estimated the aggressiveness level of flycatchers settling in the experimental zones during  
275 nest building or early egg laying stages. We followed the protocol detailed in Morinay et al  
276 (2019). In short, at the beginning of the test, an observer attached (i) clay decoys representing  
277 either a flycatcher pair or a male great tit to the nest box of the focal pair and (ii) a  
278 loudspeaker broadcasting songs of the corresponding species below the nest box. The

279 observer then sat camouflaged 8-10 m away and recorded all the behaviours of both the male  
280 and the female flycatchers for 15 minutes if both individuals were seen at least 5 minutes  
281 during this first period, or up to 25 minutes if at least one of them arrived at the end of the  
282 first 15 min only, to allow describing flycatchers' behaviour for at least 5 minutes. We  
283 conducted one test with flycatcher decoys and one with great tit decoy. However, if one  
284 individual was not seen during either test, we conducted more tests (up to 5), with a day break  
285 between two consecutive tests. To limit pseudoreplication risk, we used 10 sets of flycatcher  
286 decoys, 10 sets of great tit decoys, 5 different song tracks per species, and we randomized the  
287 song track used with a given decoy set. Aggressiveness score was then later estimated as the  
288 number of moves within 2 m from the nest box (between branches or to the box, as well as  
289 attacks on decoys) plus the number of chases performed against live intruders, standardized  
290 per 15 minutes (the repeatability of this score within and between years is around 0.25,  
291 Morinay et al. 2019). We averaged the scores obtained with the conspecific and heterospecific  
292 decoys to obtain a unique individual score. However, when including in the models either of  
293 these scores instead of the mean score led to qualitatively similar results. Over the 99  
294 flycatcher pairs that started building nests in our experimental zones, we obtained  
295 aggressiveness and age data for 77 females and 60 males.

296

### 297 *Statistical analyses*

298 We first tested whether overall flycatcher settlement in experimental zones differed between  
299 song broadcast treatments (high quality great tit song, low quality great tit song, chaffinch  
300 song as a control) by comparing nest box occupancy probability between treatments using a  
301 generalized linear mixed model with flycatcher occupancy (binary variable) as the response

302 variable and broadcast treatment (3 levels: high quality tit song, low quality tit song, and  
303 chaffinch song) as the sole fixed effect. We included the forest patch and the zone (nested in  
304 the forest patch) as random terms, to account for the non-independence of the experimental  
305 nest boxes within zones and forest patches.

306         Second, among settled pairs, we tested whether the probability for flycatchers to settle  
307 in a given song broadcast treatment depended on individual and environmental factors using  
308 generalized linear multinomial mixed models. Even though nest box choice is likely to be a  
309 joint decision by both pair members, we fitted separate models for males and females,  
310 because testing the effects of individual factors for both pair members in a single model  
311 would lead to a reduced sample size (more females are captured than males, N=57 nest box  
312 choices for which both the male and female age and aggressiveness were obtained). We fitted  
313 models with the broadcast treatment of the zone chosen by each flycatcher (3 levels) as the  
314 response variable and included as fixed effects (i) individual's age and aggressiveness score,  
315 (ii) settlement date, (iii) the presence of previously settled great tits and flycatchers (2 separate  
316 binary variables) as shown by the presence of nest material in a box in the experimental zone  
317 on the day of choice and (iv) mean song bias. We included age and settlement date because  
318 late arriving birds and yearlings have previously been found to rely more on social  
319 information from great tits compared to early arriving and older ones (Seppänen and Forsman  
320 2007). We included the presence of settled great tits and flycatchers prior to settlement of the  
321 focal bird, as well as mean song bias, to control for social attraction. Given that the  
322 aggressiveness effect on the use of heterospecific social information was previously found to  
323 be age-specific in this system (Morinay et al., in revision), we tested in a second step the two-  
324 way interaction between aggressiveness and age by adding it to the model with only main  
325 effects. We included the forest patch as a random effect, but not the experimental zone

326 because there were many zones where only one pair settled (17 over the 51 zones where  
327 flycatchers settled in total) and overall few replicates of each experimental treatment per  
328 forest patch (1.5 zone of each treatment per patch on average, with 26 zones out of 57 being  
329 the only replicate of a treatment in a given patch). The experimental zone was therefore  
330 strongly confounded with treatment choice. Consequently, including the zone as a random  
331 effect led to convergence issues and artificially high associated variances.

332 Finally, we tested whether flycatchers adjusted early reproductive investment,  
333 measured here by (i) laying date, (ii) the delay between settlement and laying, and (iii) clutch  
334 size, according to the broadcast treatment (3 levels) using (generalized) linear mixed effects  
335 models. Besides the treatment, we included the same fixed and random effects as for the  
336 preceding models, except for settlement date, which was included only in the model for clutch  
337 size.

338

### 339 *Linear model implementation*

340 We implemented Bayesian linear models with the *MCMCglmm* function  
341 (“MCMCglmm” R package, Hadfield, 2010). We scaled all continuous explanatory variables  
342 to allow comparison between factors. We did not select models for fixed effects (Mundry &  
343 Nunn, 2009). We implemented the model fitting the binary occupancy of each experimental  
344 nest box with the ‘threshold family’ and the residual variance fixed to 1 (11 x 10<sup>4</sup> iterations,  
345 burn-in = 10<sup>4</sup>, thinning-interval = 50). We implemented models fitting the treatment chosen  
346 using the ‘categorical’ family (15 x 10<sup>5</sup> iterations, burn-in = 10<sup>4</sup>, thinning-interval = 700; and  
347 when including the interaction term aggressiveness x age: 35 x 10<sup>5</sup> iterations, burn-in = 3 x  
348 10<sup>4</sup>, thinning-interval = 1,700); we fixed the variance-covariance residual matrix to 2/3 for the  
349 diagonal terms (variance) and 1/3 for all the off-diagonal terms (covariance; Hadfield 2016).



350 We implemented the models for laying date with the Gaussian family ( $12 \times 10^4$  iterations,  
351 burn-in = 6,000, thinning interval = 50) and for the delay in laying and clutch size with the  
352 Poisson family ( $15 \times 10^5$  iterations, burn-in =  $2 \times 10^4$ , thinning interval = 700). For all models,  
353 we used normally distributed priors with a mean of 0 and a large variance ( $10^8$ ) for fixed  
354 effects, expanded priors (with  $V = 1$ ,  $\nu = 1000$ ,  $\alpha \cdot \mu = 0$ ,  $\alpha \cdot V = 1$ ) for the random  
355 variance associated to the forest patch, and inverse-Gamma priors for the residual (when not  
356 fixed) and random variances. Model convergence was assessed visually and by comparing  
357 three chains per model using the *gelman.diag* and *gelman.plot* functions (Gelman & Rubin  
358 approach, Plummer et al. 2006). Autocorrelation levels were always below 0.1 and effective  
359 sample sizes above 1,500 per chain.

360

## 361 **Results**

362

### 363 *Occupancy pattern according to broadcast treatment*

364 The total number of settled flycatcher pairs was 33 in the high quality great tit song treatment,  
365 27 in the low quality tit song treatment and 39 in the chaffinch song (control) treatment. The  
366 probability for a nest box to be occupied by collared flycatchers did not differ between  
367 treatments (posterior means and 95% Credible Interval (CI) considering the control treatment  
368 as the reference: low quality tit treatment: -0.36 [-0.73; 0.12]; high quality tit treatment: -0.18  
369 [-0.56; 0.23]; zone and forest patch variances did not differ from zero;  $N=284$ ).

370

### 371 *Individual and environmental effects on the choice of a broadcast treatment*

372 The probability to choose an experimental zone of a given broadcast treatment  
373 depended on female aggressiveness score (estimate [95% CI]: 0.81 [0.07; 1.61] for high  
374 quality vs. control, from the model without interaction; N=77), but this effect differed  
375 between yearling and older females (interaction aggressiveness score by age, Table 1, Figure  
376 1). Among older females, less aggressive ones were more likely to settle in zones of the low  
377 quality great tit song treatment (relation between aggressiveness level and probability to settle  
378 in the low quality song vs. control treatment: estimate [95% CI]: -3.47 [-6.45; -0.96]; Table 1,  
379 Figure 1b), while more aggressive ones were more likely to settle in zones of the high quality  
380 great tit song treatment (relation between aggressiveness level and probability to settle in the  
381 high quality song vs. control treatment: estimate [95% CI]: 1.33 [0.14; 2.63]; Table 1, Figure  
382 1a). The probability to choose an experimental zone of a given broadcast treatment also  
383 depended on the presence of competitors previously settled in the zone: flycatchers were more  
384 likely to settle in a great tit song treatment zone (either high or low quality compared to  
385 control) when other great tits had previously settled in the same zone (Table 1); they were  
386 also more likely to settle in a control zone than in a high quality great tit song zone when  
387 other flycatchers had previously settled in the experimental zone (Table 1). Neither settlement  
388 date, song bias, male age nor male aggressiveness affected the probability to settle in a zone  
389 of a given broadcast treatment (Table 1, N=60 for the model with male factors).

390

### 391 *Early reproductive investment according to broadcast treatment*

392 We found no difference between broadcast treatments in flycatcher laying date, delay between  
393 settlement and laying, and clutch size (all 95% CI encompassed zero, N=77 or 76 for clutch  
394 size for models with female factors, and N=60 for models with male factors; Table A1). As

395 expected, yearling females were found to lay eggs later in the season than older females  
396 (Table A1). Aggressiveness scores and male age had no effect on early reproductive  
397 investment (Table A1).

398

## 399 **Discussion**

400 Using a playback experimental approach, we tested whether flycatchers use complex quality  
401 information contained in great tit songs as a source of heterospecific social information for  
402 breeding site selection. Our results confirmed the direct use of this cue by old flycatcher  
403 females for small-scale settlement decisions because we used broadcasted songs alone, i.e.  
404 decoupled from the actual presence of great tit pairs. Flycatcher choice of experimental zones  
405 depended on female aggressiveness level in interaction with female age: among old females,  
406 more aggressive ones settled preferentially in zones with high quality great tit songs, while  
407 less aggressive ones preferred zones with low quality tit songs. In addition to song presence  
408 itself, our results thus provide evidence that heterospecific song features related to emitter's  
409 quality can be used for important decision making. This source of heterospecific social  
410 information did however not affect flycatchers' early reproductive investment (laying date,  
411 clutch size, delay between settlement and laying), suggesting that different information  
412 sources are used for different breeding decisions (Doligez et al., 2008) and calling for a finer  
413 understanding of the fitness benefits of using each information source.

414

415 *Why and when using great tit song features for settlement decisions?*

416 Migratory flycatchers may not easily gather updated personal information about breeding

417 habitat quality when returning from migration and have therefore been shown to rely on  
418 resident, already settled, great tit presence and early reproductive investment for their own  
419 settlement decisions under strong time constraints (e.g. Forsman & Seppänen, 2011; Kivelä et  
420 al., 2014). They have been found to benefit from settling near great tit nests in terms of  
421 increased offspring number and condition (Forsman, Seppänen, & Mönkkönen, 2002;  
422 Forsman, Thomson, & Seppänen, 2007); old flycatcher females also adjust reproductive  
423 investment according to neighbouring tit clutch size, producing more and heavier eggs near  
424 tits with large clutches (Forsman et al., 2012). Such reproductive benefits can be achieved via  
425 the direct assessment of local habitat quality upon settlement, if a high quality great tit pair  
426 secures a high quality territory, or via indirect effects through enhanced access to food  
427 resources during nestling provisioning and/or social benefits such as protection against nest  
428 predators (Forsman et al., 2002). This shows that heterospecific cues from great tits can  
429 inform flycatchers about optimal breeding sites and thereby allow them to secure future  
430 breeding success. Great tit songs may allow flycatchers to easily assess great tit density, but  
431 also quality, from a distance, thus with limited costs, while direct information about early  
432 reproductive investment might be more difficult and costly to gather (Ahola et al., 2007;  
433 Forsman et al., 2018; Merilä & Wiggins, 1995; Samplonius & Both, 2019; Slagsvold, 1975).

434         Song production is overall costly (in terms of time, energy, predation risk and  
435 agonistic contests) and should thus be selected to honestly inform on producer's quality (Gil  
436 & Gahr, 2002), for example reflecting its past (Bischoff et al., 2009) or present parasitic load  
437 (Buchanan & Catchpole, 1999; Møller, 1991). Song features in great tit males have been  
438 shown to inform on male survival and reproductive success (McGregor et al. 1981,  
439 Lambrechts and Dhondt 1986, Rivera-Gutierrez et al. 2010), on mate quality (to females)  
440 during escalating song contests (Otter et al., 1999), and on competitive ability (to rivals) at the

441 conspecific level (Peake, Matessi, McGregor, & Dabelsteen, 2005). Great tit song features  
442 have not directly been related to territory quality (Lambrechts and Dhondt 1988, but see Hoi-  
443 Leitner et al. 1995, and Manica et al. 2014 for other species), but great tit males singing  
444 longer strophes were found to be dominant at feeders (Lambrechts & Dhondt, 1986) and more  
445 willing to engage in territorial defence (McGregor & Horn, 1992). Overall, these studies  
446 suggest that great tit song features revealing singers' high quality are likely to be associated  
447 with the acquisition and defence of a high quality territory, but also a better exploitation of  
448 habitat during nestling provisioning and nest defence against predators via increased vigilance  
449 and risk-taking (Krams, 1998). Thus, cueing on great tit song features may be an efficient  
450 proximate mechanism for flycatchers to identify and select high quality individuals close to  
451 which it can be beneficial to settle (Forsman et al., 2002; Forsman et al., 2007), as our results  
452 for old aggressive females suggest. Because songs are acquired from a distance, Yet, we  
453 cannot exclude the alternative explanation that, after the start of the experiment, the latest  
454 great tit pairs settled around our experimental zones non-randomly, in particular with respect  
455 to their own phenotype, depending on the broadcast treatment, and that flycatchers' settlement  
456 decisions were affected by the presence or phenotype of these neighbouring great tits rather  
457 than (or on top of) the experimentally broadcasted songs. However, flycatchers have been  
458 shown to prefer settling in the closest vicinity to great tits, i.e. the nearest nest box (Kivelä et  
459 al., 2014) and the average number of different great tit songs heard within or close to the  
460 experimental zones (song bias) did not affect treatment choice by flycatchers. Therefore, we  
461 believe that the alternative mechanism of an indirect effect of broadcast treatment on  
462 flycatchers via an effect on neighbouring live great tits, although possible, is unlikely here.  
463 Nevertheless, the use of broadcasted great tit songs as a social information source by  
464 flycatchers did not preclude the simultaneous use of other sources, such as the presence of

465 great tit pairs, as reflected by a higher settlement probability in presence of previously settled  
466 great tit pairs.

467 Our results are in line with recent studies examining the use of song features as a  
468 source of information at the intraspecific level in other migratory species. Wood warblers  
469 have for example been shown to cue on song rate (number of trills per minute) of conspecific  
470 males to select breeding sites: males preferred settling near broadcasts of an apparently low  
471 quality male, with a low song rate (Szymkowiak et al., 2016) probably to avoid competition  
472 costs since song rate reflects individuals' aggressiveness (Szymkowiak & Kuczyński, 2017).  
473 Similarly, yellow warblers discriminate conspecific songs reflecting pairing status based on  
474 syllable frequency and song repetition within song bouts and use this information for breeding  
475 site selection: they were more likely to settle in areas with broadcasts mimicking the presence  
476 of already paired conspecifics, presumably indicating high-quality sites (Kelly & Ward,  
477 2017). Interestingly here, our results clearly suggest that such song features informing on  
478 individuals' quality constitute cues that can cross species boundaries.

479 Nevertheless, the availability of great tit songs to newly arrived flycatchers may vary  
480 both within and between years. When flycatchers arrive on the breeding grounds, a large part  
481 of great tit females can have initiated incubation and thus great tit male singing activity can be  
482 largely reduced (Amrhein, Johannessen, Kristiansen, & Slagsvold, 2008; Mace, 1987). The  
483 time delay between great tit settlement and flycatcher arrival, as well as the time interval  
484 between the arrival of the first and last flycatchers, may strongly constrain the possibility for  
485 flycatchers to eavesdrop on great tit song and may emphasize the use of other information  
486 sources. The timing of great tit reproduction but also the synchrony of flycatcher arrival show  
487 high variability between years in this and other populations (Morinay, Forsman, Kivelä,

488 Gustafsson, & Doligez, 2018; Samplonius & Both, 2019), affecting the availability of cues  
489 linked to great tit presence and reproductive activity upon flycatcher arrival. Thus selective  
490 pressures should favour flexibility in the use of the different heterospecific cues in response to  
491 environmental variation. Great tit song characteristics may be used for flycatcher settlement  
492 decisions when tits are late and by early arriving flycatchers, while other information about tit  
493 quality and reproductive investment (e.g. clutch size, tit incubating or provisioning activity;  
494 Seppänen et al. 2011, Samplonius and Both 2017) or conspecific social information should be  
495 favoured otherwise, even though settlement date had no influence here on broadcast treatment  
496 choice. Manipulating information availability through the timing of song broadcast would be  
497 needed to explore this hypothesis. In our study, tit laying date was intermediate ( $34.8 \pm 7.8$   
498 (SD), counted from the 1st of April) compared to other years ( $26.6 \pm 6.9$  for 2016, an early  
499 year, and  $42.3 \pm 3.9$  for 2013, a late year; see Morinay et al. 2018), which may explain  
500 relatively small differences between broadcast treatments.

501

#### 502 *Role of female experience and competitive ability*

503 Old females were able to use the information about both the presence and quality of great tit  
504 individuals provided by songs to select a breeding site. Conversely, yearling females were not  
505 affected by song presence or quality, even though yearlings are usually more prone to use  
506 social information, including heterospecific one, as shown before in the pied flycatcher –  
507 great tit system (Seppänen & Forsman, 2007; Loukola et al., 2013). This difference between  
508 yearling and older females plausibly results from different past experience with great tit  
509 songs. Among songbirds, the response to songs is usually shaped by imprinting both in the  
510 conspecific (Catchpole & Slater, 2008; Kroodsma, 1982) and the heterospecific context

511 (Hansen & Slagsvold, 2003). Because flycatchers breed a couple of weeks later than great tits,  
512 flycatcher fledglings are usually not exposed to great tit songs before leaving on migration  
513 mid-August. Therefore, flycatcher yearlings arriving on breeding grounds from migration are  
514 not expected to be able to associate great tit song features with singer's quality estimates.  
515 Cueing on great tit song features may require experience obtained only during the first  
516 breeding season for flycatchers, and yearling flycatchers could use other information sources  
517 to assess great tit presence and reproductive investment (Seppänen & Forsman, 2007; Loukola  
518 et al., 2013).

519         Among older females, the difference in choice of great tit song broadcast treatment  
520 according to aggressiveness level could result from two mechanisms. First, old flycatcher  
521 females may adjust their settlement decisions depending on the balance between expected  
522 benefits in terms of habitat quality and costs in terms of competition level and agonistic risks.  
523 While flycatchers benefit from breeding close to great tits, the latter bear costs from this  
524 proximity, with (depending on years) either lower number, quality, size or survival of  
525 offspring reared close to flycatcher nests (Forsman, et al., 2007), likely due to competition for  
526 food resources. Great tits may therefore be expected to show aggressiveness towards  
527 flycatchers at the settlement stage. In this context, only more aggressive flycatcher females  
528 may be able to cope with increased costs associated to settling near more competitive /  
529 aggressive great tits and benefit from the most favourable habitats (as reflected by higher  
530 quality great tit songs); less aggressive females still preferred settling near great tits, i.e. in  
531 habitats of supposedly higher quality than control (chaffinch song) zones, but they avoided  
532 zones where agonistic risk and competition with great tits was expected to be highest. This  
533 could be in line with previous intraspecific results showing higher settlement of great tits near  
534 broadcasts of great tit songs with smaller repertoires, i.e. reflecting potentially lower quality



535 individuals (Krebs et al., 1978): later-settlings individuals could indeed be low competitive  
536 individuals more prone to avoid potential competitive costs. Alternatively, flycatcher females  
537 may have adjusted their response to our aggressiveness test after settlement, depending on the  
538 song broadcast treatment and thus apparent competitive level of neighbouring great tits. In  
539 this population, the repeatability of our aggressiveness score is around 0.2, meaning that this  
540 trait is largely plastic (Morinay et al., 2019). Furthermore, we measured aggressiveness after  
541 settlement, during nest building, at a time when songs were still broadcasted for most  
542 flycatcher pairs, and higher singing performance was suggested to induce social aggression, at  
543 least at the intraspecific level (Gil & Gahr, 2002). In the case of post-settlement adjustment of  
544 aggressiveness level, however, it would be surprising that only females, but not males,  
545 respond to the broadcasted song treatment, since males are as much involved in territory  
546 defence against heterospecific intruders as females (unpublished results). Furthermore, such  
547 adjustment of aggressiveness level implies that individuals respond in the absence of great tit  
548 individuals actually defending their neighbourhood. Importantly, both mechanisms, i.e. the  
549 adjustment of settlement choice according to female aggressiveness level or the post-  
550 settlement adjustment of aggressiveness response by females according to broadcasted songs,  
551 imply that old flycatcher females are able to discriminate great tit songs features reflecting  
552 high and low quality individuals, use them as a heterospecific social information source and  
553 adjust their behaviour accordingly, whether pre- or post-settlement.

554

#### 555 *No role of male factors*

556           Interestingly, male age and aggressiveness score did not influence pair settlement with  
557 respect to the broadcast treatment. Even though nest site selection is a joint behaviour by both

558 pair members, our results thus suggest that only female flycatchers were capable of adjusting  
559 this behaviour in response to great tit songs, which could reflect a higher ability to  
560 discriminate song features compared to males. Selective pressures may be higher in flycatcher  
561 females compared to males for the use of songs in the context of species recognition (when  
562 facing hybridization risk with sympatric pied flycatchers; Qvarnström, Rice, & Ellegren,  
563 2010; Wheatcroft & Qvarnström, 2017) and/or mate selection (with higher constraints on  
564 females than males due to facultative polygyny; Gustafsson & Qvarnström, 2006;  
565 Qvarnström, Sheldon, Pärt, & Gustafsson, 2003). Former studies have shown differential  
566 auditory processes between sexes in several species (Del Negro, Kreutzer, & Gahr, 2000;  
567 Williams, 1985), upon which selection could act differently. Alternatively, males could  
568 discriminate song features just as well as females (as suggested by the widespread ‘dear  
569 enemy’ effect; Moser-Purdy & Mennill, 2016), but may be less prone to use this information  
570 for settlement decisions if other social cues are more relevant at the spatial scale of site choice  
571 for males, supposedly involving smaller scales compared to females (Arlt & Pärt, 2008;  
572 Doligez, Pärt, & Danchin, 2004; Greenwood, 1980; Morinay et al., 2018; Samplonius & Both,  
573 2017). The different selective pressures acting on male and female settlement and  
574 reproductive investment may also favour the acquisition and use of complex social  
575 information such as tit clutch size or tit song features by females, allowing them to adjust  
576 decisions (e.g. Forsman et al., 2002, 2012, 2007), while males must quickly secure nest sites  
577 to attract mates in the face of strong male-male competition, and thus cannot take time for  
578 gathering such complex information (see Samplonius & Both, 2017b). Theoretically, the sex-  
579 specific pattern observed here could also result from different breeding costs and benefits of  
580 settling close to high (or low) quality great tits between males and females. Such sex-specific  
581 costs and benefits may however be difficult to estimate here because both sexes participate in

582 nest defence and offspring provisioning. Further work would be needed to assess whether  
583 flycatcher males can discriminate great tit song features and in this case which other  
584 information sources would be more valuable to them compared to females.

585

586 Overall, our results shed further light on the complexity of social information use by  
587 providing evidence for the use of refined heterospecific information sources such as the  
588 quality-related information contained in heterospecific acoustic signals for settlement  
589 decisions. Interestingly, the resulting global occupancy pattern was unaffected by our  
590 broadcast treatment, emphasizing the importance of accounting for individual variability to  
591 understand the complex use of social information. Further work is needed to assess how and  
592 when different information sources are used for different breeding decisions (see e.g. Doligez  
593 et al., 2008) depending on individual and environmental conditions, including the  
594 quantification of fitness benefits of using each information source in a given context. In the  
595 case of great tit songs, this could include manipulating another information source  
596 simultaneously (e.g. territory quality, through food supplementation; Récapet, Bize, &  
597 Doligez, 2017), or manipulating individuals' phenotype (e.g. body condition), on top of song  
598 broadcasts, to explore how individuals' characteristics (sex, age, condition, aggressiveness but  
599 also previous experience) affect which information is used for decisions along the breeding  
600 period, from nest site choice to parental care investment until (and possibly after) fledging.

601

## 602 **Data, code and materials**

603 The dataset supporting this article has been uploaded as Supplementary Material 1 and 2.

604 **Competing interests**

605 The authors declare no competing interests.

606

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827 Table 1. Effect of individual and environmental variables on the probability to settle in experimental zones of a given broadcast treatment.

	Low quality tit vs. Control		High quality tit vs. Control	
	Posterior mean	95% CI	Posterior mean	95% CI
<b>Model with female factors N=77</b>				
Intercept	-1.24	[ -3.28 ; 0.61 ]	0.50	[ -0.88 ; 1.91 ]
Age ♀ ( <i>yearling</i> )	-0.13	[ -2.50 ; 2.42 ]	-1.77	[ -3.62 ; 0.29 ]
Aggressiveness ♀	-3.57	[ -6.58 ; -0.94 ] *	1.38	[ 0.17 ; 2.75 ] *
Aggressiveness x Age ♀ ( <i>yearling</i> )	3.49	[ 0.25 ; 6.72 ] *	-1.07	[ -2.99 ; 0.59 ]
Day of choice	-0.21	[ -1.18 ; 0.80 ]	0.13	[ -0.79 ; 1.06 ]
Presence of other great tits ( <i>yes</i> )	2.73	[ -0.03 ; 5.35 ]	3.79	[ 1.19 ; 6.64 ] *
Presence of other flycatchers ( <i>yes</i> )	-1.26	[ -3.38 ; 0.44 ]	-2.67	[ -4.65 ; -0.64 ] *
Song bias	0.45	[ -0.31 ; 1.29 ]	0.51	[ -0.34 ; 1.34 ]
Forest patch variance	1.09 [0.00; 3.69]			
<b>Model with male factors N=60</b>				
Intercept	0.07	[ -1.70 ; 1.92 ]	1.22	[ -0.42 ; 3.31 ]
Age ♂ ( <i>yearling</i> )	-1.35	[ -3.68 ; 0.93 ]	-2.21	[ -4.93 ; 0.38 ]
Aggressiveness ♂	-0.01	[ -0.04 ; 0.02 ]	-0.03	[ -0.08 ; 0.00 ] □
Day of choice	-0.23	[ -1.30 ; 0.81 ]	0.59	[ -0.57 ; 1.59 ]

Presence of other great tits ( <i>yes</i> )	2.55 [ 0.14 ; 5.41 ] *	3.34 [ 0.89 ; 6.22 ] *
Presence of other flycatchers ( <i>yes</i> )	-0.89 [ -2.94 ; 1.23 ]	-2.59 [ -5.06 ; -0.59 ] *
Song bias	0.14 [ -0.71 ; 1.11 ]	0.75 [ -0.24 ; 1.71 ]
Forest patch variance	1.12 [0.00; 3.90]	

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832 Model outputs are estimates (posterior means and 95% Credible Intervals) for settlement in an experimental zone of the low quality great tit song  
833 vs. the control (chaffinch song) treatment (left) and the high quality great tit song vs. the control treatment (right; i.e. the control treatment served  
834 as reference here), for females and males separately (see text). For qualitative covariates, the estimated category is given in parentheses. Stars  
835 indicate estimates whose 95% CI do not overlap zero. The 95% CI for the estimate of male aggressiveness score on the probability to settle in  
836 experimental zones of the high quality tit song treatment just reached 0; however, this trend did not appear robust because it disappeared when  
837 using a larger sample size including males not captured later on and which could not be aged (i.e. when excluding the age effect from the model).

838 Table A1. Output of models fitting flycatchers' early-reproductive investment including either female or male age and aggressiveness score.

	Model with female age and aggressiveness		Model with male age and aggressiveness	
	Posterior mean	95% CI	Posterior mean	95% CI
<b><i>Model fitting laying date</i></b>		<i>N</i> = 77		<i>N</i> = 60
Intercept	51.95 [ 51.03 ; 52.89 ] *		52.19 [ 51.11 ; 53.22 ] *	
Treatment ( <i>low quality</i> )	-0.21 [ -1.35 ; 0.83 ]		-0.47 [ -1.63 ; 0.73 ]	
( <i>high quality</i> )	0.04 [ -1.01 ; 1.18 ]		0.00 [ -1.28 ; 1.26 ]	
Aggressiveness	0.36 [ -0.06 ; 0.78 ]		0.25 [ -0.24 ; 0.74 ]	
Age ( <i>yearling</i> )	1.19 [ 0.29 ; 2.13 ] *		-0.25 [ -1.46 ; 0.96 ]	
Presence of other great tits ( <i>yes</i> )	-0.95 [ -1.91 ; 0.09 ]		-0.82 [ -1.88 ; 0.24 ]	
Presence of other flycatchers ( <i>yes</i> )	1.29 [ 0.46 ; 2.23 ] *		1.31 [ 0.34 ; 2.29 ]	
Song bias	-0.05 [ -0.45 ; 0.37 ]		-0.30 [ -0.81 ; 0.24 ]	
Forest patch variance	0.06 [ 0.00 ; 0.27 ]		0.20 [ 0.00 ; 0.89 ]	
Residual variance	3.23 [ 2.25 ; 4.35 ]		3.29 [ 2.04 ; 4.59 ]	
<b><i>Model fitting delay between settlement and laying</i></b>		<i>N</i> = 77		<i>N</i> = 60
Intercept	2.34 [ 2.16 ; 2.52 ] *		2.33 [ 2.13 ; 2.53 ] *	
Treatment ( <i>low quality</i> )	0.01 [ -0.20 ; 0.21 ]		0.01 [ -0.23 ; 0.23 ]	
( <i>high quality</i> )	-0.03 [ -0.22 ; 0.20 ]		-0.15 [ -0.41 ; 0.08 ]	
Aggressiveness	-0.02 [ -0.11 ; 0.07 ]		-0.08 [ -0.18 ; 0.01 ]	



Age ( <i>yearling</i> )	-0.12 [ -0.30 ; 0.06 ]	0.06 [ -0.17 ; 0.29 ]
Presence of other great tits ( <i>yes</i> )	-0.02 [ -0.22 ; 0.18 ]	0.05 [ -0.18 ; 0.25 ]
Presence of other flycatchers ( <i>yes</i> )	-0.29 [ -0.47 ; -0.11 ] *	-0.37 [ -0.57 ; -0.19 ] *
Song bias	-0.01 [ -0.10 ; 0.06 ]	0.05 [ -0.05 ; 0.14 ]
Forest patch variance	0.01 [ 0.00 ; 0.03 ]	0.01 [ 0.00 ; 0.04 ]
Residual variance	0.01 [ 0.00 ; 0.03 ]	0.01 [ 0.00 ; 0.02 ]
<b>Model fitting clutch size</b>	<b>N = 76</b>	<b>N = 60</b>
Intercept	1.84 [ 1.63 ; 2.06 ] *	1.83 [ 1.60 ; 2.06 ] *
Treatment ( <i>low quality</i> )	0.01 [ -0.24 ; 0.24 ]	0.03 [ -0.24 ; 0.29 ]
( <i>high quality</i> )	0.01 [ -0.23 ; 0.26 ]	0.01 [ -0.27 ; 0.28 ]
Aggressiveness	-0.02 [ -0.12 ; 0.08 ]	-0.01 [ -0.12 ; 0.09 ]
Age ( <i>yearling</i> )	-0.07 [ -0.30 ; 0.14 ]	-0.06 [ -0.33 ; 0.21 ]
Presence of other great tits ( <i>yes</i> )	-0.02 [ -0.25 ; 0.18 ]	-0.02 [ -0.28 ; 0.20 ]
Presence of other flycatchers ( <i>yes</i> )	0.06 [ -0.13 ; 0.29 ]	0.05 [ -0.19 ; 0.30 ]
Song bias	-0.01 [ -0.10 ; 0.09 ]	0.00 [ -0.11 ; 0.11 ]
Settlement date	-0.02 [ -0.13 ; 0.09 ]	-0.03 [ -0.15 ; 0.10 ]
Forest patch variance	0.00 [ 0.00 ; 0.02 ]	0.01 [ 0.00 ; 0.02 ]
Residual variance	0.00 [ 0.00 ; 0.01 ]	0.00 [ 0.00 ; 0.01 ]

839

840 Estimated levels are given in parentheses; older females, the control treatment, and the absence of other great tits or flycatchers serve as references. Stars

841 indicate estimates which 95% CI do not overlap zero.

842

## Figure legends

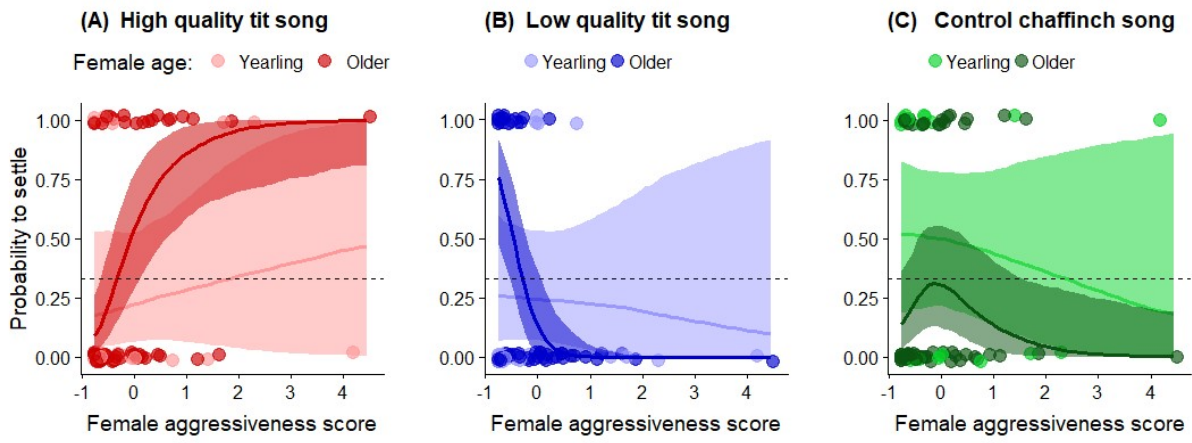
843 Figure 1. Probability for flycatchers to settle in an experimental zone according to the  
844 broadcast treatment (3 levels: (a) high quality tit song, (b) low quality tit song, (c) chaffinch  
845 song as a control) depending on female aggressiveness score and age (light red/blue/green:  
846 yearling females; dark red/blue/green: older females). Predicted mean probabilities (solid  
847 lines) and their 95% Credible Intervals (shaded areas) were derived for average estimates of  
848 all other model parameters. Points indicate actual settlements (1 for settlement in the  
849 broadcast treatment considered, 0 for settlement in one of the other two treatments). The  
850 horizontal dashed line represents the probability to settle at random in a zone of the broadcast  
851 treatment considered (i.e. 0.33).

852

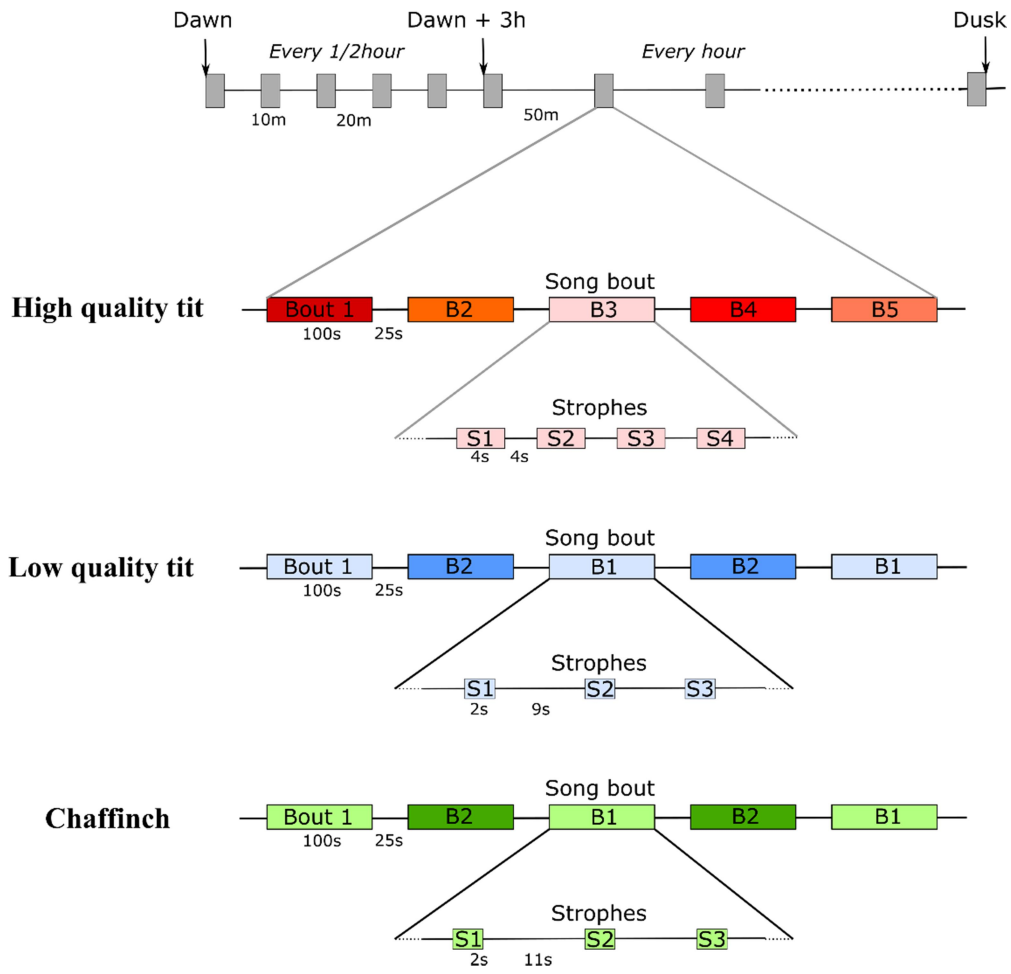
853 Figure A1. Structure of a song track (top), composed of a succession of 10 minute-long song periods.  
854 Song periods are composed of song bouts (B1, B2...), which are composed of strophes (S1, S2 ...).  
855 All strophes in the same song bout were composed of the same type of syllable. Depending on the  
856 great tit natural song used for building the song track, the syllables within a strophe slightly varied in  
857 rhythm, amplitude, and, before transformation, in length. To standardize strophe length, we duplicated  
858 or deleted syllables. (a) Playback tracks mimicking a good quality great tit song had a repertoire size  
859 of 5 song bout types, composed of 4 second-long strophes separated by 4 seconds of silence. (b)  
860 Playback tracks mimicking a low quality song had a repertoire size of 2 song bout types, composed of  
861 2 second-long strophes separated by 9 seconds of silence. (c) Chaffinch song track followed the same  
862 temporal pattern than low quality tit treatment (but with one strophe every 11 seconds), as it better  
863 matches their natural singing rhythm. The two different chaffinch song bout types per individual B1  
864 and B2 were composed of a fixed syllable structure that could vary between individuals but was quite

865 conserved within individuals. The order of song bouts within a song period - and of strophes within  
866 song bouts- were alternated between song periods and song bouts to avoid habituation.

867



870 **Figure A1**



871