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

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## Abstract

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

## Introduction

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

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

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

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

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

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

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

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

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

## **Materials and methods**

### *Animal welfare note*

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

### *Study area and population monitoring*



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

### *Playback experimental design*

In the 13 forest patches chosen for the study on the basis of a sufficiently high number 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

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

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

#### *Playback song structure*

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

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

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

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

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

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

### *Aggressiveness test*

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

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

### *Statistical analyses*

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

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

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

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

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

#### *Linear model implementation*

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



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

## Results

### *Occupancy pattern according to broadcast treatment*

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

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

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

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

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

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

## Discussion

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

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

Migratory flycatchers may not easily gather updated personal information about breeding

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

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

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

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

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

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

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

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

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

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



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

#### *No role of male factors*

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

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

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

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

## **Data, code and materials**

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

## Competing interests

The authors declare no competing interests.

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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					
<i>Model with female factors</i>	<i>N=77</i>										
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]									
<i>Model with male factors</i>	<i>N=60</i>										
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]													

851

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>		<b><i>N = 77</i></b>				<b><i>N = 60</i></b>	
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>		<b><i>N = 77</i></b>				<b><i>N = 60</i></b>	
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><i>Model fitting clutch size</i></b>	<b><i>N = 76</i></b>	<b><i>N = 60</i></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.

## Figure legends

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

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



