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

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Assessing local habitat quality via social cues provided by conspecific 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 various species have been shown to be attracted to breeding sites by conspecific 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, and whether this depends on the individual's own phenotype and especially its competitive ability, remains unknown. We used a playback experiment in a wild population of collared flycatchers, Ficedula albicollis, a species known to eavesdrop on the presence and performance of dominant great tits, Parus major. We tested whether flycatchers, whose aggressiveness was experimentally assessed, preferred to settle near playback 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 playback of high-quality tit song and avoided playback of low-quality tit song, while less aggressive females preferred to settle near playback 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, although this depended 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.

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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 between 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, that is, its personal experience

('personal information', such as its own reproductive success, Switzer, 1997). Alternatively, information can be acquired from observing the interactions of other individuals sharing similar needs (either conspecific 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 conspecifics 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 provides easily accessible information but does not directly inform about the fitness consequences of others' decisions. Individuals can also use the performance of others, that is, their success after making a

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decision; this 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 about 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, & Lehikoinon, 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 with information gathering, on the other, may require reducing such costs. This should favour the use of cues reflecting others' performance obtained at 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. antipredator strategies involving eavesdropping on conspecific and heterospecific alarm calls; reviewed in Magrath, Haff, Fallow, & Radford, 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 & Schlossberg, 2004). Importantly, signals used in sexual communication, which include acoustic signals, are selected (1) to be conspicuous, allowing signallers 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, for example, have been shown to eavesdrop on male 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, 1999; 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, *Setophaga petechia*, Kelly & Ward, 2017; song rate in wood warblers, *Phylloscopus sibilatrix*, Szymkowiak, Thomson, & Kuczyński, 2016). Such refined acoustic information use could occur not only within but also between species; however, this has not yet been explored 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, Hjernquist, Taipale, &

Gustafsson, 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 for nestlings and predators, and tits start breeding only a couple of weeks before flycatchers arrive from migration, thus providing flycatchers with valuable information for their own choice of breeding habitat. Flycatchers have been shown to gain fitness benefits from using this heterospecific information for settlement decisions and invest more in their reproduction when copying great tits' choices (Forsman, Seppänen, & Mönkkönen, 2002; Forsman, Thomson, & Seppänen, 2007). Prospecting nests of tits 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, & Doligez, n.d.; Samplonius & Both, 2017).

Upon flycatchers' arrival from migration, we played 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 the experimental zones. If flycatchers are attracted by great tit songs when choosing where to breed, they should settle preferentially in zones where tit songs are played; in addition, if flycatchers use information about great tit quality as reflected by song features, they should settle preferentially in zones with playback of high-quality tit songs, presumably indicating high-quality habitat. We also tested whether the choice of a zone with high- versus low-quality tit song depended on the 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), according to the experimental song treatment.

METHODS

Ethical Note

To minimize disturbance during aggressiveness tests, we approached nestboxes 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 J.M. and 471:M043 to Cécile Vansteenberghe). 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 min depending on nestling age (30 min when nestlings were 5 days old or younger), to avoid nestlings starving if parents did not resume feeding during the catching period; we checked traps every 5−10 min, and removed the traps as soon as adults had been caught. We started catching sessions after 0600 h to let birds feed and provision nestlings undisturbed for at least 2 h after the night period (sunrise is at ca. 0400 h in spring). We handled adults for 5−10 min and released them straight after manipulation or

(when catching both parents during nestling feeding) kept them until we caught the partner (up to 40 min). 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 nestboxes provided in excess in the study area (Doligez, Pärt, Danchin, Clobert, & Gustafsson, 2004; Gustafsson, 1988); they also partly feed the same food to nestlings (in particular caterpillars) and share predators (Lundberg & Alatalo, 1992). Collared flycatchers start arriving on the breeding grounds late April–early May, that is, 2 weeks on average after the beginning of the tit breeding season. Over 2012–2017, 33.5% of the nestboxes 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, *Sitta europaea*, sparrows, *Passer domesticus*, coal tits, *Periparus ater*) or by tits that abandoned their nest before identification, and 28.7% remained empty. In all nestboxes 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 versus older adults; Svensson, 1992). Nestboxes 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 nestboxes (>30, and up to 180), we established experimental zones composed of five neighbouring nestboxes (except for one zone, which had four), with four boxes (three for the four-box zone) spread around a central nestbox (approximately 20 m away); experimental zones were separated from each other by at least 40 m (i.e. each zone was surrounded by at least one row of nonexperimental nestboxes). Each selected forest patch contained three to nine experimental zones (total $N = 57$, 19 of each treatment; four patches with three zones, seven patches with four or five zones and two patches with eight or nine zones). We conducted the playback experiment between 29 April and 27 May, that is, throughout the period of flycatcher settlement. During these 29 days, at the centre of each experimental zone we played either (1) a great tit song track with high-quality song features, that is, mimicking the singing activity of high-quality individuals (i.e. large repertoire, long strophes, high song rate, Lambrechts & Dhondt, 1986; McGregor et al., 1981; Rivera-Gutierrez, Pinxten, & Eens, 2010), (2) a great tit song track with song features of low-quality individuals (i.e. with a small repertoire size, short strophes, low song rate) or (3) a song track from a generalist and widespread forest-dwelling bird species with no previously shown influence on flycatcher settlement decisions, the common chaffinch, *Fringilla coelebs*, as a control. Common chaffinches are migrant (on Gotland) open-cup nesters and are larger than collared flycatchers as are great tits. Even though chaffinches and flycatchers partly feed the same food to nestlings (insect larvae), chaffinches are habitat generalists and their presence should not reflect a specific resource. There is currently no direct

evidence of resource or interference competition or interspecific information use between chaffinches and flycatchers. Consequently, chaffinches appear to be a good control species for the song playback experiment. We ensured that each patch contained at least one experimental zone of each treatment. The distance between experimental zones reliably reflected the natural density of great tit breeding pairs in our forest patches (average ± SD minimum distance between breeding great tits in our experimental forest patches in the preceding year, i.e. 2016: 59.8 ± 9.3 m; $N = 403$). Because great tit and chaffinch songs can be heard from a long distance (>100 m in our forest patches), a prospecting flycatcher should thus have been able to simultaneously hear several experimental playbacks and to choose between treatments.

Song tracks were played from dawn (1 h before sunrise) for 17 h, corresponding to dusk at the beginning of the experiment and up to 1 h 30 min before dusk at its end. During the experiment, the start of the playback was adjusted (15 min earlier every 10 days) to match the seasonal change in the timing of dawn, but the length of the track remained unchanged. To match the natural singing activity of great tits, we played 10 min of song every 30 min from dawn to 3 h after dawn, and then every hour till the end of the sequence (see Fig. A1), similarly to Krebs, Ashcroft, and Webber (1978). Tracks were played at ca. 85–95 dB, close to the natural sound amplitude of great tit songs (McGregor & Horn, 1992; sound amplitude checked at 1 m distance with a sound level meter 'Dr. Meter MS10'). In each experimental zone, the song track was played from a camouflaged loudspeaker (Zealot S1) attached 1.5–2 m above ground on a tree next to the central nestbox of each experimental zone.

Playback Song Structure

To create the sound tracks while limiting the risk of pseudoreplication, we used songs from four different great tits to mimic songs of high-quality tits, from four others to mimic songs of low-quality tits and from four different chaffinches for controls. Great tit songs were recorded in the same population in 2016, at dawn, with a Sennheiser MKH70 microphone and a Zoom H4N recorder. Chaffinch songs were recorded either on Gotland in 2016 (one individual) or on the Swedish mainland (three individuals); these are available online (Xeno Canto online database, www.xeno-canto.org, accessed in April 2017; recording 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 remained unchanged throughout the experiment, to avoid mixing signals from different individuals in case flycatchers were able to recognize individual 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 Fig. A1) and amplified. We amplified whole song bouts (see Fig. 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 nestboxes in the experimental zones available to flycatchers and avoid songs from live great tits interfering with our playback, we prevented great tits (but not blue tits) settling in our experimental zones from early April by narrowing the entrance

hole of all experimental nestboxes to 28 mm diameter with drilled chipboards attached around the nestbox hole. At the beginning of the experiment, on 29 April, we removed the chipboards to expand the nestbox entrance hole to 32 mm diameter (recommended size for both great tits and flycatchers, L. Gustafsson, personal communication, May 2016). Late blue and great tits could thus also settle in the experimental zones during the experiment. When this happened before the first flycatcher pair had settled in the experimental zone and the nestbox density was sufficiently low (for three of the 57 zones), we slightly relocated the experimental zone by adding one nestbox on the edge of the zone and excluding the box occupied by the tit pair, to provide the same number of available nestboxes (five) to the first flycatcher pair to settle in all zones. Of the 57 experimental zones, 30 (52%) remained unoccupied by great tits throughout the experiment.

As the singing performance of local great tits might have affected our treatment, we controlled for the singing activity of tits within or in close vicinity of each experimental zone. We counted the different songs that could be heard close by from the tree where the loudspeaker was placed, for 10 min picked at random before 1000 h and in between two playback songs. We recorded this measure of singing activity by live great tits for each zone for 4–7 days a week depending on the experimental zone and field time constraints, obtaining between 16 and 27 measures per zone; we averaged this over the whole experiment 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, following the protocol detailed in Morinay, Daniel, Gustafsson, and Doligez (2019). In short, at the beginning of the test, an observer attached (1) clay decoys representing either a flycatcher pair or a male great tit to the nestbox of the focal pair and (2) a loudspeaker playing songs of the corresponding species below the nestbox. The observer then sat camouflaged 8–10 m away and recorded all the behaviours of both the male and the female flycatchers for 15 min if both individuals were seen for at least 5 min during this first period, or up to 25 min if at least one of them arrived only at the end of the first 15 min, to allow the observer to record the flycatchers' behaviour for at least 5 min. We conducted one test with flycatcher decoys and one with a great tit decoy. However, if one individual was not seen during either test, we conducted more tests (up to five), with a day's break between two consecutive tests. To limit the risk of pseudoreplication, we used 10 sets of flycatcher decoys, 10 sets of great tit decoys, five different song tracks per species and randomized the song track used with a given decoy set. Aggressiveness score was then later estimated as the number of movements within 2 m from the nestbox (between branches or onto the box, as well as attacks on decoys) plus the number of chases of live intruders, standardized per 15 min (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, including either of these scores in the models 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 treatments (high-quality great tit song, low-quality great tit song, chaffinch song as a control) by comparing nestbox occupancy probability between treatments using a generalized linear mixed model with flycatcher occupancy (binary variable) as the response variable and treatment (three 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 nonindependence of the experimental nestboxes within zones and forest patches.

Second, among settled pairs, we used generalized linear multinomial mixed models to test whether the probability of flycatchers settling in a given treatment depended on individual and environmental factors. Even though nestbox 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 were captured than males, $N = 57$ nestbox choices for which both male and female age and aggressiveness were obtained). We fitted models with the treatment of the zone chosen by each flycatcher (three levels) as the response variable and included as fixed effects (1) the individual's age and aggressiveness score, (2) settlement date, (3) the presence of previously settled great tits and flycatchers (two separate binary variables) as shown by the presence of nest material in a box in the experimental zone on the day of choice and (4) 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 than early arriving and older ones (Seppänen & 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 effect of aggressiveness on the use of heterospecific social information has been found to be age specific in this system (Morinay et al., n.d.), in a second step we tested 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 zones 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 (1) laying date, (2) the delay between settlement and laying and (3) clutch size, according to the treatment (three 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 nestbox with the 'threshold family' and the residual variance fixed to 1 (11×10^4 iterations, burn-in $= 10^4$, thinning interval $= 50$). We implemented models fitting the treatment chosen using the

Table 1
Effect of individual and environmental variables on the probability of settling in experimental zones of a given treatment

	Low-quality tit vs Control		High-quality tit vs Control	
	Posterior mean	95% CI	Posterior mean	95% CI
Model with female factors, N=77				
Intercept	−1.24	[−3.28; 0.61]	0.50	[−0.88; 1.91]
Age ♀ (yearling)	−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*Age ♀ (yearling)	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 (yes)	2.73	[−0.03; 5.35]	3.79	[1.19; 6.64]*
Presence of other flycatchers (yes)	−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]
Model with male factors, N=60				
Intercept	−0.11	[−1.56; 1.50]	0.24	[−1.22; 1.66]
Age ♂ (yearling)	−1.33	[−3.67; 0.87]	−2.16	[−5.11; 0.37]
Aggressiveness ♂	−0.17	[−1.11; 0.77]	−1.01	[−2.18; 0.08]
Day of choice	−0.25	[−1.29; 0.78]	0.58	[−0.53; 1.63]
Presence of other great tits (yes)	2.54	[0.01; 5.20]*	3.34	[1.05; 6.47]*
Presence of other flycatchers (yes)	−0.87	[−2.95; 1.17]	−2.60	[−4.93; −0.50]*
Song bias	0.14	[−0.82; 1.04]	0.74	[−0.21; 1.74]

Model outputs are estimates (posterior means and 95% credible intervals, CI) for settlement in an experimental zone of the low-quality and high-quality great tit song versus the control (chaffinch song) treatment (i.e. the control treatment served as reference here), for females and males separately (see text). For qualitative covariates, the estimated category is given in parentheses. Asterisks indicate estimates whose 95% CI do not overlap zero.
Variances associated with the forest patch were negligible (posterior mean [95%CI] = 1.09 [0.00; 3.69] for the model with female factors; 1.08 [0.00; 3.75] for the model with male factors).

'categorical' family (15×10^5 iterations, burn-in = 10^4, thinning interval = 700; including the interaction term aggressiveness∗ age: 35×10^5 iterations, burn-in = 3×10^4, thinning interval = 1700); we fixed the variance−covariance residual matrix to 1 for the diagonal terms (variance) and 0.5 for all the off-diagonal terms (covariance; Hadfield, 2016). We implemented the models for laying date with the Gaussian family (12×10^4 iterations, burn-in = 6×10^3, thinning interval = 50) and for the delay in laying and clutch size with the Poisson family (11×10^5 iterations, burn-in = 10^4, thinning interval = 500). 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 with the forest patch for models fitting the treatment chosen, and inverse-Gamma priors for the residual (when not fixed) and other 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, Best, Cowles, & Vines, 2006). Autocorrelation levels were always below 0.1 and effective sample sizes above 1500 per chain.

RESULTS

Occupancy Pattern according to 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 of a nestbox being 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 [−0.74; 0.04]; high-quality tit
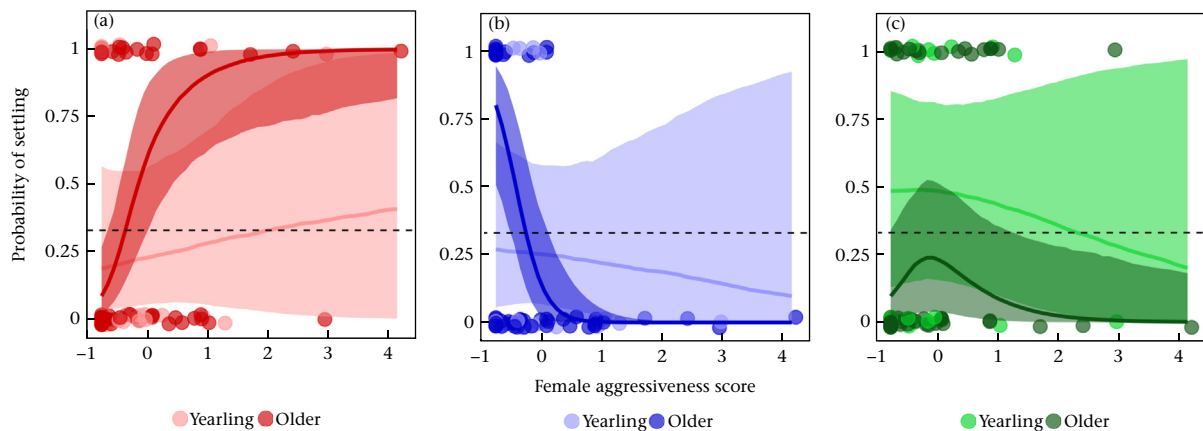

Figure 1. Probability of flycatchers settling in one of three experimental zones in relation to female aggressiveness score and age. There were three playback treatments: (a) high-quality great tit song, (b) low-quality great tit song and (c) chaffinch song as a control. Predicted mean probabilities (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 playback treatment, 0 for settlement in one of the other two treatments). The horizontal dashed line represents the probability of settling at random in one of the three treatments (i.e. 0.33).

treatment: −0.17 [−0.55; 0.21]; zone and forest patch variances did not differ from zero; $N = 284$).

Individual and Environmental Effects on Treatment Choice

The probability of choosing an experimental zone of a given treatment depended on the female's aggressiveness score (estimate [95% CI]: 0.81 [0.06; 1.61] for high-quality versus control, from the model without interaction; $N = 77$), but this effect differed between yearling and older females (interaction aggressiveness score∗age; Table 1, Fig. 1). Among older females, more aggressive ones were more likely to settle in zones of the high-quality great tit song treatment (relation between aggressiveness level and probability of settling in the high-quality song versus control treatment: estimate [95% CI]: 1.38 [0.17; 2.75]; Table 1, Fig. 1a), while less aggressive ones were more likely to settle in zones of the low-quality great tit song treatment (relation between aggressiveness level and probability of settling in the low-quality song versus control treatment: estimate [95% CI]: −3.57 [−6.58; −0.94]; Table 1, Fig. 1b). The probability of choosing an experimental zone of a given treatment also depended on the presence of competitors already settled there: flycatchers were more likely to settle in a zone (either high or low quality compared to the control) when great tits had already settled in it (Table 1) and were more likely to settle in a control zone than in a high-quality great tit song zone when other flycatchers were already settled there (Table 1). Settlement date, song bias, male age and male aggressiveness did not affect the probability of settling in a zone of a given treatment (Table 1, $N = 60$ for the model with male factors).

Early Reproductive Investment according to Treatment

We found no difference between 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 laid 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 an experimental playback 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. As our playbacks were decoupled from the presence of great tit pairs we were able to confirm the direct use of this cue by old flycatcher females for small-scale settlement decisions. Choice of experimental zones depended on the female's aggressiveness level in interaction with her age: among old females, more aggressive ones settled preferentially in zones with high-quality great tit songs, while less aggressive ones settled in zones with low-quality tit songs. In addition to song presence itself, our results thus provide evidence that heterospecific song features related to the singer's quality can be used for important decision making. This source of heterospecific social information did not, however, 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 are Great Tit Song Features Used?

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 et al., 2002; Forsman et al., 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 not only great tit density but also quality from a distance, and 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).

Songs are costly to produce (in terms of time, energy, predation risk and agonistic contests) and should thus be selected to honestly inform about the singer'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 about male survival and reproductive success (Lambrechts & Dhondt, 1986; McGregor et al., 1981; Rivera-Gutierrez et al., 2010), mate quality (to females) during escalating song contests (Otter et al., 1999) and competitive ability (to rivals) at the conspecific level (Peake, Matessi, McGregor, & Dabelsteen, 2005). Great tit song features have not directly been related to territory quality (Lambrechts & Dhondt, 1988; but see Hoi-Leitner, Nechtelberger, & Hoi, 1995, and Manica, Maia, Dias, Podos, & Macedo, 2014 for other species), but great tit males singing longer strophes were found to be dominant at feeders (Lambrechts & Dhondt, 1986) and more willing to engage in territorial defence (McGregor & Horn, 1992). Overall, these studies suggest that great tit song features revealing singers' high quality are likely to be associated with not only the acquisition and defence of a high-quality territory but also better exploitation of habitat during nestling provisioning and nest defence against predators via increased vigilance and risk taking (Krams, 1998). Thus, cueing on great tit song features may be an efficient proximate mechanism for flycatchers to identify and select high-quality individuals to settle near (Forsman et al., 2002, 2007), as our results for old aggressive females suggest. Because songs are acquired from a distance, however, we cannot exclude the alternative explanation that, after the start of the experiment, the later great tit pairs settled around our experimental zones nonrandomly, in particular with respect to their own phenotype, depending on the treatment, and that flycatchers' settlement decisions were affected by the presence or phenotype of these neighbouring great tits rather than (or on top of) the songs being played. However, flycatchers have been shown to prefer settling close to great tits, that is to the nearest nestbox (Kivelä et al., 2014), and the average number of different great tit songs heard within or close to the experimental zones (song bias) did not affect

treatment choice by flycatchers. Therefore, we believe that the alternative mechanism of an indirect effect of treatment on flycatchers via an effect on neighbouring live great tits, although possible, was unlikely. Nevertheless, the use of great tit songs as a social information source by flycatchers did not preclude the simultaneous use of other sources, as reflected in this study by a higher settlement probability in the presence of already 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, for example, have been shown to cue on song rate (number of trills/min) of conspecific males to select breeding sites: males preferred settling near playbacks 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 playbacks 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 about 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. By the time flycatchers arrive on the breeding grounds, most great tit females can be incubating and thus the males are singing less (Amrhein, Johannessen, Kristiansen, & Slagsvold, 2008; Mace, 1987). The time delay between great tit settlement and flycatcher arrival, as well as the time between the arrival of the first and last flycatchers, may strongly constrain the opportunity for flycatchers to eavesdrop on great tit song and may emphasize the use of other information sources. Both the timing of great tit reproduction and the synchrony of flycatcher arrival vary markedly 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 & Both, 2017) or conspecific social information should be favoured otherwise, even though settlement date had no influence here on treatment choice. Manipulating information availability through the timing of song playback would be needed to explore this hypothesis. In our study, tit laying date was intermediate (34.8 ± 7.8 (SD), counted from 1 April) compared to other years (26.6 ± 6.9 for 2016, an early year, and 42.3 ± 3.9 for 2013, a late year; see Morinay et al., 2018), which may explain relatively small differences between treatments.

Role of Female Experience and Competitive Ability

Old females were able to use the information about both the presence and the 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 they are usually more prone to use social, including heterospecific, information, as shown before in the pied flycatcher, *Ficedula hypoleuca* — great tit system (Loukola et al., 2013; Seppänen & Forsman, 2007). This difference between yearling and older females plausibly results from different experience with great tit songs. Among songbirds, the response to songs is usually shaped by imprinting in both 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 in mid-August. Therefore, flycatcher yearlings arriving on the breeding grounds from migration are not expected to be able to associate great tit song features with the singer's quality. Cueing on great tit song features may require experience obtained only during the first breeding season, and yearling flycatchers could use other information sources to assess great tit presence and reproductive investment (Loukola et al., 2013; Seppänen & Forsman, 2007).

Among older females, the difference in choice of great tit song 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 suffer costs from this proximity, with (depending on the year) either lower number, quality, size or survival of offspring reared close to flycatcher nests (Forsman, et al., 2007), probably because of competition for food resources. Great tits may therefore be expected to be aggressive towards flycatchers at the settlement stage. In this context, only more aggressive flycatcher females may be able to cope with increased costs associated with 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 settled near great tits, that is, 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 results showing higher settlement of great tits near playbacks of great tit songs with smaller repertoires, reflecting potentially lower-quality individuals (Krebs et al., 1978): later-settling individuals could indeed be less 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 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 being played for most flycatcher pairs, possibly stimulating flycatchers to adjust their aggressiveness response according to the apparent level of competition in the neighbourhood. Indeed, higher singing performance has been suggested to induce social aggression, at least at the intraspecific level (Gil & Gahr, 2002). If flycatchers adjusted their aggressiveness level after settlement, however, it would be surprising that only females, but not males, responded to the treatment, since males are as much involved in territory defence against heterospecific intruders as females (Morinay, 2018, p. 168). Furthermore, such an adjustment of aggressiveness level implies that individuals respond in the absence of great tit individuals defending their neighbourhood. Importantly, both mechanisms, the adjustment of settlement choice according to female aggressiveness level and the post-settlement adjustment of aggressiveness response by females according to treatment, imply that old flycatcher females are able to discriminate great tit song features reflecting high- and low-quality

individuals, use them as a heterospecific social information source and adjust their behaviour accordingly, whether pre- or postsettlement.

No Role of Male Factors

Interestingly, male age and aggressiveness score did not influence pair settlement with respect to treatment. Even though nest site selection is a joint behaviour by both pair members, our results thus suggest that only female flycatchers could adjust 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 to use 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). Previous studies have shown differential auditory processes between the 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 change their 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, 2017). 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 be difficult to estimate for flycatchers, however, 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 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' phenotypes (e.g. body condition), on top of song playback, to explore how individuals' characteristics (sex, age, condition, aggressiveness but also previous experience) affect which information is used for decisions during the breeding period, from nest site choice to parental care investment until (and possibly after) fledging.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.anbehav.2020.01.002.

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Appendix

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
Model fitting laying date		*N* = 77		*N* = 60
Intercept	51.95	[51.03;52.89]*	52.19	[51.11;53.22]*
Treatment (low quality)	−0.21	[−1.35;0.83]	−0.47	[−1.63;0.73]
(high quality)	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 (yearling)	1.19	[0.29;2.13]*	−0.25	[−1.46;0.96]
Presence of other great tits (yes)	−0.95	[−1.91;0.09]	−0.82	[−1.88;0.24]
Presence of other flycatchers (yes)	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]
Model fitting delay between settlement and laying		*N* = 77		*N* = 60
Intercept	2.34	[2.16;2.52]*	2.33	[2.13;2.53]*
Treatment (low quality)	0.01	[−0.20;0.21]	0.01	[−0.23;0.23]
(high quality)	−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 (yearling)	−0.12	[−0.30;0.06]	0.06	[−0.17;0.29]
Presence of other great tits (yes)	−0.02	[−0.22;0.18]	0.05	[−0.18;0.25]
Presence of other flycatchers (yes)	−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]
Model fitting clutch size		*N* = 76		*N* = 60
Intercept	1.84	[1.63;2.06]*	1.83	[1.60;2.06]*
Treatment (low quality)	0.01	[−0.24;0.24]	0.03	[−0.24;0.29]
(high quality)	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 (yearling)	−0.07	[−0.30;0.14]	−0.06	[−0.33;0.21]
Presence of other great tits (yes)	−0.02	[−0.25;0.18]	−0.02	[−0.28;0.20]
Presence of other flycatchers (yes)	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]

Model outputs are estimates (posterior means and 95% credible intervals, CI) for early reproductive investment for females and males separately (see text), given the playback treatment (the control treatment served as reference here) and other covariates. Estimated levels are given in parentheses; older females, the control treatment and the absence of other great tits or flycatchers serve as references. Asterisks indicate estimates whose 95% CI do not overlap zero.
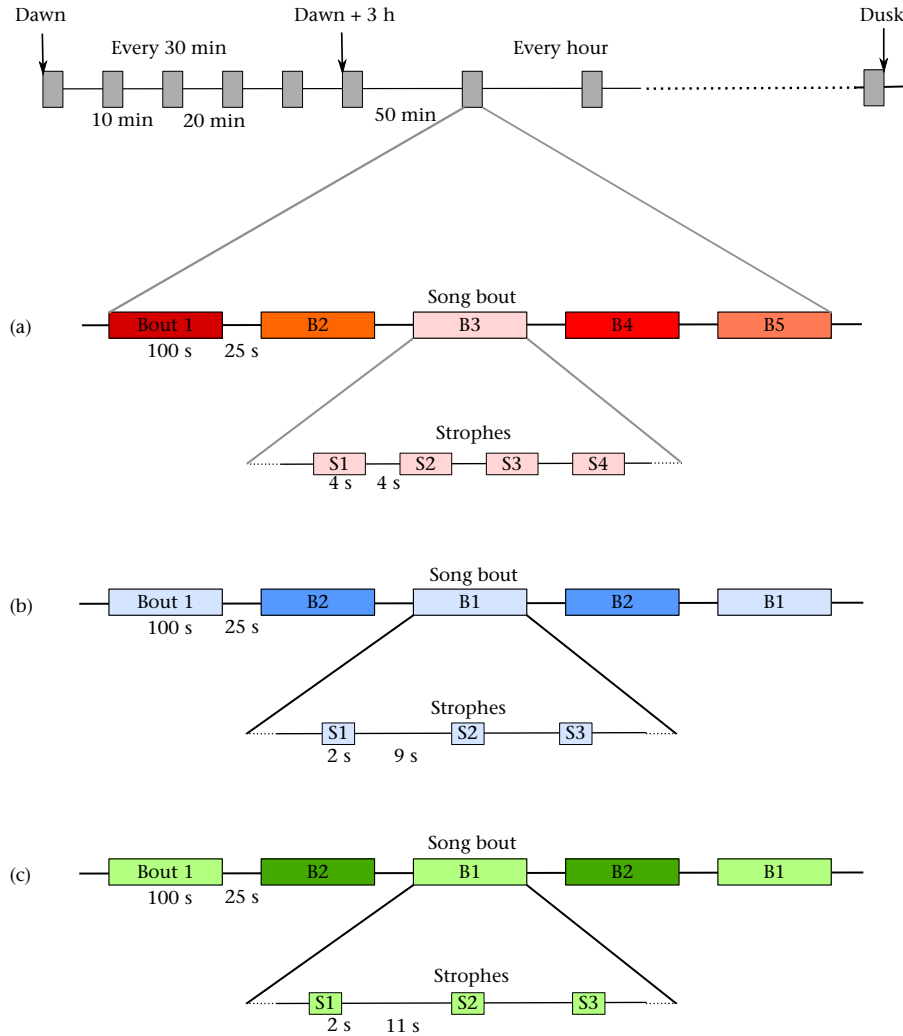
Figure A1. Structure of a song track (top), composed of a succession of 10 min song periods. Song periods are composed of song bouts (B1, B2 …), which are composed of strophes (S1, S2 …). All strophes in the same song bout were composed of the same type of syllable. Depending on the natural great tit song used for building the song track, the syllables within a strophe varied slightly in rhythm, amplitude and, before transformation, 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 five song bout types, composed of strophes of 4 s separated by 4 s of silence. (b) Playback tracks mimicking a low-quality song had a repertoire size of two song bout types, composed of 2 s strophes separated by 9 s of silence. (c) Chaffinch song tracks followed the same temporal pattern as low-quality tit tracks (but with one strophe every 11 s), as this 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 conserved within individuals. The order of song bouts within a song period and of strophes within song bouts were alternated between song periods and song bouts to avoid habituation.