Interactive vocal communication at the nest by parent Great Tits *Parus major*

INGRID C. A. BOUCAUD,[1*] PÉNÉLOPE A. VALÈRE,[1] MÉLISSA L. N. AGUIRRE SMITH,[1] BLANDINE DOLIGEZ,[2,3] LAURE CAUCHARD,[4] FANNY RYBAK[5] & CLÉMENTINE VIGNAL[1]

[1]*Univ Lyon, UJM-Saint-Etienne, CNRS, Neuro-PSI/ENES UMR 9197, Saint-Etienne, France*
[2]*LBBE, CNRS UMR 5558, Université Lyon 1/Université de Lyon, Lyon, France*
[3]*Department of Animal Ecology, EBC, University of Uppsala, Uppsala, Sweden*
[4]*Département de Sciences Biologiques, Université de Montréal, Montreal, QC, Canada*
[5]*Neuro-PSI, CNRS UMR 9197, Université Paris Sud, Paris, France*

Although most bird species show monogamous pair bonds and bi-parental care, little is known of how mated birds coordinate their activities. Whether or not partners communicate with each other to adjust their behaviour remains an open question. During incubation and the first days after hatching, one parent – generally the female – stays in the nest for extended periods, and might depend on acoustic communication to exchange information with its mate outside. The Great Tit *Parus major* is an interesting study system to investigate intra-pair communication at the nest because males address songs to their mate while she is in the nest cavity, and females answer the male from the cavity with calls. However, the function of this communication remains unknown. In this study, we recorded the vocalizations and observed the resulting behaviour of Great Tit pairs around the nest at different breeding stages (laying, incubation and chick-rearing). We observed vocal exchanges (vocalization bouts, alternated on the same tempo, between the female inside the nest and her male outside) in three contexts with different outcomes: (1) the female left the nest, (2) the male entered the box with food, and the female then used specific call types, (3) mates stopped calling but did not leave or enter the nest. The structure of vocal exchanges was globally stable between contexts, but females used calls with an up-shifted spectrum during exchanges, at the end of which they left the nest or the male entered the nest. Birds vocalized more and at higher tempo during exchanges that ended up in feeding inside the nest. Birds also vocalized more during exchanges taking place during laying – a period of active mate guarding – than during incubation. We conclude that vocal exchanges could signal the females' need for food and the males' mate guarding behaviour, and discuss other possible functions of this communication.

Keywords: acoustic communication, bi-parental care, coordination, hole-nesting, intra-pair communication, monogamy, pair bond, songbird.

INTRODUCTION

Bi-parental care can be considered as a form of both conflict and cooperation between mates (Trivers 1972, Black 1996). Each parent adjusts its workload to that of its partner, but surprisingly little is known about how the division of labour is achieved (McNamara *et al.* 1999). During parental care, each mate could benefit from sending information to and receiving information from its partner. This might be especially crucial during incubation and chick-rearing. During these periods, the parent staying in the nest has no or limited visual information about the surroundings because the nest is either completely enclosed except for

*Corresponding author.
Email: ingrid.c.a.boucaud@gmail.com

the small entrance opening (cavities, burrows, spherical or bottle-shaped nests) or limits greatly the bird's movements and positions (cups or platforms). Acoustic signals are likely to play a key role in communication between mates when one of them is at the nest, but this acoustic communication between mates and its role in coordination of parental behaviour has been little studied.

Acoustic cues may be used by the bird at the nest to assess the situation outside, such as the presence or absence of predators (Burns 1983, Johnson & Kermott 1991, Ziolkowski *et al.* 1997, Elie *et al.* 2010, Mainwaring & Griffith 2013). A bird may also use acoustic communication from the nest to give information to its distant mate. In Northern Cardinals *Cardinalis cardinalis*, the female expresses her own needs for food or the need of her nestlings by singing from the nest and allows her mate to adjust his feeding visits to the nest. This limits predation risks, as males are highly conspicuous with their bright red plumage (Halkin 1997). In other bird species, females vocalize upon departing from and arriving at their nest, and this might inform their mate of their activities and reproductive state (Beletsky & Orians 1985), increase their mate's nest defence against predators (Yasukawa 1989) or signal female identity (Collias 1963, McDonald & Greenberg 1991). Finally, pair partners might use vocalizations when they meet at the nest. Each time they meet at the nest during incubation or nestling period, Zebra Finch *Taeniopygia guttata* mates perform simple coordinated mutual vocal displays (Elie *et al.* 2010). Nest meeting ceremonies using vocalizations have been described in several species, particularly in water birds (Johnsgard 1965) and seabirds (Aubin & Jouventin 2002), and are thought to contribute to pair bond maintenance; however, the functions of these vocalizations remain largely unknown (Wachtmeister 2001).

The Great Tit *Parus major* provides an excellent study system to investigate intra-pair communication at the nest and to test whether it relates to partners' coordination during breeding. Great Tits are cavity-nesters and the female builds the nest, incubates the eggs and broods the hatchlings alone (Cramp & Perrins 1993). Males are known to address songs to their mate located in the cavity, as they stop the dawn chorus just after the emergence of their female from the nest (Mace 1986), and females respond to the playback of the song

of their mate by leaving the nest (Lind *et al.* 1996). After leaving the cavity, the female is often fed by the male (Hinde 1952, Royama 1966, Lind *et al.* 1996). During nest-building, laying and incubation, females respond to their mate's song from the nest using nine different call types (Gorissen & Eens 2005) and this interactive vocal communication occurs both during and outside the dawn chorus (Gorissen & Eens 2004, Halfwerk *et al.* 2011). Because most of these female calls are produced with a low sound pressure level, they are probably used in short-range communication directed at the mate only (Gorissen & Eens 2004, 2005). Males adjust their singing behaviour depending on the female response. Indeed, males sing closer to the nest when their female is exposed to a playback of noise inside the cavity (Halfwerk *et al.* 2012), confirming that male song in this context is addressed to the mate and suggesting that female response is used as a feedback by the male. Great Tit mates thus show interactive vocal communication at the nest, but what information is exchanged and whether this communication contributes to the coordination of partners' activities remain unknown.

In this study, we recorded vocal interactions at the nest between Great Tit mates over the course of a breeding attempt from egg-laying to the young nestling stage, both during and after the dawn chorus. Simultaneously, we made direct observations of pair behaviour. We observed vocal exchanges between the female inside the nest and her male outside in three contexts with different outcomes: (1) the female left the nest, (2) the male entered the box with food, (3) mates stopped calling but did not either leave or enter the nest. To test the hypotheses that mates might communicate their readiness to enter or leave the nest and that the acoustic structure of the vocal exchange might predict its outcome, we compared the acoustic structure of vocal exchanges between contexts and between breeding stages.

METHODS

Study site

Our study was conducted in wooded areas close to the University of St-Etienne campus, France (45°25′N, 4°25′E), with 24 nest-boxes provided in 2013 and 54 nest-boxes in 2014 (wood nest-boxes, 150 × 150 × 250 mm, entrance hole 32 mm in

diameter). Nest-boxes were checked weekly beginning at the end of March, and three times a week when occupied by a breeding pair.

Recording of parental acoustic and behavioural activities around the nest

Data were collected in April–May 2013 on seven Great Tit pairs and in April–May 2014 on 12 pairs. In 2013, each pair was recorded on one morning during three different reproductive stages: laying, incubation and young nestlings (4 days old or less; at this stage females spend most of their time in the nest brooding the nestlings before they are able to thermoregulate). In 2014, each pair was recorded only once, during incubation. On the evening before a recording day, a recorder (Song-Meters SM2 + , 16-bit, 44 100-Hz sampling rate; Wildlife Acoustics Inc., Concord, MA, USA) was positioned near the nest-box, connected to a microphone (SMX-II, Wildlife Acoustics Inc.; omnidirectional, flat frequency response 20 Hz–20 kHz, sensitivity –36 ± 4 dB; 0 dB = 1 V/Pa at 1 kHz) inside the nest-box just below the ceiling (in-built pre-amplifier gain set at +24 dB) and a microphone outside, fixed on the tree trunk at the height of the nest-box (in-built pre-amplifier gain set at +42 dB). Pairs were recorded between 05:30 and 09:00 h in the laying and young nestling stages. The duration of recording was increased in the incubation stage (between 05:30 and 14:30 h) because behavioural events were less frequent at this stage. During incubation and young nestling stages, direct visual observations were performed simultaneously with acoustic recordings: an observer sat under a camouflage net 10–15 m from the nest-box and used a headphone to record vocalizations and partners' behaviour (e.g. entrance or exit from the nest) simultaneously. Direct observations were not necessary during the laying stage because behaviour during this period has been described previously in great detail (Mace 1987): only the female enters and leaves the nest during this stage, and these movements as well as periods of female presence or absence inside the nest were easily identified on acoustic recordings (Halfwerk *et al.* 2012). Moreover, direct observations were not necessary in 2014, as data from 2013 showed that each possible event was easily recognizable using the acoustic recording only. Thus, spectrograms of recordings were visualized using SONGSCOPE software (Wildlife Acoustics Inc.) to detect vocal exchanges as well as exits and entrances and presence inside the nest.

Definition of vocal exchanges

We defined a vocal exchange as the vocal interaction of a female inside her nest with her mate. Because females never called in the absence of their mate, vocal exchanges included all vocalizations produced by females from inside their nest. We considered that the vocal exchange started with the male song strophe or call preceding the first vocalization of the female, and ended with the last female vocalization. In some rare cases, the male's last vocalization bout overlapped that of the female and ended later. In such cases, the vocal exchange ended with this last male vocalization bout. A vocal exchange stopped when the female stopped calling for at least 30 s, so two successive vocal exchanges were separated by at least 30 s. Sometimes, we observed females vocalizing outside the nest, but these vocalizations were difficult to record with our recording setup, so only female vocalizations produced inside the nest-box were considered here.

Vocal exchanges occurred in three different contexts. In all cases, the male initiated the vocal exchange by either singing or calling outside the nest-box and the female responded from inside, but the three contexts differed by their outcome:

- Simple exchange: mates stopped calling but did not leave or enter the nest (Fig. 1a; Sound S1);
- Exit exchange: the female left the nest (Fig. 1b; Sound S2);
- Feeding exchange: the male entered the nest to feed the female or the nestlings. While the male was inside, the female used specific call types (Fig. 1c; Sound S3). Note that the male sometimes entered the nest-box directly without any preceding vocal exchange (incubation: one of 10 cases in 2013, and six of 20 cases in 2014; young nestling stage: eight of 12 cases in 2013).

We extracted two vocal exchanges from each context in each breeding stage. Only one context was sufficiently frequent to be analysed in laying and young nestling stages, and three contexts in the incubation stage, so in 2013 the maximum sample size per pair is thus 10 vocal exchanges. One of the seven recorded females called only twice inside the nest-box and so was not included
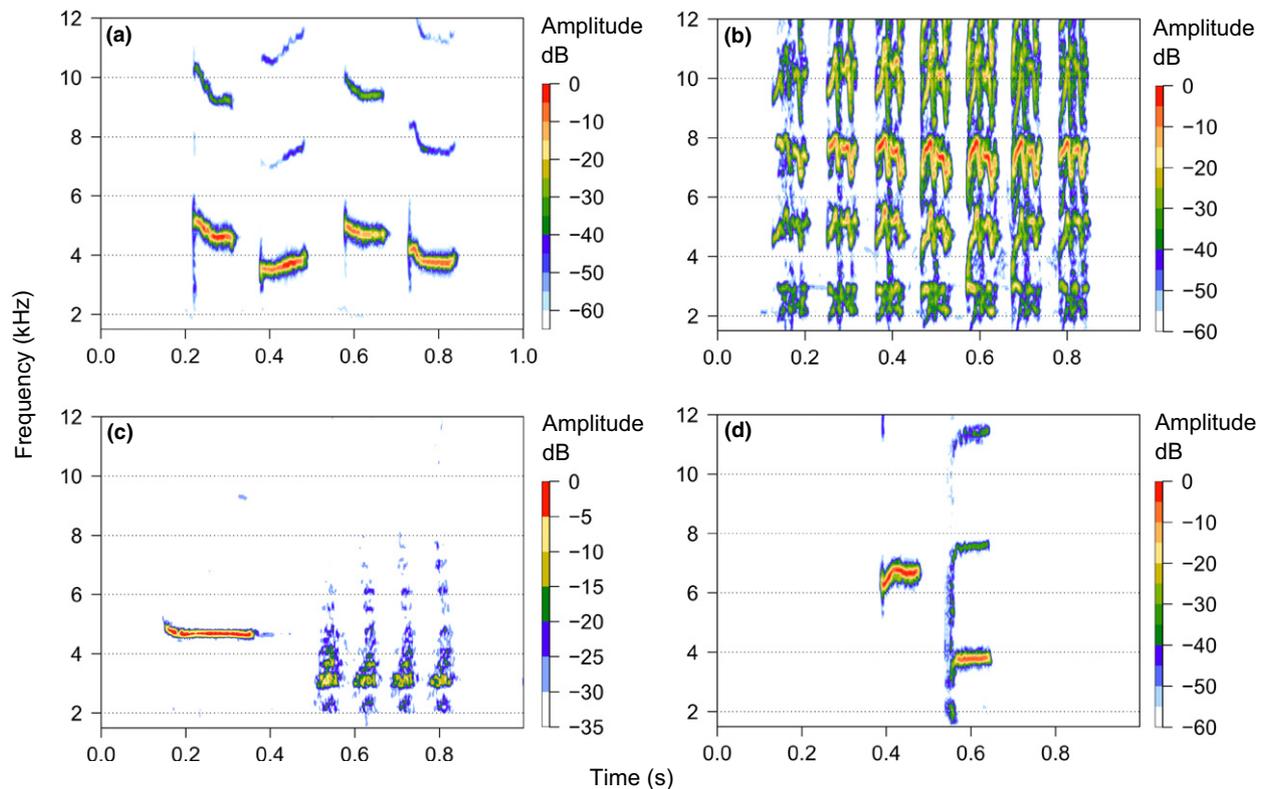
Figure 1. Spectrograms showing extracts of the three contexts of vocal exchanges recorded at the nest between Great Tit mates (microphone inside the nest-box): (a) Simple exchange, (b) Exit exchange, (c) Feeding exchange (see text for the description of these contexts); M and F: male and female vocalization bouts, respectively. Spectrograms were prepared using the Seewave package (Sueur *et al.* 2008) in ʀ software (R Development Core Team 2014).

in the acoustic analyses of vocal exchanges, but was included in other quantifications. Two other pairs had missing vocal exchanges (four and three, respectively), so a total of 53 vocal exchanges were analysed in 2013. In 2014, whenever possible, we extracted two vocal exchanges per context and per pair (maximum sample size per pair = 6 vocal exchanges). Missing vocal exchanges in some pairs led to a total of 51 vocal exchanges analysed in 2014. On these vocal exchanges, we performed acoustic analyses describing the vocal repertoire and acoustic structure of female calls and the temporal structure of the exchange.

Vocal repertoire and analysis of the acoustic structure of female calls

Both males and females produce different call and song types during vocal exchanges (Hinde 1952, Gompertz 1961). Females predominantly produced bouts of calls (series of identical calls produced with silences between calls that were shorter or equal to the call duration; Fig. 1). These bouts mainly contained chattering, a high-pitched call with rapid frequency modulations (described by Gorissen & Eens 2005, Fig. 2b; Sound S5). Females occasionally used songs (only during incubation, two females out of six in 2013 and three females out of 12 in 2014, Fig. 2a; Sound S4). Great Tit songs are notes (continuous traces on

the spectrogram separated by silences) assembled to form motifs (generally two different notes per motif), which are repeated to form a phrase (Fig. 1b). The song type produced by females sometimes matched the song type of their mate; in other words, it showed the same spectro-temporal shape and properties. Females also occasionally used contact calls (four females of 12 in 2014). Contact calls are song-like notes that can be associated to form a motif. Contrary to songs, however, these motifs are not repeated to form a phrase (Fig. 2d; Sound S7).

All males produced songs and contact calls in all vocal exchange contexts. Males occasionally used alarm calls (four males in a total of six vocal exchanges in 2013 and four males in a total of five vocal exchanges in 2014; Fig. 2c; Sound S6). Alarm calls were produced during Simple and Feeding exchanges but never during Exit exchanges.

We performed an analysis of the acoustic structure of female chattering calls extracted from recordings in 2014 (n = 1529 calls from 12 individuals, mean ± sd per individual = 127.4 ± 126.7) using custom-written codes based on the Seewave package (Sueur *et al.* 2008) implemented in ʀ (R Development Core Team 2014). The duration of each call (in s) was measured between edges manually labelled using ᴘʀᴀᴀᴛ software (http://www.fon.hum.uva.nl/praat/). After band-

Figure 2. Spectrograms of vocalizations used during exchanges: (a) female song, (b) female bout of chattering calls, (c) male alarm call, (d) male contact call. Spectrograms were prepared using the Seewave package (Sueur *et al.* 2008) in R software (R Development Core Team 2014).

pass filtering (500–20 000 Hz encompassing the spectral bandwidth of Great Tit vocalizations, 'fir' function), the amplitude of the call was measured as the root-mean-square of the amplitude envelope of the call ('rms' function) and the following spectral parameters were computed using the 'specprop' function (FFT using a Hamming window and a window length of 512):

- as the frequency spectrum is a distribution, it can be characterized using classic descriptive statistics (all in Hertz). We used the mean, the standard deviation (sd), the median, and the first (Q25) and third (Q75) quartiles of the spectrum of the call – which represent the frequencies below which lie respectively 50, 25 and 75% of the energy of the call. The interquartile range (IQR) was defined as Q75–Q25;
- the frequency of highest amplitude – the dominant frequency – can be measured over the duration of the call (obtained via the 'dfreq' function, window length of 512 and overlap of 50%) and characterized using its mean (average

dominant frequency) and its standard deviation (in Hertz);
- the call's noisiness can be quantified using the Shannon spectral entropy. The Shannon entropy of a noisy signal tends towards 1, whereas for a pure tone it tends towards 0.

Temporal structure of vocal exchanges

The temporal structure of vocal exchanges was manually labelled using PRAAT software before being analysed using custom-written codes implemented in R. For each vocalization (call or song motif), we recorded the identity of the caller and the call or song type. Then, we measured temporal parameters for each vocal exchange: the duration of the exchange and, for each sex, the numbers of (1) song motifs, (2) calls and (3) vocalization bouts (call bouts or song phrases) and their durations. For females, we also measured the number of female vocalization bouts per exchange that overlapped a male vocalization bout.

To compare the tempo of male and female vocalizations, we measured inter-bout intervals (IBIs), the duration between the start of two successive vocalization bouts of the same individual. To quantify the reaction time of the female to her male's vocalizations, we measured the mean latency in each vocal exchange, i.e. the duration between the beginning of a male vocalization bout and the beginning of the following female vocalization bout.

Statistical analyses

All statistical tests were performed using R software. Following all linear mixed models (LMMs, lmer function, lme4 package), equivariance and distribution of the residuals were graphically checked using plotresid function (RVAideMemoire package). The stability of the models and absence of influential cases were checked by removing levels of the random effects one at a time (infl.-model and cook.distance functions, influence.ME package, Nieuwenhuis *et al.* 2012). For each model, marginal and conditional coefficients of determination are presented (R2m and R2c, r.squaredGLMM function, MuMIn package; Nakagawa & Schielzeth 2013) as well as effect sizes using estimates, standard errors and 95% confidence intervals of fixed factors. *P*-values of models were obtained using Wald Chi-square tests (Anova function, car package). *Post-hoc* tests were performed using multiple comparisons tests (glht function, multcomp package, with Tukey contrasts). If equivariance and distribution of the residuals were violated or if the model was unstable, non-parametric statistics were used. Non-parametric tests (for paired data: Wilcoxon sign test; for independent data: Wilcoxon test, coin package) are presented with their effect size as $r = Z/\sqrt{N}$, where Z is the statistic and N the total sample size.

To compare between breeding stages the number of vocal exchanges of each context (Simple, Exit, Feeding) as well as the number of female exits without any vocalization and the time spent by the female in the nest during recording, we used non-parametric Friedman tests on 2013 data recorded during 05:30–09:00 h. *Post-hoc* tests were performed using pairwise multiple comparisons for ranked data (Nemenyi 1963; posthoc.friedman.nemenyi.test function, PMCMR package and wilcoxsign_test function to get the effect size and confidence interval on the significant difference).

We tested the temporal coordination between mates' vocal productions using incubation-stage data collected in 2013 and 2014. We carried out four different analyses:

- First, we tested the regressions between the mean numbers of male and female vocalization bouts per exchange, and between the mean male and female IBI per exchange. We used LMM, taking into account repeated measures within pairs (random factor) and testing also the potential interaction with the context (three levels: Simple, Exit, Feeding). As recommended for a within-subjects design with a covariate (Schielzeth & Forstmeier 2009), the covariate was also included as a random slope using the following R code: Male parameter ~ Female parameter * Context + (1 + Female parameter | Pair identity). In each LMM, one pair was identified as overly influential on the regression outcomes (see method above) so it was removed from the dataset, leading to $n = 74$ exchanges from 17 pairs.

- To test whether individuals adjusted the tempo of their vocalizations to that of their partner in alternated bouts (series MFMF..., where M is a male vocalization and F is a female vocalization), we compared each male IBI to the corresponding female IBI (in $M_1F_1M_2F_2M_3F_3$, the interval M_1M_2 is compared with the interval F_1F_2, and so on). In this analysis, we thus considered only alternated vocalization between mates (Male–Female or Female–Male transitions) so excluding successive bouts of the same individual (for instance in MFMFFF, only MFMF is studied). A positive regression between male and female IBI should indicate that mates adjust the tempo of their vocalizations to each other. This was assessed by the following R code: $\log_{10}$(Male IBI) ~ $\log_{10}$(Female IBI) + (1 + $\log_{10}$(Female IBI)| Pair identity). The sample size of this analysis was $n = 124$ dyads of male and female IBI from 14 pairs.

- If male and female have the same vocalization tempo, then we expect that male and female average IBI will not differ. Moreover, if male and female vocalizations show antiphasic alternation (same duration between female response to the preceding male bout and male response to the preceding female bout), we expect that both male and female IBI will not differ from twice the latency (delay between the beginning

of a male vocalization bout and the beginning of the female response). We tested these hypotheses on interval values (average per exchange) using an LMM with the type of interval (three levels: male IBI, female IBI or 2*Latency) as fixed factor, and the pair identity and the exchange identity as random factors using the following R code: $\log_{10}$(interval) ~ type + (1 | Pair identity) + (1 | exchange). The sample size was $n = 240$ from 80 exchanges of 18 pairs.

- To test whether the number of female vocalization bouts overlapping male bouts was random or occurred more or less often than expected by chance given the vocalization rate of the partners, we used the duty cycle method outlined by Ficken *et al.* (1974), which is commonly used to estimate chance levels of overlap (Maynard *et al.* 2012, Hall *et al.* 2015). We computed the proportion of female vocalization bouts per exchange that overlapped a male vocalization bout (observed proportion of overlaps). We compared this with the proportion of female bouts expected to overlap a male bout by chance, given the amount of time the male was vocalizing (expected proportion of overlaps = male duty cycle = sum of male bout durations/total duration of exchange). The comparison between observed and expected proportions of overlaps was done using a Wilcoxon signed rank test on all exchanges showing at least one male–female transition ($n = 52$ exchanges from 17 pairs). We also performed this comparison using only the exchanges showing at least one overlap ($n = 29$ exchanges from 15 pairs). We confirmed the results of both comparisons using only mean values per pair, controlling for pseudo-replication.

The acoustic structure of female chattering calls was studied using the 2014 incubation recordings ($n = 1529$ calls from 12 females). To test whether the acoustic structure of calls differed when compared between the three contexts of vocal exchange, we first built composite scores of acoustic structure using a principal component analysis (PCA) (dudi.pca function, ade4 package). Before being included in the PCA, symmetrical distribution of parameters was verified. The resulting PCA had two principal components (PC1 and PC2) with eigenvalues > 1 (Kaiser criterion), which

explained respectively 48.8 and 22.5% of the variance (see variable loadings in Table 1A). PC1 and PC2 were analysed using an LMM with the context (three levels: Simple, Exit, Feeding) as fixed factor and the female identity as random factor (12 levels) using the following R code: PC ~ Context + (1 | Female identity).

Because all three contexts of vocal exchange (Simple, Exit, Feeding) were not observed in every breeding stage, it was not possible to test in the same model whether acoustic parameters differed between the three contexts within the same breeding stage, or whether acoustic parameters differed between breeding stages for the same context. We thus answered these questions separately.

To test whether the temporal structure of the three contexts of vocal exchange differed when compared within the same breeding stage (which was possible only in incubation, using both 2013

Table 1. Variable loadings of the PCA on (A) the acoustic structure of females' chattering calls, (B) the temporal structure of the three contexts of vocal exchange in incubation, and (C) the temporal structure of Simple exchange in egg-laying and incubation stages.

Variable	PC1	PC2
(A)		
Duration	−0.34	0.00
Mean	−0.90	−0.34
sd	−0.75	0.51
Median	−0.80	−0.48
First quartile (Q25)	−0.33	−0.85
Third quartile (Q75)	−0.94	0.06
Interquartile range (IQR)	−0.78	0.55
Shannon spectral entropy	−0.86	0.26
Average dominant frequency	−0.54	−0.72
sd of the dominant frequency	−0.61	0.06
Amplitude	0.47	−0.50
(B)		
Duration of the vocal exchange	0.86	0.40
Number of female vocalizations	0.95	−0.04
Mean duration of a female bout	0.36	−0.85
Mean number of calls in one female bout	0.31	−0.90
Number of male vocalizations	0.85	0.36
Female's latency response to male vocalizations	−0.38	0.08
(C)		
Duration of the vocal exchange	−0.85	0.37
Number of female vocalizations	−0.97	0.05
Mean duration of a female bout	−0.43	−0.79
Mean number of calls in one female bout	−0.59	−0.67
Number of male vocalizations	−0.85	0.31
Female's latency response to male vocalizations	0.30	−0.37

and 2014 data), we first built composite scores of acoustic structure using a PCA (dudi.pca function, ade4 package). To run the PCA, we kept only parameters showing symmetrical distribution (all log-transformed to reach this criterion). The number of male and female bouts was excluded based on this criterion. IBIs were also excluded as they had no value for birds producing only one vocalization bout in a vocal exchange. The resulting PCA had two principal components (PC1 and PC2) with eigenvalue above 1 (Kaiser criterion), which explained respectively 45.7 and 30.6% of the variance (see variable loadings in Table 1B). PC1 and PC2 were analysed using an LMM with the context (three levels: Simple, Exit, Feeding) as fixed factor and the pair identity as a random factor (18 levels) with the following R code: PC ~ Context + (1 | Pair identity). The LMM on PC1 showed no overly influential pair, so the data set was $n = 77$ exchanges from 18 pairs. In the LMM on PC2, two pairs were sequentially identified as overly influential on the outcome of the model, so they were removed from the dataset to reach model stability, leading to $n = 66$ exchanges from 16 pairs. Finally, the total number of vocalization bouts and the IBI were compared between contexts using a Kruskal–Wallis test followed by pairwise multiple comparisons for ranked data (posthoc.friedman.nemenyi.test function, PMCMR package and wilcoxsign_test function to get the effect size and confidence interval on the significant difference) on average value per pair and per context to correct for pseudoreplication.

To test whether the temporal structure of the same context of vocal exchange differed between breeding stages (which was possible only for Simple vocal exchanges using 2013 data), we compared the temporal structure of exchanges between laying and incubation stages. To do so, we built composite scores of acoustic structure using a PCA (see above). PC1 and PC2 explained respectively 50 and 24.1% of the variance (see variable loadings in Table 1C). Because the sample size was small ($n = 22$ exchanges from six pairs), PC1 and PC2 were compared between laying and incubation stages using non-parametric tests on average value per pair (Wilcox sign test for paired data). The number of vocalization bouts and the IBI were also compared between stages using non-parametric tests (Wilcoxon sign test for paired data) on average value per pair and per stage to correct for pseudoreplication.

RESULTS

Frequency of the three contexts of vocal exchanges between mates across breeding stages

All three contexts of vocal exchanges (Simple, Exit and Feeding) were observed during incubation and young nestling stages, but during laying, only Simple exchanges were performed by the birds (Fig. 3). The absence of the two other contexts during laying was not simply explained by a shorter time spent by the female in the nest during this period, as this time was shorter during young nestling stage but not during laying ($\chi_2^2 = 8.0$, $P = 0.02$, $n = 7$; *posthoc* $Z = 2.37$, $P = 0.018$, $r = 0.63$). From laying to young nestling stage, the number of Simple exchanges decreased ($\chi_2^2 = 7.44$, $P = 0.024$, $n = 7$; *posthoc* $Z = 2.31$, $P = 0.021$, $r = 0.62$, Fig. 3a), whereas the number of feeding visits by the male increased ($\chi_2^2 = 13.04$, $P = 0.001$, $n = 7$; *posthoc* $Z = -2.37$, $P = 0.018$, $r = 0.63$, Fig. 3b). The number of Exit exchanges also tended to increase across breeding stages ($\chi_2^2 = 6.12$, $P = 0.047$, $n = 7$; Fig. 3c) but *post-hoc* tests did not show any pairwise significant difference. The number of female exits without vocalization increased ($\chi_2^2 = 11.62$, $P = 0.003$, $n = 7$; $Z = -2.37$, $P = 0.018$, $r = 0.63$, Fig. 3d).

Temporal coordination between mates during vocal exchanges

In all three contexts, the numbers of male and female vocalization bouts during the incubation stage were positively related (Table 2A, Fig. 4a), indicating vocal interaction between mates. Male and female IBI were also positively related (Table 2B), indicating temporal coordination. This was also true when considering only alternated vocalization bouts (male–female or female–male transitions) (Table 2C, Fig. 4b). Moreover, in each exchange, the average female IBI did not differ from the average male IBI (female 5.89 s: 95% CI 5.01–6.92, male 5.25 s: 95% CI 4.47–6.17) (Table 2D), confirming that male and female vocalizations had the same tempo. Furthermore, the delay between the beginning of a male vocalization bout and the following female bout (latency 1.2 s: 95% CI 1.04–1.37) was shorter than half the male or the female IBI (Table 2D). This result shows that vocal exchanges were not
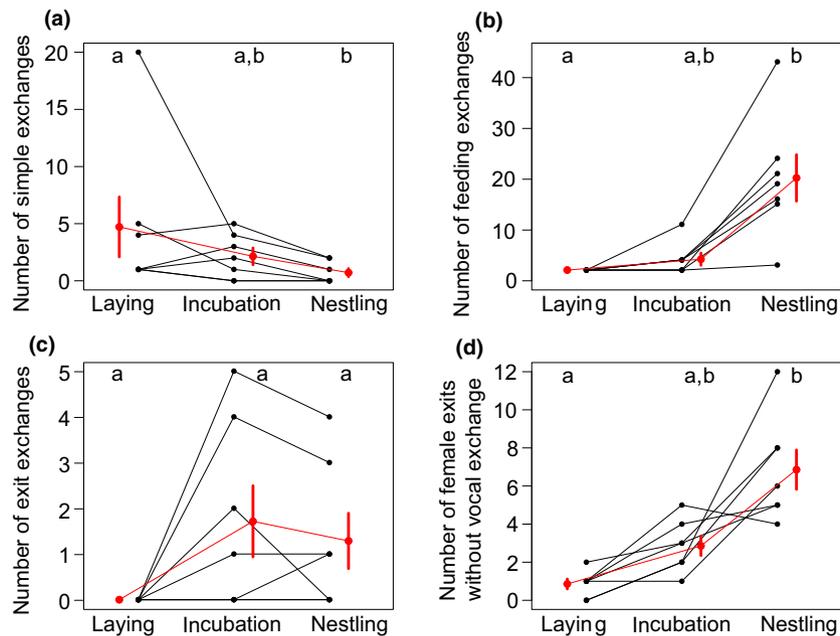
Figure 3. Number of vocal exchanges and female exits recorded between 05:30 and 09:00 h along the three phases of the breeding cycle. Lines connect values for each given nest, and red points are means with standard error on all individuals. Letters refer to significant differences among breeding stages, *n* = 7.

fully antiphasic male–female interactions, but that females responded to male vocalizations more rapidly than the reverse.

On average, 26.8% of female vocalization bouts overlapped the preceding male bout. This proportion did not differ from chance, given the vocalization rates of both partners and the duration of male vocalizations ($Z = 0.045$, $P = 0.964$, $r = 0.004$). But when considering only exchanges with at least one overlap (55.8% of the exchanges), females overlapped significantly more often with male bouts than expected by chance ($Z = -3.665$, $P = 0.0002$, $r = 0.681$). These results suggest that females matched male tempo.

Effect of the context on the acoustic structure of female calls during vocal exchanges

The first composite score of acoustic structure of the female chattering calls (PC1) showed that females used calls with up-shifted frequency spectrum (higher mean, median, Q75 and average dominant frequency), wider frequency bandwidth (higher sd and IQR), larger modulations of frequency (higher sd of the dominant frequency), more spectral noise and lower amplitude in Exit

than in Simple exchanges (Table 3, Fig. 5a). PC2 showed that females used calls with up-shifted frequency spectrum (higher Q25 and average dominant frequency), narrower frequency bandwidth (lower sd and IQR) and higher amplitude in Feeding than in Simple exchanges (Table 3, Fig. 5a). The same differences in PC2 showed tendencies between Feeding and Exit exchanges, as well as between Exit and Simple exchanges.

Effect of the context on the temporal structure of vocal exchanges

The first composite score of acoustic structure of the vocal exchange (PC1) showed that Feeding exchanges differed significantly from Simple and Exit exchanges (Table 3, Fig. 5b): Feeding exchanges were longer, with more male and female vocalizations. The second composite score (PC2 of the PCA) showed that Exit exchanges differed significantly from Simple exchanges (Table 3, Fig. 5b): females used longer bouts and more calls per bout during Exit exchanges than during Simple exchanges. Furthermore, Feeding exchanges tended to have more vocalization bouts than Exit exchanges ($\chi_2^2 = 5.54$, $P = 0.063$; *post-hoc* $Z = -2.31$, $P = 0.021$, $r = 0.44$) and shorter IBI than

Table 2. Results of LMM on the temporal coordination between mates during vocal exchanges.

	Estimate	se		χ^2	df	P-value
(A)						
Number of male vocalization bouts (R2m = 0.72, R2c = 0.85)						
(Intercept)	0.4544	0.3527				
Number of female vocalization bouts	0.7455	0.1525				
Feeding exchanges	−0.4808	0.5372				
Simple exchanges	−0.1096	0.5109				
Number of female vocalization bouts: Feeding Exchanges	0.2126	0.1465				
Number of female vocalization bouts: Simple Exchanges	0.1393	0.1855				
Number of female vocalization bouts				67.68	1.0	**<0.001**
Context				0.23	2.0	0.891
Number of female vocalization bouts: Context				2.11	2.0	0.349
(B)						
Mean male IBI (R2m = 0.34, R2c = 0.60)						
(Intercept)	3.5268	1.5677				
Female IBI	0.4022	0.2309				
Feeding exchanges	0.4907	2.0732				
Simple exchanges	−0.5414	1.9989				
Female IBI: Feeding exchanges	−0.2216	0.3504				
Female IBI: Simple exchanges	0.0850	0.2772				
Female IBI				10.79	1.0	**0.001**
Context				0.88	2.0	0.643
Female IBI: Context				1.05	2.0	0.593
(C)						
Male IBI in alternated vocalization bouts (R2m = 0.35, R2c = 0.47)				54.04	1.0	**<0.001**
(Intercept)	0.2365	0.0509				
Female IBI (log)	0.5877	0.0800				
			CI 95%	z-value		
(D)						
IBI type (R2m = 0.34, R2c = 0.54)				131.39	2.0	**<0.001**
2*Female latency response	0.3812	0.0301	[0.320; 0.442]			
Female IBI	0.7689	0.0348	[0.699; 0.839]			
Male IBI	0.7181	0.0347	[0.648; 0.788]			
Female IBI - 2*Female latency response				10.33		**<0.001**
Male IBI - 2*Female latency response				8.96		**<0.001**
Male IBI - Female IBI				−1.27		0.410

Significant results are displayed in bold.

Simple exchanges ($\chi_2^2 = 5.85$, $P = 0.054$; *post-hoc* $Z = −2.33$, $P = 0.020$, $r = 0.45$). Thus, longer vocal exchanges in which birds produced more vocalizations at higher bout rate had a higher probability of concluding with a feeding event, and the outcome of vocal exchanges with more female calls per bout was more likely to be an exit.

Effect of the breeding stage on the temporal structure of vocal exchanges

The first composite score of acoustic structure of the vocal exchange (PC1) showed that Simple exchanges during laying were significantly longer,

with more male and female vocalizations, longer female vocalization bouts and more calls per female bouts, than during incubation ($Z = −2.02$, $P = 0.043$, $r = 0.58$). The breeding stage did not affect PC2 or mean IBI per exchange, or total number of vocalization bouts per exchange (respectively $Z = 0.67$, $P = 0.50$, $r = 0.19$; $Z = 0.40$, $P = 0.686$, $r = 0.13$; $Z = 1.62$, $P = 0.10$, $r = 0.51$).

DISCUSSION

We studied the characteristics of vocal exchanges around the nest between mates in the Great Tit, and found that vocal exchanges are coordinated
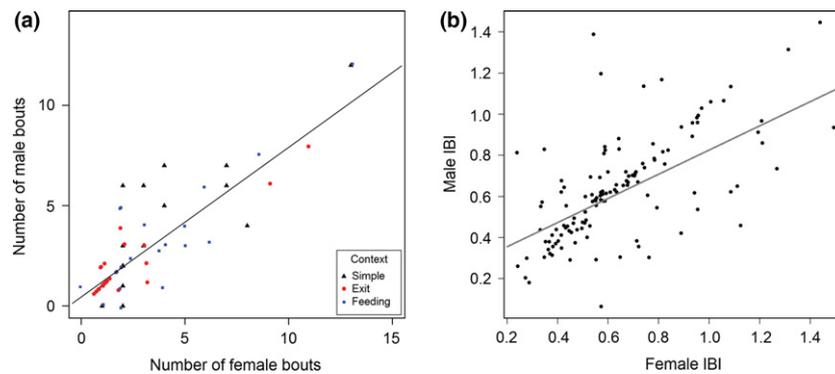
Figure 4. Temporal coordination between mates during vocal exchanges: linear regressions between (a) numbers of male and female bouts per exchange, and (b) male and female IBI in alternated sequences (see Methods). Regression lines result from the LMM analyses.

Table 3. Effect of the context on the acoustic structure of the female chattering calls and on the structure of the vocal exchange.

	Estimate	se	CI 95%	z-value	χ^2	df	P-value
PC1 of the PCA on chattering calls structure (R2m = 0.002, R2c = 0.54)					6.98	2	**0.030**
Exit exchange	−0.7660	0.5530	[−1.98; 0.44]				
Feeding exchange	−0.6320	0.5510	[−1.84; 0.58]				
Simple exchange	−0.3990	0.5520	[−0.72; −1.61]				
Feeding exchange - Exit exchange	0.1337	0.1306		1.02			0.561
Simple exchange - Exit exchange	0.3669	0.1431		2.56			**0.028**
Simple exchange - Feeding exchange	0.2332	0.1231		1.89			0.140
PC2 of the PCA on chattering calls structure (R2m = 0.015, R2c = 0.27)					24.49	2	**<0.001**
Exit exchange	0.1707	0.2512	[−0.37; 0.71]				
Feeding exchange	−0.0484	0.2486	[−0.59; 0.49]				
Simple exchange	0.4301	0.2503	[−0.11; 0.97]				
Feeding exchange - Exit exchange	−0.2191	0.1027		−2.13			0.083
Simple exchange - Exit exchange	0.2594	0.1125		2.31			**0.055**
Simple exchange - Feeding exchange	0.4785	0.0969		4.94			**<0.001**
PC1 of the PCA on acoustic structure of vocal exchanges (R2m = 0.17, R2c = 0.24)					16.47	2	**<0.001**
Exit exchange	−0.6020	0.3100	[−1.22; 0.02]				
Feeding exchange	1.0320	0.3350	[0.36; 1.70]				
Simple exchange	−0.3680	0.2940	[−0.96; 0.22]				
Feeding exchange - Exit exchange	1.6339	0.4319		3.78			**<0.001**
Simple exchange - Exit exchange	0.2341	0.4010		0.58			0.828
Simple exchange - Feeding exchange	−1.3998	0.4205		−3.33			**0.003**
PC2 of the PCA on acoustic structure of vocal exchanges (R2m = 0.09, R2c = 0.39)					8.76	2	**0.013**
Exit exchange	−0.1620	0.2660	[−0.70; 0.38]				
Feeding exchange	0.1211	0.2860	[−0.46; 0.70]				
Simple exchange	0.6630	0.2520	[0.15; 1.18]				
Feeding exchanges - Exit exchange	0.2833	0.3197		0.89			0.649
Simple exchange - Exit exchange	0.8258	0.2860		2.89			**0.011**
Simple exchange - Feeding exchanges	0.5424	0.3038		1.79			0.174

Significant results are displayed in bold.

because male and female alternate their vocalizations, and male and female tempos are correlated. Although much simpler, these coordinated vocalizations share acoustic characteristics of the song duets of tropical bird species (Marshall-Ball *et al.* 2006, Molles & Waas 2006, Bradley & Mennill 2009, Koloff & Mennill 2011). Indeed, avian duets are mutual acoustic displays between two birds, generally a mated pair, that make temporally coordinated vocal or non-vocal sounds (Farabaugh 1982, Hall 2004). Temporal coordination in duets is often considered a marker of pair bond strength and the mates' commitment in pair bond activities (Hall 2004). The rich field of study on song duets
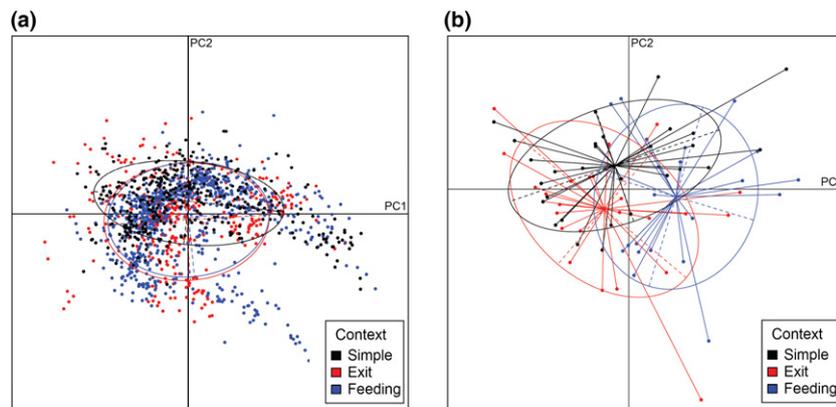
Figure 5. Effect of context on (a) the acoustic structure of female chattering calls and (b) the temporal structure of vocal exchanges between mates. In (a), lower values of PC1 indicate calls with up-shifted frequency spectrum (higher mean, median, Q75 and average dominant frequency), wider frequency bandwidth (higher sd and IQR), larger modulations of frequency (higher sd of the dominant frequency), more spectral noise and lower amplitude. Lower values of PC2 indicate calls with up-shifted frequency spectrum (higher Q25 and average dominant frequency), narrower frequency bandwidth (lower sd and IQR) and higher amplitude. In (b), higher PC1 values indicate longer vocal exchanges with more male and female vocalizations. Lower PC2 values indicate longer female vocalization bouts with more calls. Results from the corresponding PCAs. Ellipses contain 67% of the data points in each group.

is thus a valuable theoretical background to the formulation of hypotheses on the structure and functions of coordinated communication between mates at the nest. Further studies using playback experiments could determine more precisely the mechanisms of this coordination and which bird leads the exchange.

Simple exchanges were significantly longer, with more male and female vocalizations, longer female vocalization bouts and more calls per female bout during laying than during incubation. This difference matches with the peak of male song observed during the female fertility period (Mace 1987, Cramp & Perrins 1993). During laying, male vocalizations have been hypothesized to stimulate the female to lay eggs and to copulate, as well as to reduce the risk of extra-pair copulations (Mace 1987). For instance, males can modify the acoustic features of their song according to female fertility and this capacity is correlated with female sexual fidelity: males that switch to a low-pitched version of their song at the peak of female fertility get cuckolded less often (Halfwerk *et al.* 2011). Thus, Simple exchanges observed in this study could contribute to mate guarding and pair bond maintenance.

Males and females use different vocal repertoires during vocal exchanges at the nest. Our sample size was rather small, so the precise composition of the repertoire remains to be fully studied using more recordings per pair. Like Gorissen and Eens (2005),

we found that the chattering call was the most common female call and was used in all three contexts. Thus, this call type is not specifically associated with female exit from the nest and is not only a departure call that aims at promoting vigilance and nest defence by the male (Yasukawa 1989, McDonald & Greenberg 1991, Grunst *et al.* 2014), as suggested by Gorissen and Eens (2004), but is a call produced in response to the male's vocalizations.

Some females occasionally used songs during vocal exchanges. In female Great Tits, song is very uncommon and its function is poorly known (Hinde 1952, Gompertz 1961), although it is primarily reported during reproductive fighting or when the male is absent from the territory, which was not the case here. Because this vocalization had a higher amplitude than other calls used by the female inside the nest cavity, female song may contribute to extra-pair communication by signalling ownership of the nest cavity and thus play a role in nest or territory defence. The use of vocalizations at the nest as a territorial signal has been reported in other species. For instance, the nest calls of female Red-winged Blackbirds *Agelaius phoeniceus* might signal ownership of the nest and advertise the presence of a settled female (Small & Boersma 1990). The use of vocal exchanges between pair members for joint territory defence is also one of the main functions identified for duets of tropical bird species (Marshall-Ball *et al.* 2006, Molles & Waas 2006, Bradley & Mennill 2009, Koloff & Mennill 2011).

Finally, some males used alarm calls. Interestingly, females never emerged from their nest when males produced alarm calls. Our sample size concerning this vocalization type is rather small, but this result may suggest that vocal exchanges can be used as an anti-predator strategy: the male could signal to the female when it is safe, or not, to leave the nest cavity. Japanese Great Tits *Parus major minor* produce acoustically distinct calls for different nest predators, which elicit appropriate predator searching and escape behaviours from both adults and nestlings (Suzuki 2011, 2012). It remains to be studied whether male Great Tits use different alarm calls during vocal exchanges with the female at the nest.

Within a given breeding stage, the outcome of the vocal exchange could be determined by differences in acoustic structure. During incubation, longer vocal exchanges in which birds produced more vocalizations at a higher tempo had a higher probability of concluding in a feeding event in the nest. The outcome of vocal exchanges with more female calls per bout was more likely to be an exit from the nest by the female, which might lead to feeding by the mate outside the nest-box (Royama 1966). Moreover, females used chattering calls with an up-shifted spectrum during Feeding and Exit exchanges. Female calls had narrower frequency bandwidth and higher amplitude in Feeding than in Simple exchanges, and wider frequency bandwidth, larger modulations of frequency, more spectral noise and lower amplitude in Exit than in Simple exchanges. All these results show that females could indicate their energetic needs to their mate both in the structure of their calls and in the temporal structure of the vocal exchange. In Northern Cardinals, females change the male's probability of coming to the nest with food by singing from the nest in response to his vocalizations (Halkin 1997). This could allow the male to limit his feeding visits to the nest to times when they are really needed and therefore to reduce flights to the nest that might attract predators. As acoustic signals produced by the female from the nest might also attract predators (Yasukawa 1989), the net benefit of mates' vocal exchanges might lie in the multiple functions of this communication.

Our results suggest that females might encode their need for food in the temporal structure of the vocal exchange and in the structure of their calls. We also found that Feeding exchanges as well as Exit exchanges were both absent during egg-laying and started during incubation. Thus, these vocal exchanges do not only reflect female fertility and male mate guarding as suggested by previous studies (Gorissen & Eens 2004). In several passerine species, females signal their need for food with begging calls, whose intensity is condition-dependent and determines male feeding (Tobias & Seddon 2002, Otter *et al.* 2007, Moore & Rohwer 2012, Cantarero *et al.* 2014). Mate feeding in the early breeding stages has been suggested to have evolved as a compensatory energetic strategy in species in which the female incubates and builds the nest alone (Galván & Sanz 2011). In Great Tits, mate feeding starts at egg-laying, increases during incubation and continues until the young leave the nest. Thus, it takes place when the energetic demands are high for egg or heat production and, more importantly, when female foraging movements are limited during incubation (Hinde 1952, Royama 1966). Whether female nutritional state affects the rate of male feeding remains to be experimentally tested.

At the young nestling stage, both the number of Feeding exchanges and the number of female exits without vocal exchanges increased. This is consistent with the fact that nestling nutritional needs are added to the female's needs, and is in agreement with the possibility that a females may use vocalizations to signal their own needs as well as the needs of their offspring (Halkin 1997, Ellis *et al.* 2009). Feeding vocal exchanges could thus play a role in the communication between mates to organize parental care.

In conclusion, we have shown that Great Tit pairs use vocal interactions around the nest cavity throughout breeding, and that these interactions take place in three contexts. These vocal exchanges could possibly signal a female's needs to the male, and contribute to predator vigilance and pair bond maintenance. Future studies could also investigate to what extent the coordination of this communication relates to the coordination of pair members during breeding or to pair bond strength, and thus the possible impact of this communication on reproductive success.

REFERENCES

Aubin, T. & Jouventin, P. 2002. How to vocally identify kin in a crowd: the penguin model. In Slater, P.J.B., Rosenblatt, J.S., Snowdon, C.T. & Roper, T.J. (eds) *Advances in the Study of Behavior*: 243–277. London: Academic Press.

Beletsky, L.D. & Orians, G.H. 1985. Nest-associated vocalizations of female Red-winged Blackbirds, *Agelaius phoeniceus*. *Z. Tierpsychol.* **69**: 329–339.

Black, J.M. 1996. *Partnerships in Birds: the Study of Monogamy*. Oxford: Oxford University Press.

Bradley, D.W. & Mennill, D.J. 2009. Strong ungraded responses to playback of solos, duets and choruses in a cooperatively breeding Neotropical songbird. *Anim. Behav.* **77**: 1321–1327.

Burns, J. T. 1983. *Mate switching in House Wrens*. Unpublished PhD thesis, University of Minnesota.

Cantarero, A., López-Arrabé, J., Palma, A., Redondo, A.J. & Moreno, J. 2014. Males respond to female begging signals of need: a handicapping experiment in the Pied Flycatcher, *Ficedula hypoleuca*. *Anim. Behav.* **94**: 167–173.

Collias, N.E. 1963. A spectrographic analysis of the vocal repertoire of the African Village Weaverbird. *Condor* **65**: 517–527.

Cramp, S. & Perrins, C.M. 1993. *Handbook of the Birds of Europe, the Middle East, and North Africa: Volume VII: Flycatchers to Shrikes*. Oxford: Oxford University Press.

R Development Core Team 2014. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Elie, J.E., Mariette, M.M., Soula, H.A., Griffith, S.C., Mathevon, N. & Vignal, C. 2010. Vocal communication at the nest between mates in wild Zebra Finches: a private vocal duet? *Anim. Behav.* **80**: 597–605.

Ellis, J.M.S., Langen, T.A. & Berg, E.C. 2009. Signaling for food and sex? Begging by reproductive female White-throated Magpie-jays. *Anim. Behav.* **78**: 615–623.

Farabaugh, S. 1982. The ecological and social significance of duetting. In: Kroodsma, D.E. & Miller, E.H. (eds) *Acoustic Communication in Birds*, Vol. 2: 85–124. New York: Academic Press.

Ficken, R.W., Ficken, M.S. & Hailman, J.P. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. *Science* **183**: 762–763.

Galván, I. & Sanz, J.J. 2011. Mate-feeding has evolved as a compensatory energetic strategy that affects breeding success in birds. *Behav. Ecol.* **22**: 1088–1095.

Gompertz, T. 1961. The vocabulary of the Great Tit. *Br. Birds* **54**: 369–417.

Gorissen, L. & Eens, M. 2005. Complex female vocal behaviour of Great and Blue Tits inside the nesting cavity. *Behaviour* **142**: 489–506.

Gorissen, L. & Eens, M. 2004. Interactive communication between male and female Great Tits (*Parus major*) during the dawn chorus. *Auk* **121**: 184–191.

Grunst, M.L., Grunst, A.S. & Rotenberry, J.T. 2014. Phenotypic plasticity in nest departure calls: weighing costs and benefits. *Anim. Behav.* **90**: 31–39.

Halfwerk, W., Bot, S., Buikx, J., van der Velde, M., Komdeur, J., ten Cate, C. & Slabbekoorn, H. 2011. Low-frequency songs lose their potency in noisy urban conditions. *Proc. Natl Acad. Sci. USA* **108**: 14549–14554.

Halfwerk, W., Bot, S. & Slabbekoorn, H. 2012. Male Great Tit song perch selection in response to noise-dependent female feedback. *Funct. Ecol.* **26**: 1339–1347.

Halkin, S.L. 1997. Nest-vicinity song exchanges may coordinate biparental care of Northern Cardinals. *Anim. Behav.* **54**: 189–198.

Hall, M. 2004. A review of hypotheses for the functions of avian duetting. *Behav. Ecol. Sociobiol.* **55**: 415–430.

Hall, M.L., Rittenbach, M.R.D. & Vehrencamp, S.L. 2015. Female song and vocal interactions with males in a neotropical wren. *Front. Evol. Ecol.* **3**: 12.

Hinde, R.A. 1952. The behaviour of the Great Tit (*Parus major*) and some other related species. *Behaviour* **2**(Suppl): 1–207.

Johnsgard, P.A. 1965. *Handbook of Waterfowl Behavior*. Ithaca, NY: Cornell University Press.

Johnson, L.S. & Kermott, L.H. 1991. The functions of song in male House Wrens (*Troglodytes aedon*). *Behaviour* **116**: 190–209.

Koloff, J. & Mennill, D. 2011. Aggressive responses to playback of solos and duets in a Neotropical antbird. *Anim. Behav.* **82**: 587–593.

Lind, H., Dabelsteen, T. & McGregor, P.K. 1996. Female Great Tits can identify mates by song. *Anim. Behav.* **52**: 667–671.

Mace, R. 1986. Importance of female behaviour in the dawn chorus. *Anim. Behav.* **34**: 621–622.

Mace, R. 1987. The dawn chorus in the Great Tit *Parus major* is directly related to female fertility. *Nature* **330**: 745–746.

Mainwaring, M.C. & Griffith, S.C. 2013. Looking after your partner: sentinel behaviour in a socially monogamous bird. *PeerJ* **1**: e83.

Marshall-Ball, L., Mann, N. & Slater, P.J.B. 2006. Multiple functions to duet singing: hidden conflicts and apparent cooperation. *Anim. Behav.* **71**: 823–831.

Maynard, D.F., Ward, K.-A.A., Doucet, S.M. & Mennill, D.J. 2012. Calling in an acoustically competitive environment: duetting male Long-tailed Manakins avoid overlapping neighbours but not playback-simulated rivals. *Anim. Behav.* **84**: 563–573.

McDonald, M.V. & Greenberg, R. 1991. Nest departure calls in female songbirds. *Condor* **93**: 365–373.

McNamara, J.M., Gasson, C.E. & Houston, A.I. 1999. Incorporating rules for responding into evolutionary games. *Nature* **401**: 368–371.

Molles, L.E. & Waas, J.R. 2006. Are two heads better than one? Responses of the duetting Kokako to one- and two-speaker playback. *Anim. Behav.* **72**: 131–138.

Moore, S.D. & Rohwer, V.G. 2012. The functions of adult female begging during incubation in sub-Arctic breeding Yellow Warblers. *Anim. Behav.* **84**: 1213–1219.

Nakagawa, S. & Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**: 133–142.

Nemenyi, P. B. 1963. *Distribution-free multiple comparisons*. Unpublished PhD thesis, University of Princeton.

Nieuwenhuis, R., Grotenhuis, M. & Pelzer, B. 2012. influence.ME: tools for detecting influential data in mixed effects models. *R Journal* **4**: 38–47.

Otter, K.A., Atherton, S.E. & van Oort, H. 2007. Female food solicitation calling, hunger levels and habitat differences in the Black-capped Chickadee. *Anim. Behav.* **74**: 847–853.

Royama, T. 1966. A re-interpretation of courtship feeding. *Bird Study* **13**: 116–129.

Schielzeth, H. & Forstmeier, W. 2009. Conclusions beyond support: overconfident estimates in mixed models. *Behav. Ecol.* **20**: 416–420.

Small, M.P. & Boersma, P.D. 1990. Why female Red-winged Blackbirds call at the nest. *Wilson Bull.* **102**: 154–160.

Sueur, J., Aubin, T. & Simonis, C. 2008. Seewave: a free modular tool for sound analysis and synthesis. *Bioacoustics* **18**: 213–226.

Suzuki, T.N. 2011. Parental alarm calls warn nestlings about different predatory threats. *Curr. Biol.* **21**: R15–R16.

Suzuki, T.N. 2012. Referential mobbing calls elicit different predator-searching behaviours in Japanese Great Tits. *Anim. Behav.* **84**: 53–57.

Tobias, J.A. & Seddon, N. 2002. Female begging in European Robins: do neighbors eavesdrop for extrapair copulations? *Behav. Ecol.* **13**: 637–642.

Trivers, R.L. 1972. Parental investment and sexual selection. In Campbell, B. (ed.) *Sexual Selection and the Descent of Man 1871–1971*: 136–179. University of California, Los Angeles: Aldine Publishing Company.

Wachtmeister, C.A. 2001. Display in monogamous pairs: a review of empirical data and evolutionary explanations. *Anim. Behav.* **61**: 861–868.

Yasukawa, K. 1989. The costs and benefits of a vocal signal: the nest-associated 'Chit' of the female Red-winged Blackbird, *Agelaius phoeniceus*. *Anim. Behav.* **38**: 866–874.

Ziolkowski, D.J., Jr, Johnson, L.S., Hannam, K.M. & Searcy, W.A. 1997. Coordination of female nest attentiveness with male song output in the cavity-nesting House Wren *Troglodytes aedon*. *J. Avian Biol.* **28**: 9–14.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Sound S1. Simple exchange
Sound S2. Exit exchange
Sound S3. Feeding exchange
Sound S4. Song
Sound S5. Chattering calls
Sound S6. Alarm call
Sound S7. Contact call