



Original Article

# Acoustic communication in zebra finches signals when mates will take turns with parental duties

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Bi-parental care may involve both cooperation and conflict between parents. Parents adjust their workload to that of their partner and this ability is likely to affect reproductive success. Whether mates communicate, either to resolve the sexual conflict or to coordinate their joint investment in parental care is a largely unaddressed question which we examined by recording wild zebra finches at the nest during incubation. Zebra finch (*Taeniopygia guttata*) partners produce vocal exchanges at the nest that can be characterized as duets. Some duets end in nest-relief (when birds take turns incubating and foraging) but some do not (when the foraging mate vocally interacts with its incubating partner by coming inside or in the vicinity of the nest). Our data indicate that the structure of the duet predicted its outcome (relief or not), with a parent calling differently before leaving or staying in the nest by modifying its vocal repertoire as well as the acoustic structure of one particular call type which is typically used inside the nest. Zebra finch partners may thus exchange on the time to take turns with parental duties. Our results show that acoustic communication between partners might be of importance in the organization of parental care and could help in understanding sexual conflict resolution or cooperation phenomena in future studies.

**Key words:** bi-parental care, coordination, duets, intra-pair communication, monogamy, negotiation.

## INTRODUCTION

Bi-parental care is an excellent model system to study cooperation and conflict between unrelated individuals. Indeed, the adjustment of an individual's workload to that of its partner can be considered as the result of an evolutionary conflict: each parent may increase its lifetime reproductive success by reducing its investment in current offspring care at the expense of the other sex (Trivers 1972). Models predict that parents may either compensate (Houston and Davies 1985; McNamara et al. 1999; Jones et al. 2002; McNamara et al. 2003) or match (Johnstone and Hinde 2006) the parental effort of their mate. Several empirical studies have tested these models by experimentally decreasing or increasing the parental effort of an individual to observe modifications in the behavior of its partner (Lessells 2012). But whenever partners breed together more than once,

they share the cost of the current breeding effort on future reproduction and should cooperate to optimize breeding for the pair as a whole. In this framework, the adjustment of an individual's workload to that of its partner would be the result of a coordinated teamwork and the pair-bond would represent a cooperative partnership (Black 1996). Indeed, parents may synchronize their activities, like foraging trips or nest visits to feed the chicks (Lee et al. 2010; Mariette and Griffith 2012; van Rooij and Griffith 2013; Mariette and Griffith 2015) and the degree of synchrony can correlate with the reproductive success (Mariette and Griffith 2012; Mariette and Griffith 2015). Breeding success increases with pair-bond duration in many long-term monogamous species, and this has been attributed to the progressive improvement of coordination between partners (mate familiarity effect: Forslund and Part 1995; Black 1996; Black 2001). Regardless of whether behavioral adjustments between mates result from conflict or cooperative optimization of bi-parental care, their mechanisms have seldom been studied. Although

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effective communication can promote conflict resolution as well as cooperation, communication between partners during parental care has been surprisingly unexplored.

Behavioral adjustments between mates might be particularly important in species with bi-parental incubation. In these species, partners take turns incubating the eggs and the transition when the foraging partner relieves the incubating partner, a nest-relief, is a crucial step. A failure of relief would leave the nest unattended and could have important impacts on the clutch (Ball and Silver 1983; Spoon et al. 2006).

The duration of the incubation bout (measured as the period during which only one parent incubates) may be controlled by the returning bird, especially in species that have to forage far from the nest (Williams and Croxall 1991; Widmann et al. 2015). But in species in which mates can stay in contact during incubation, the incubating bird can control the duration of a bout by deciding to leave the nest when its partner is nearby (Ball and Silver 1983). Finally, mates may decide together when it is time to do the relief and this process may involve communication.

In the ring dove (*Streptopelia risoria*), male and female incubate the eggs and the non-incubating bird can initiate a nest-relief by various behaviors such as allopreening (Ball and Silver 1983). In several species, mates perform a display referred to as a nest-relief ceremony when taking turns incubating and foraging but little is known about the mechanisms underlying the behavioral exchange and the function of the display (Wachtmeister 2001). Because female vocalizations have long been neglected (Riebel 2003; Riebel et al. 2005; Odom et al. 2014), little is known on interactive communication between males and females with the exception of acoustic duets (Farabaugh 1982; Hall 2004; Benedict 2008; Hall 2009; Dahlin and Benedict 2013). Avian duets are joint acoustic displays between 2 birds that make temporally coordinated vocal or non-vocal sounds. Among them, the highly coordinated song duets of tropical songbirds are the most studied (Farabaugh 1982; Hall 2004; Benedict 2008; Hall 2009; Dahlin and Benedict 2013). These duets have been hypothesized to fulfil several functions, such as pair-bond maintenance, mate guarding, territory defense, or synchronization of reproductive effort. A recent study suggested that the evolution of duets is associated with year-round territoriality and long-term pair-bonds (Tobias et al. 2016). But the possibility that duets could play a role in parental care, and more precisely in the coordination of bi-parental incubation, has never been explored (Hall 2004; Hall 2009; Dahlin and Benedict 2013).

Although song duetting is relatively rare (estimates ranging from 4.3% of all bird species (420 species, Hall 2009) to 15.6% of songbirds [58 out of 372 sampled species, Logue and Hall 2014]), interactive communication between mates involving simpler and less conspicuous vocalizations is likely to be more widespread (Todt et al. 1981; Lamprecht et al. 1985; Morton and Derrickson 1996; Wright and Dahlin 2007). Until recently, most research on bioacoustics has focused on high amplitude signals that project over long distances and can simultaneously influence multiple types of receivers (Anderson and Reichard 2015; Reichard and Anderson 2015). But in songbirds there is increasing evidence that not only songs but also calls, which are usually discrete low amplitude signals, play a role during breeding (Elie et al. 2010; Ter Maat et al. 2014; Gill et al. 2015). Intra-pair acoustic communication at the nest using calls has been described in some species (Halkin 1997; Gorissen and Eens 2004; Elie et al. 2010; Halfwerk et al. 2012; Grunst et al. 2014) and could be used by mates to coordinate nest-relief.

Zebra finches (*Taeniopygia guttata*) maintain life-long pair bonds and both parents contribute to nest building, incubation and chicks provisioning (Zann 1996). Mates show a high degree of coordination of their activities during nestlings feeding (Mariette and Griffith 2012; Mariette and Griffith 2015) and by sharing incubation time equally (El-Wally 1966; Delesalle 1986; Zann and Rossetto 1991; Gorman et al. 2005; Gilby et al. 2013). There is a striking correlation in the investment of partners on the first day of incubation, when it is difficult to understand how the male is aware that the female has laid her last egg (Zann and Rossetto 1991). The coordination of partners when foraging was positively related to overall reproductive success, and this was driven primarily by hatching success, indicating the benefits of good coordination during incubation (Mariette and Griffith 2012). Zebra finches use lots of calls throughout the year and some of them are particularly used during breeding (Zann 1996; Elie et al. 2010; Elie and Theunissen 2016; Gill et al. 2015). Moreover, during breeding, parents perform call duets each time they meet at the nest (Elie et al. 2010; Boucaud et al. 2016). The duets performed during incubation shift changes (when one partner swaps with the other—hereafter a nest-relief), function as a vocal negotiation process over incubation share (Boucaud et al. 2016). Indeed, in domestic birds, partners' calling behaviors during the relief duet depend on the previous shift's duration, and predict partners' respective time off nest during the subsequent shifts (Boucaud et al. 2016). But all duets do not end in relief: between 2 reliefs, partners often perform call duets without swapping roles at the end (with one bird calling from outside the nest to the other bird in the nest or with one bird visiting the other into the nest). If partners communicate to adjust the time of the nest-relief, the acoustic structure of the duet should predict its outcome (relief or not). In this study, we tested this hypothesis by recording wild zebra finch pairs during incubation. We analyzed the temporal structure and vocal repertoire of the duets as well as the acoustic structure of one call type specifically used by both male and female in the nest. We compared relief duets produced by 1) the returning male and the incubating female and 2) the returning female and the incubating male to see if acoustic features predict who is returning/leaving. We also tested whether the acoustic features of duets produced by the incubating female and the returning male could predict 1) male entrance in the nest and 2) male's relief of the female.

## METHODS

### Study site

Data were collected from October to early November 2012 at Fowlers Gap Arid Zone Research Station, western New South Wales, Australia (31°05'13.1"S 141°42'17.4"E). The study area at Gap Hills is typical zebra finch breeding habitat (Acacia spp. trees and shrubs; Griffith et al. 2008). It had been provided with 191 identical nest-boxes constructed of 8-mm plywood with internal dimensions of 140 mm (length) × 93 mm (breadth) × 180 mm (depth at the back) × 120 mm (depth at the front) and with an entrance hole of 30 mm diameter. All nest-boxes were fixed on individual steel stakes 1–1.8 m off the ground and within 2 m of an acacia bush (Griffith et al. 2008).

### Recording

Eighteen breeding pairs were recorded during incubation on 2 consecutive days [except for 2 pairs that were recorded for the second time 2 days after the first recording; first day of

recording during the incubation cycle mean  $\pm$  standard deviation (SD) =  $6 \pm 3$ ]. The birds were not banded but no pair or individual could have been recorded at 2 different nests because all recordings took place in a short time window (25 days) relative to the length of a pair's breeding attempt and because monogamy is strict in this species (Zann 1996; Griffith et al. 2010).

Just before recording, a digital recorder (Zoom H4n, 44.1 kHz, 16 bit, flat frequency response from 50 to 20000 Hz) was positioned near the nest-box, connected to a tie microphone (Audio-Technica AT803, flat frequency response from 30 to 20000 Hz) in the nest-box just below the ceiling and a tie microphone outside, fixed on a branch near the nest-box entrance. During the recording session an observer sitting in a hide 10–15 m from the nest, recorded partners' behavior (presence of partners in the nest area and movements in and out of the nest-box). Recordings started between 07:30 and 14:00. Some birds showed signs of disturbance (such as hesitating to enter the nest) the first time they saw the equipment, but that behavior rapidly disappeared (birds took  $11 \pm 2$  min – mean  $\pm$  standard error (SE) – to return on the eggs after the beginning of the recording). The observer stopped the recording after observing 3 relief duets. Thus the mean duration of a recording was  $3.7 \pm 0.2$  h.

### Data overview and duet description

We defined duets as a sequence of male and female calls that either alternated or partly overlapped (Elie et al. 2010). A duet started with the first call of one mate answered by its partner within 10 s, and lasted until 1 bird left or both birds stopped calling for at least 10 s. We distinguished 3 different duetting contexts:

- 1) Relief duets were performed when partners replaced one another during incubation. The returning bird relieved its incubating partner on the nest, so they alternated foraging trips.
- 2) Nest visit duets were performed when the returning mate just visited its mate by entering into the nest but did not take its turn incubating and left the nest at the end of the duet.
- 3) Sentinel duets were performed with one mate inside the nest and the other staying outside, located between 20 cm and 5 m from the nest (Elie et al. 2010).

In the majority of relief and visit duets, the returning bird brought nest material, so this behavior did not discriminate the 2 types of duets and did not differ between males and females (Supplementary Appendix A).

Between 2 reliefs, a bird spent around  $45 \pm 26$  min (mean  $\pm$  SD) on the eggs and this time did not differ between males and females (Supplementary Appendix A). Considering 2 incubation bouts per bird, visit, and sentinel duets occurred more when the female was incubating than when the male was incubating (Supplementary Appendix A). So, nest visits and sentinels with the male incubating were rare and our sample size was too limited for an analysis of these events. Thus, for each pair, we extracted when possible 2 reliefs (one with the female returning to the nest and one with the male returning), as well as one nest visit and one sentinel (both with the female incubating). For each recording, we used GoldWave software (<https://www.goldwave.com/>) to extract the duets and we took care to extract only duets occurring after the first relief to be sure that both birds already saw the equipment inside and around the nest and consequently that their behavior was not disturbed. From a total of 36 recordings (2 recording days for 18 pairs), we obtained 35 reliefs with the

female returning to the nest, 33 reliefs with the male returning to the nest, 36 nest visits, and 29 sentinels, so a total of 133 duets was analyzed.

Reliefs and nest visits were split into 3 different phases (described in Boucaud et al. 2016, Figure 1):

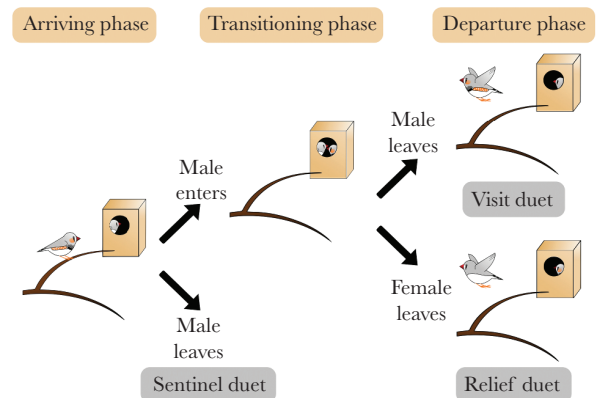
- 1) Arriving phase: the duet begins when the returning mate is still outside the nest (usually less than 2 m from the nest entrance) whereas its incubating partner is inside.
- 2) Transitioning phase: the returning bird meets its partner inside the nest.
- 3) Departure phase: the departure phase starts when the incubating bird (in reliefs), or the returning bird (in nest visit) comes out of the nest. During this phase, mates continue interacting vocally until the duet ends when the leaving bird leaves the nest area (or when both birds stop calling for more than 10 s).

Note that in reliefs, the transitioning phase could happen outside the nest: the incubating bird met its partner at the nest's entrance. In these cases, the 2 birds vocalize outside the nest during this phase and the departure phase starts when the returning bird goes inside the nest.

The duration of these 3 phases was measured manually on the acoustic recordings using Praat software (<http://www.fon.hum.uva.nl/praat/>). Birds make characteristic noises (mechanically with their feet or bodies passing through the entrance) when entering or exiting the boxes allowing us to detect precisely these events.

### Duet analysis

Each extracted duet was manually labeled using Praat software which displays both the oscillogram and the spectrogram of the recording (view range: 0–20 kHz; window length: 0.02 s; dynamic range: 60 dB). For each vocalization, we recorded the identity of the caller and the call type. The identity of the caller was determined by visual observation of the birds' behaviors (described above) and the characteristics of the recordings. At the beginning and the end of the duets, caller identity was easily established because one bird was calling from inside the box and the other one from outside. The bird inside the box was closer to the microphone than the bird outside, and its calls were therefore a lot louder on recordings. When both birds were inside the



**Figure 1**

Diagram showing the 3 different duetting contexts, as well as the 3 different phases of a duet. In this diagram the male returns the nest, the same is true when the female returns.

nest-box, we managed to attribute calls to individuals using the individual signature of the calls.

In zebra finches, males and females use the same vocal repertoire, except song which is produced only by males (Zann 1996). Moreover, the repertoire used during duets does not depend on the bird's sex but depends on the bird's position inside or outside the nest (Elie et al. 2010). In this study, we distinguished 3 types of vocalizations and one non-vocal sound (Zann 1996):

- 1) Short calls. Short calls are harmonic stacks generally shorter than 100 ms. Zebra finches show a continuum of soft short calls used in close social context (Tets, Cackles, and Arks) as well as louder Distance Calls (around 100 ms for males, 200 ms for females; Zann 1996). The acoustic conditions of the nest-boxes (creating attenuation and reverberation of the sound) did not allow us to accurately discriminate between these different short calls, so we grouped them into the single call type "Short Call".
- 2) Whines. Whine is a soft, long (around 300 ms, but with high variation) and high pitched moan. This "pleading" sound is a vocalization specifically uttered inside the nest (Zann 1996).
- 3) Song. Males sang in 22 out of the 133 duets.
- 4) Bill clicking. Bill clicking is beak clattering that have already been described in zebra finches searching for a nest site and performing nest ceremony (Zann 1996).

After labeling, each recording was analyzed using custom-written codes implemented in R (R Development Core Team 2014). From the list of calls, we measured temporal parameters of the duet sequence and of each phase separately: the total duration, the total number of calls, the average call rate (number of calls per minute defined as the total number of calls divided by the time spent calling). The relative participation of the partners was measured as the proportion of male calls among the total number of calls. To describe the repertoire used, as song was rare and birds used 2 call types (whines and short calls), we measured whine proportion, as the percentage of whine calls among all calls in the duet. Because song and bill-clicking were not systematically used in duets we only considered if they were present or not.

### Analysis of the acoustic features of whine calls

Because most short calls were produced either outside the nest or when the 2 birds were inside the nest-box creating overlaps, the quality of the recordings did not permit the analysis of short calls' acoustic features. On the contrary, the acoustic features of male and female whine calls could be measured. To automatically select whine calls without overlap and of good recording quality, we selected whines produced when only one bird was inside the nest-box. We analyzed a total of 625 whines from the females (nest visits: 144; sentinels: 121; reliefs with the female returning: 185; reliefs with the male returning: 175) and 335 whines for the males (reliefs with the female returning: 107; reliefs with the male returning: 228).

Whine calls were then analyzed using custom-written codes implemented in R. The duration of each call (s) was measured between edges labeled using Praat software. After bandpass filtering (400–18 000 Hz encompassing the spectral bandwidth of this type of vocalizations, "fir" function), the following spectral parameters were computed using the "specprop" function (FFT using a Hamming window and a window length of 512):

1. As the frequency spectrum is a distribution, it can be characterized using classic descriptive statistics (all in Hertz). We used the median, 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 IQR (Inter Quartile Range) was defined as Q75–Q25. We also used the mean and standard deviation (SD) of the spectrum.

2. The call's noisiness can be quantified using the Shannon spectral entropy. The Shannon entropy of a noisy signal tends towards 1 whereas it tends towards 0 for a pure tone.

## Statistical analysis

### Overview

Our aim was to determine whether birds call differently during duets before staying in or leaving the nest. We asked 2 main questions:

- 1) Do partners' vocal behaviors differ depending on whether they were returning or leaving the nest? To this end, we compared relief duets with the female returning the nest to relief duets with the male returning.
- 2) Do the characteristics of the duet predict its outcome? To this end, we compared the 3 types of duets with the female incubating at the beginning of the interaction. In a first step, we compared the sentinel duets to the arriving phase of visit and relief duets to determine whether duet characteristics predict male entrance into the nest. In a second step, we compared complete visit and relief duets to determine whether duet characteristics predict that the male will take its turn incubating.

All statistical tests were performed using R software (R Development Core Team 2014). Comparisons of proportions were performed using tests of equal or given proportion ("prop.test" and "pairwise.prop.test" functions). Following all linear mixed models (LMM, "lmer" function of the lme4 library), equivariance and distribution of the residuals were graphically checked using "plotresid" function (RVAideMemoire library). For each model, marginal and conditional coefficients of determination are presented (r2m and r2c, "rsquaredGLMM" function of the MuMIn library; Nakagawa and Schielzeth 2013). *P* values on models were obtained using Wald Chi-square tests ("Anova" function, car library). Post hoc tests were performed using the "lsmeans" function (lsmean library) using Tukey contrasts. The same function was used to obtain estimates and SE in models.

To limit multiple testing, PCA were used to compute composite scores whenever more than 3 parameters were correlated (e.g. correlated parameters describing the temporal structure: number of calls, duration, duration of the arriving phase, duration of the transitioning phase). Before being included in the PCA, some parameters were transformed to reach a symmetrical distribution (Supplementary Appendix B). Principal components with eigenvalue above 1 (Kaiser criterion) were selected. All variable loadings are given in Supplementary Appendix B.

### Do partners' vocal behaviors differ depending on whether they were returning or leaving the nest?

A first PCA was computed on the number of calls, the duration, the duration of the arriving phase, and the duration of the transitioning phase of the relief duets (Supplementary Appendix B). Two other PCA were performed on the acoustic parameters of the whine calls to compare 1) calls of returning and leaving females and 2) calls of returning and leaving males during relief duets (Supplementary Appendix B). After each PCA, PC1 and PC2 were analyzed using LMMs. LMMs included the sex of the returning bird (2 levels) as fixed factor and the pair identity (18 levels) and the day (2 levels: 1st day and 2nd day) as random factors. LMMs were

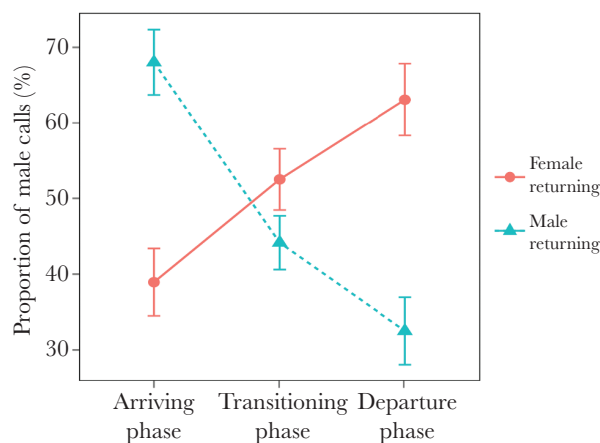


**Table 1**

**Statistical analysis of the effect of the sex of the returning bird on relief duets: a) structure of the duet, b) acoustic structure of returning and leaving male whine calls, and c) acoustic structure of returning and leaving female whine calls**

a)	Estimate ± SE	R2m	R2c	T-ratio	Chi <sup>2</sup>	df	P value
PC1		0.02	0.27		1.91	1	0.167
Female	0.19 ± 0.40						
Male	-0.26 ± 0.41						
PC2		0.01	0.08		0.43	1	0.510
Female	-0.11 ± 0.27						
Male	0.06 ± 0.28						
Whine proportion (%)		<0.01	0.19		0.07	1	0.798
Female	25.02 ± 3.25						
Male	26.00 ± 3.35						
Proportion of male calls (%)		0.21	0.22				
Sex of the returning bird					1.00	1	0.318
Phase					1.17	1	0.558
Sex of the returning bird * Phase					49.14	1	<b>&lt;0.001</b>
Sex of the returning bird (arriving phase)				-4.75		174	<b>&lt;0.001</b>
Sex of the returning bird (transitioning phase)				1.38		173	0.727
Sex of the returning bird (departure phase)				5.03		174	<b>&lt;0.001</b>
Female, arriving phase	38.96 ± 4.21						
Male, arriving phase	68.03 ± 4.56						
Female, transitioning phase	52.57 ± 4.16						
Male, transitioning phase	44.34 ± 4.42						
Female, departure phase	63.07 ± 4.36						
Male, departure phase	32.66 ± 4.36						
b)	Estimate ± SE	R2m	R2c	Chi <sup>2</sup>	df	P-value	
PC1		0.02	0.33	9.11	1	<b>0.002</b>	
Leaving	0.42 ± 0.58						
Returning	-0.32 ± 0.57						
PC2		0.05	0.37	19.48	1	<b>&lt;0.001</b>	
Leaving	0.99 ± 0.40						
Returning	0.20 ± 0.39						
c)	Estimate ± SE	R2m	R2c	Chi <sup>2</sup>	df	P-value	
PC1		0.06	0.48	21.17	1	<b>&lt;0.001</b>	
Returning	-0.36 ± 0.43						
Leaving	0.78 ± 0.44						
PC2		<0.01	0.44	0.16	1	0.685	
Returning	-0.49 ± 0.34						
Leaving	-0.56 ± 0.34						

Significant P values are shown in bold. PC: principal component of the principal component analysis.



**Figure 2** Proportion of male calls during the 3 phases of a relief duet when the returning partner is the female (F, red) or the male (M, blue). Points are means and bars are standard errors.

written as follows: Variable ~ Sex of the returning bird + (1|Pair identity) + (1|Day). The same LMM was used to analyze the whine proportion during relief duets.

The relative participation of partners (measured as the proportion of male calls) during relief duets was analyzed using a similar model including also the phase (3 levels: arriving, transitioning, departure) as an additional fixed factor and the interaction. This LMM was written as follows: Proportion of male calls ~ Sex of the returning bird \* Phase + (1|Pair identity) + (1|Day).

***Does the acoustic structure of the arriving phase of the duet predict male entrance in the nest?***

To test whether the structure of the duet predicts male entrance, we compared sentinel duets with the arriving phase of visit and relief duets with the male returning. A PCA was performed on the acoustic structure of the whine calls of incubating females (Supplementary Appendix B). PC1 and PC2 of this PCA, as well as the parameters describing the temporal structure (duration, number of calls, call rate, whine proportion)

were each analyzed using LMMs with the context (3 levels: sentinel, visit, and relief) as fixed factor and the pair identity (18 levels) and the day (2 levels: 1st day and 2nd day) as random factors. LMMs were written as follows: Variable  $\sim$  context + (1 | Pair identity) + (1 | Day).

The proportion of duets containing bill clicking or song was compared between contexts (sentinel, visit, and relief) using a test of equal or given proportion.

### *Does the acoustic structure of the duet predict that the male will take its turn incubating?*

The parameters of visit and relief duets (duration, number of calls, call rate, whine proportion of the male, whine proportion of the female, proportion of male calls) were each analyzed using LMMs with the context (2 levels: visit and relief), the phase (3

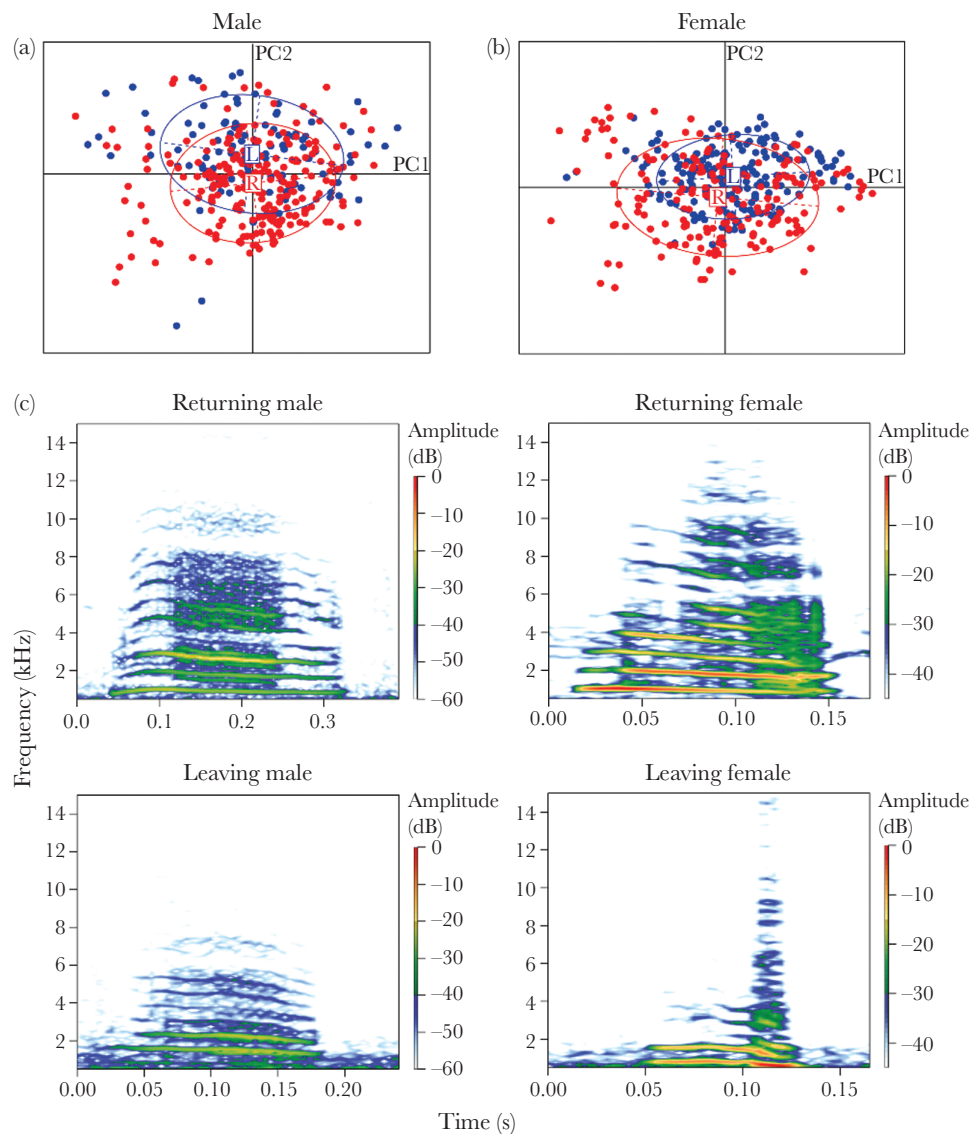
levels: arriving, transitioning, departure) and their interaction as fixed factors, and the pair identity (18 levels) and the day (2 levels: 1st day and 2nd day) as random factors. LMMs were written as follows: Variable  $\sim$  Context \* Phase + (1 | Pair identity) + (1 | Day).

Note that in all models, using the day of recording as a fixed factor did not change any of the results, so we decided to present the results of the models using the day as a random factor.

## RESULTS

### Partners' vocal behaviors differ depending on whether they were returning or leaving the nest

There were no significant difference in PC1 and PC2 values related to the temporal structure of the duet (number of calls,



**Figure 3**

Acoustic structure of whine calls of returning and leaving birds (A) PCA analysis of male whine calls, (B) PCA analysis of female whine calls (R: returning; L: leaving), and (C) spectrograms of whine calls produced by one male and one female when leaving and returning the nest. In (A) lower values of PC1 indicate energy in higher frequency bands (higher mean, median and Q25), larger frequency bandwidth (higher IQR) and more spectral noise (higher entropy). Lower values of PC2 indicate longer calls with energy in higher frequency bands (higher mode and Q25) and lower frequency bandwidth (lower SD). In (B) lower values of PC1 indicate energy in higher frequency bands (higher mean, median, Q25 and Q75), larger frequency bandwidth (higher IQR and SD) and more spectral noise (higher entropy). Lower values of PC2 indicate longer calls with energy in higher frequency bands (higher mode and Q25). Ellipses show 67% of the data points in each group.

duration of the duet, duration of the arriving phase, and duration of the transitioning phase) nor in call repertoire (whine proportion) depending on which bird was returning or leaving the nest (Table 1a). So there was no evidence of an effect of the sex of the bird returning/leaving neither on the temporal structure nor on the repertoire of the duet.

The relative participation of partners to a relief duet (measured as the proportion of male calls) depended on which bird was returning or leaving the nest: during the arriving phase, the returning bird produced more calls than its incubating partner, and during the departure phase, the departing bird produced more calls than its partner who just took its turn incubating (Figure 2; Table 1a). Overall, the bird outside the nest contributed more to the corresponding phase of the duet.

PC1 and PC2 values related to the structure of whine calls differed between returning and leaving birds. When males returned to the nest, their whine calls were longer with energy in higher frequency bands (higher mean, mode, median, Q25 and Q75) and

more spectral noise (higher entropy) than when they were leaving the nest (Table 1b; Figure 3A, lower values of PC1 and PC2). This difference between returning and leaving calls was similar in females. When females returned to the nest, their whine calls had energy in higher frequency bands (higher mean, median, Q75), larger frequency bandwidth (higher IQR and SD) and more spectral noise (higher entropy) (Table 1c; Figure 3B, lower values of PC1).

### The acoustic structure of the arriving phase of the duet predict male entrance in the nest

The arriving phase of relief, visit, and sentinel duets performed between the returning male and the incubating female differed neither in call rate (call/s) nor in call repertoire (whine proportion) (Table 2a). Contrastingly, the number of calls was significantly lower in visits than in relief duets, and the duration was significantly lower in visits than in relief and sentinel duets

**Table 2**

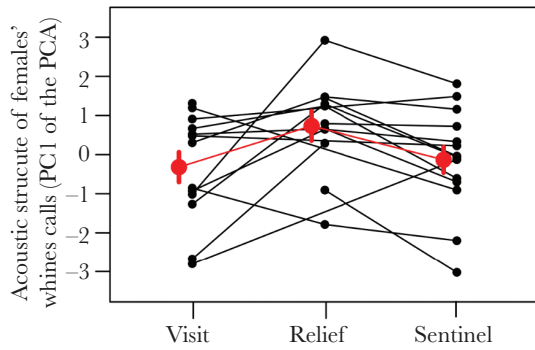
**Statistical analysis comparing the structure of the arriving phase between relief, visit and sentinel duets: a) temporal structure of the duet and, b) acoustic structure of female whines**

a)	Estimate ± SE (without transformation)	R2m	R2c	T-ratio	Chi <sup>2</sup>	df	P value
Duration (s, log10 + 1)		0.07	0.16		8.12	2	<b>0.017</b>
Relief vs. visit				-2.12		77	0.093
Sentinel vs. visit				-2.41		71	<b>0.048</b>
Sentinel vs. relief				-0.47		74	0.887
Visit	6.51 ± 0.19						
Relief	11.50 ± 0.21						
Sentinel	13.19 ± 0.25						
Number of calls (log10 + 1)		0.07	0.18		8.18	2	<b>0.017</b>
Relief vs. visit				-2.79		77	<b>0.018</b>
Sentinel vs. visit				-1.61		71	0.250
Sentinel vs. relief				0.92		74	0.631
Visit	7.84 ± 0.17						
Relief	15.05 ± 0.19						
Sentinel	11.88 ± 0.22						
Call rate (call/s; log10 + 1)		0.04	0.08		2.91	2	0.233
Visit	1.43 ± 0.08						
Relief	1.59 ± 0.09						
Sentinel	1.11 ± 0.11						
Whine proportion (%)		0.02	0.20		2.57	2	0.277
Visit	6.58 ± 0.34						
Relief	5.99 ± 0.37						
Sentinel	11.30 ± 0.43						
b)	Estimate ± SE	R2m	R2c	T-ratio	Chi <sup>2</sup>	df	P-value
PC1		0.05	0.35		16.83	2	<b>&lt;0.001</b>
Relief vs. visit				-1.80		371	0.170
Sentinel vs. visit				2.05		369	0.101
Sentinel vs. relief				4.04		364	<b>&lt;0.001</b>
Visit	0.13 ± 0.53						
Relief	0.62 ± 0.51						
Sentinel	-0.50 ± 0.53						
PC2		0.05	0.38		20.38	2	<b>&lt;0.001</b>
Relief vs. visit				3.80		365	<b>&lt;0.001</b>
Sentinel vs. visit				0.11		286	0.993
Sentinel vs. relief				-3.59		364	<b>0.001</b>
Visit	0.52 ± 0.27						
Relief	-0.16 ± 0.26						
Sentinel	0.49 ± 0.28						

Significant P values are shown in bold. PC: principal component of the principal component analysis. Note that estimates and SE are given on raw data, but models were computed on transformed data when necessary (transformation given in parentheses).

(Table 2a). In sentinel duets, the incubating female never used bill clicking whereas she did in the arriving phase of visit and relief duets (Test of equal or given proportions: relief = 0.30, visit = 0.28, sentinel = 0.00,  $\text{Chi}^2 = 10.63$ ,  $\text{df} = 2$ ,  $P = 0.005$ ,  $\text{p}(\text{relief-sentinel}) = 0.012$ ,  $\text{p}(\text{relief-visit}) = 1.000$ ,  $\text{p}(\text{visit-sentinel}) = 0.012$ ). Moreover the males sang more often in sentinel duets (relief = 0.15, visit = 0.00, sentinel = 0.48,  $\text{Chi}^2 = 24.52$ ,  $\text{df} = 2$ ,  $P < 0.001$ ,  $\text{p}(\text{relief-sentinel}) = 0.022$ ,  $\text{p}(\text{relief-visit}) = 0.050$ ,  $\text{p}(\text{visit-sentinel}) < 0.01$ ).

During the arriving phase, PC1 and PC2 values, which are related to the acoustic structure of whine calls of the incubating female, differed significantly between relief and sentinel duets and PC2 values differ between relief and visit duets. In relief duets, whine calls were shorter with energy in lower frequency bands



**Figure 4** Comparison of the acoustic structure of the whine calls of the incubating female between sentinel duets, and the arriving phase of visit and relief duets. Higher values of PC1 indicate more energy in lower frequency bands (lower mean, median and Q75), smaller frequency bandwidth (lower IQR and SD) and less spectral noise (lower entropy). Lines connect means for each given female, and points with bars are means + SE on all individuals.

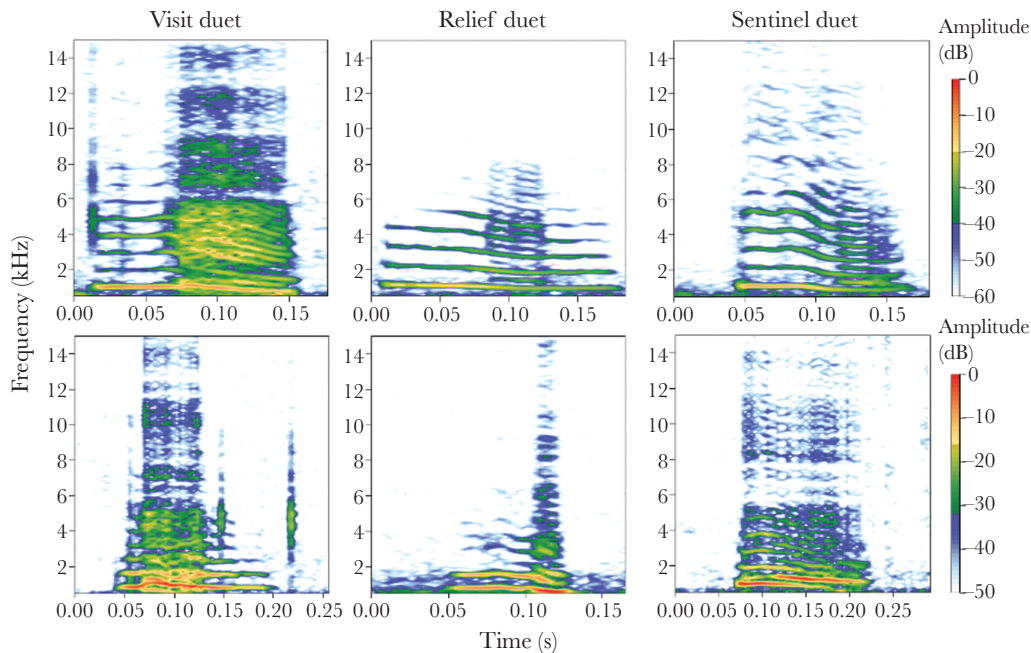
(lower mean, median, mode, Q25 and Q75), smaller frequency bandwidth (lower IQR and SD) and less spectral noise (lower entropy) (higher values of PC1 and lower values of PC2, Table 2b; Figures 4 and 5). So, males were more likely to enter and take their turn incubating when the females used shorter, lower pitched and more harmonically structured calls.

**The acoustic structure of the duet predict that the male will take its turn incubating**

When comparing the whole duet performed between the returning male and the incubating female, relief duets were longer with more calls than visit duets (Table 3). During the transitioning phase, the call rate was higher in relief than in visit duets (Table 3). The proportion of whine calls used by returning males was higher during the transitioning and departure phases in relief than in visit duets (Table 3, Figure 6). The proportion of whine calls used by incubating females was lower in all phases of relief duets compared to visit duets (Table 3, Figure 6). Finally, the proportion of male calls in the departure phase was higher in visit than in relief duets (Table 3).

**DISCUSSION**

In this study, we show that when the male and the female met in the nest during reliefs, the vocalizations differed between returning and leaving birds: the returning bird called more during the arriving phase and then used a higher proportion of whines during the transitioning and the departure phase, whereas the leaving bird called more and used less whines during the departure phase. Returning and leaving birds also differed in the acoustic structure of their whine calls. Returning birds used high-pitched and noisy whines, whereas leaving birds produced low-pitched whines with less spectral noise. These results are congruent with the changes in acoustic structure of incubating females' whines, which were



**Figure 5** Spectrograms of whine calls from 2 females (top and bottom) produced in visit, relief and sentinel duets.



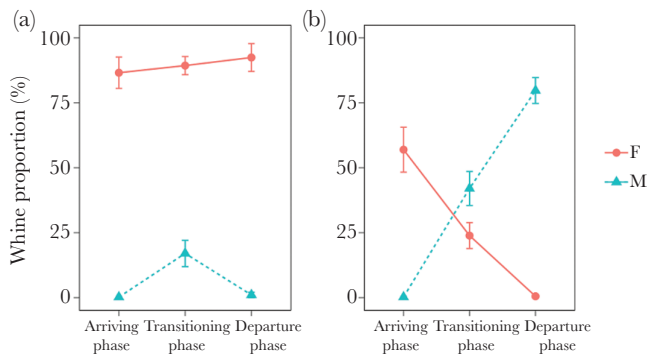
**Table 3**  
**Statistical analysis comparing the structure of relief and visit duets**

	Estimate ± SE (without transformation)	R2m	R2c	Chi <sup>2</sup>	T-ratio	df	P-value
<b>Duration (s; log10 + 1)</b>							
Duet type		0.12	0.21	27.29		1	<0.001
Phase				0.78		2	0.676
Duet type * phase				2.09		2	0.351
Visit, arriving phase	6.51 ± 0.17						
Relief, arriving phase	11.57 ± 0.18						
Visit, transitioning phase	5.82 ± 0.17						
Relief, transitioning phase	10.18 ± 0.18						
Visit, departure phase	4.67 ± 0.17						
Relief, departure phase	12.51 ± 0.18						
<b>Number of calls (log10 + 1)</b>							
Duet type		0.30	0.35	72.94		1	<0.001
Phase				10.96		2	0.004
Duet type * phase				5.15		2	0.076
Visit, arriving phase	7.84 ± 0.14						
Relief, arriving phase	14.87 ± 0.16						
Visit, transitioning phase	8.42 ± 0.14						
Relief, transitioning phase	29.62 ± 0.15						
Visit, departure phase	6.02 ± 0.15						
Relief, departure phase	17.15 ± 0.15						
<b>Call rate (calls/s; log10 + 1)</b>							
Duet type		0.12	0.15	5.60		1	0.018
Phase				14.60		2	<0.001
Duet type * phase				6.98		2	0.031
Duet type (arriving phase)					-0.31	177	0.999
Duet type (transitioning phase)					-3.52	176	0.007
Duet type (departure phase)					-0.24	177	0.999
Visit, arriving phase	1.52 ± 0.08						
Relief, arriving phase	1.61 ± 0.09						
Visit, transitioning phase	1.80 ± 0.08						
Relief, transitioning phase	3.18 ± 0.09						
Visit, departure phase	1.59 ± 0.09						
Relief, departure phase	1.66 ± 0.09						
<b>Whine proportion of the male</b>							
Duet type		0.55	0.56	81.28		1	<0.001
Phase				74.74		2	<0.001
Duet type * phase				78.59		2	<0.001
Duet type (arriving phase)					0.01	167	1.000
Duet type (transitioning phase)					-4.06	166	0.001
Duet type (departure phase)					-11.89	170	<0.001
Visit, arriving phase	0.27 ± 4.04						
Relief, arriving phase	0.23 ± 4.36						
Visit, transitioning phase	17.07 ± 4.03						
Relief, transitioning phase	40.32 ± 4.24						
Visit, departure phase	1.11 ± 4.16						
Relief, departure phase	74.80 ± 4.76						
<b>Whine proportion of the female</b>							
Duet type		0.56	0.68	197.17		1	<0.001
Phase				33.99		2	<0.001
Duet type * phase				24.06		2	<0.001
Duet type (arriving phase)					3.70	145	0.004
Duet type (transitioning phase)					9.51	141	<0.001
Duet type (departure phase)					10.88	142	<0.001
Visit, arriving phase	83.93 ± 6.68						
Relief, arriving phase	55.23 ± 6.55						
Visit, transitioning phase	85.29 ± 5.92						
Relief, transitioning phase	22.41 ± 6.84						
Visit, departure phase	81.39 ± 6.84						
Relief, departure phase	1.82 ± 6.08						
<b>Proportion of male's calls</b>							
Duet type		0.33	0.35	30.38		1	<0.001
Phase				44.30		2	<0.001
Duet type * phase				24.95		2	<0.001
Duet type (arriving phase)					1.91	179	0.397

**Table 3.**  
**Continued**

	Estimate $\pm$ SE (without transformation)	R2m	R2c	Chi <sup>2</sup>	T-ratio	df	P-value
Duet type (transitioning phase)					2.35	177	0.180
Duet type (departure phase)					7.17	178	<0.001
Visit, arriving phase	80.03 $\pm$ 4.30						
Relief, arriving phase	67.99 $\pm$ 4.72						
Visit, transitioning phase	46.87 $\pm$ 4.24						
Relief, transitioning phase	44.27 $\pm$ 4.58						
Visit, departure phase	76.47 $\pm$ 4.31						
Relief, departure phase	32.57 $\pm$ 4.52						

Note that estimates and SE are given on raw data, but models were computed on transformed data when necessary (transformation given in parentheses).

**Figure 6**

Effect of the context (A: visit duet; B: relief duet) on the proportion of whine calls used by the returning male (blue) and the incubating female (red) throughout the duet. Points are means and bars are standard errors.

lower pitched and less noisy before leaving the nest (i.e. during a relief duet) than before staying in the nest (i.e. during a sentinel or a visit of the male). To sum up, both the phonology (repertoire use, i.e. proportion of whine calls) and the prosody (spectral modifications of whine calls) predicted whether a bird stayed in the nest at the end of a duet. These differences could result from either the male or the female signaling its decision to leave/stay. As our study is only correlational, it does not allow disentangling whether the changes in vocalizations are causes of decisions or consequences of other changes (motivation, internal timing mechanisms...) that might be involved in the turn-taking in incubation. Experimental manipulations of the acoustic signal using playback experiments would allow testing the possibility that birds communicate their readiness to take turns incubating.

In the zebra finch, a physiological stress induces modifications of the acoustic structure of contact calls (Perez et al. 2012) and mates can perceive these modifications in their partner's calls (Perez et al. 2015). In males stressed by social isolation or by an oral administration of corticosterone, contact calls had energy in higher frequency bands (Perez et al. 2012). In our study, the bird using whine calls with energy in higher frequency bands was the bird which was going to stay in the nest. If stress is encoded in whine calls using the same parameters as in contact calls, birds staying would be more stressed (in higher frequencies) than birds leaving the nest. This is either inconsistent with the idea that the duration of the incubation bout is determined by an energy reserves threshold, because in that case birds leaving the nest should be more stressed. Alternatively, it could be that the information about stress is encoded differently in

contact calls and whine calls. Another hypothesis is that the modulation of whine calls' structure encodes another piece of information, such as the motivation of the bird to stay in the nest. Looking at the relationship between whine calls' frequency features and the duration of the bird's subsequent incubation bout could test this hypothesis.

Some acoustic features of the duets produced by the incubating female and the returning male were associated with male entrance into the nest and male's relief of the female. Indeed, males never entered the nest if the female did not use bill clicking during the arriving phase, and duets with more calls during the arriving and transitioning phases were more likely to end in a nest-relief. The fact that relief duets were longer with more calls than visit duets could be mechanistically linked to the time spent by the male inside the nest (longer in reliefs than in visits), but relief and visit duets also differed on other aspects—repertoire (proportion of whine calls) and relative participation of the partners (proportion of male calls)—that cannot be mechanistically explained by the time spent by the male inside the nest, and may have signaling functions in the organization of incubation. Duets produced by the incubating male and the returning female may probably work the same way but our dataset did not allow testing this hypothesis.

The temporal structure of the duet changed between visit and relief duets. Relief duets were longer with more calls and a higher call rate. Such modifications of the temporal structure of the duets have been previously found to play a role in incubation share between male and female (Boucaud et al. 2016). Indeed, we found in this previous study that a delay in male return to the nest induced accelerated relief duets with higher call rates. Moreover, the more accelerated the duet, the longer the time off nest of the female after the relief. A higher call rate could thus code the urgency to do the relief: a low call rate indicating that the relief can be done later and a high call rate that the relief is urgent.

When outside the nest, males show a tendency to perform more sentinel duets than females. We also observed that returning males used more song during sentinel than visit or relief duets. In this species, the amount of singing given by the male after the female entered the nest is positively related to the time she subsequently spent inside the nest during the laying period (Dunn and Zann 1996). If male song encourages the female to remain in the nest during laying, it may have a similar function during incubation by informing that the male will not enter the nest. Interestingly, in our recordings the vocal behavior of the female was also different between sentinel and other duets as females almost never used bill clicking in sentinel duets. Bill clicking has

been described as part of the nest ceremony occurring when a pair is searching for a nest site (Zann 1996). In other species, bill clicking or clattering is considered as part of the courtship display (Eda-Fujiwara et al. 2004; Soma and Mori 2015; Yoon et al. 2015). Here, we describe for the first time their use during incubation in the zebra finch. Because bill clicking was never used in sentinel duets in our study, but only when birds met in the nest (visits, reliefs), it could be part of a physical or behavioral greeting ceremony (Wachtmeister 2001). Greeting or meeting ceremonies in birds are observed when the partners meet after a period of separation and in many species occur throughout the duration of the pair bond (Wachtmeister 2001).

In this study, we showed that duets performed by zebra finch mates during incubation differed in temporal structure and more importantly in vocal repertoire and spectral structure of calls depending on the context (sentinel, visit, or relief). The vocal behavior of each bird indicated whether it will stay or leave the nest. Whether these modifications result only from changes in birds' motivation or whether mates use duets to decide when it is time to make a nest-relief remains to be experimentally tested.

## SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Ethics: This work was conducted under the authorities of the Animal Ethics Committee at Macquarie University, and a Scientific Research Permit from the New South Wales Parks and Wildlife Service.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Boucaud et al. (2016).

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