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Vocal negotiation over parental care? Acoustic communication at the nest predicts partners' incubation share

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In species with biparental care, individuals adjust their workload to that of their partner to either compensate or match its investment. Communication within a pair might be crucial for achieving this adjustment. Zebra finches, *Taeniopygia guttata*, form life-long monogamous pair bonds, in which partners are highly coordinated and both incubate the eggs. When relieving each other during incubation, partners perform a structured call duet at the nest. If this duet functions to coordinate incubation workload, disrupting the pair's usual nest-relief pattern by delaying the male's return to the nest should affect the structure of the duet. Using domesticated birds breeding in a large aviary, we found that delaying the male's return induced shorter duets with higher call rates. In addition, we tracked the location of individuals with a transponder at the nest and the feeder, and showed that these accelerated duets were associated with an increased haste of the partners to take turns incubating and foraging. Females also spent less time incubating during their subsequent shift, and females' time off-nest was best predicted by their mate's calling behaviour in the previous duet. Taken together, these results suggest that duets may function as 'vocal negotiation' over parental care. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, 117, 322–336.

ADDITIONAL KEYWORDS: coordination – duet – monogamy – negotiation – pair bond – zebra finch.

INTRODUCTION

Biparental care in birds has been a long-term focus of studies testing theoretical models on cooperation versus conflict equilibrium between unrelated individuals (Trivers, 1972). In particular, sexual conflict theory predicts that each parent increases its lifetime reproductive success by reducing its investment in current offspring care at the expense of the other sex that compensates for this reduction (Trivers, 1972). Subsequent research has examined how two parents reach their division of labour not only through evolutionary responses, but also through behavioural adjustment (i.e. sequential modification of one's parental effort in response to the prior effort of its mate) (McNamara, Gasson & Houston, 1999). Specifically, when an individual decreases its invest-

ment, its partner may either increase its own workload to at least partially compensate for that loss (full or partial compensation models; McNamara *et al.*, 1999) or decrease its own workload to match the reduced effort of its partner (matching model; Johnstone & Hinde, 2006). Overall, there is more empirical support towards partial compensation (meta-analysis; Harrison *et al.*, 2009); however, some cases clearly do not follow that pattern (Hinde, 2006; Hinde & Kilner, 2007; Meade *et al.*, 2011).

The adjustment of an individual's workload to that of its partner could also derive from the coordination of their activities resulting in a cooperative teamwork (Black, 1996). Many long-term monogamous species increase their breeding success with increased pair-bond duration, which may be attributed to the improved coordination of partners over time (mate familiarity effect: Forslund & Part, 1995; Black, 1996, 2001). Mates may progressively

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fine-tune how they function as a pair, making the division of labour during breeding more efficient. In some species, parents coordinate their foraging activities or synchronize their nest visits to feed the chicks (Lee, Kim & Hatchwell, 2010; Mariette & Griffith, 2012, 2015; Van Rooij & Griffith, 2013). In species where both parents incubate, hatching success may be increased when partners synchronize foraging trips (Coulson, 1966; Morris, 1987; Davis, 1988) or coordinate incubation bouts (measured by periods during which only one parent at a time incubates; Spoon, Millam & Owings, 2006). The coordination of partners during breeding could also reflect their coordination in other activities and be linked to pair-bond strength. Mates can alert each other to danger (Krams, Krama & Igaune, 2006; Mainwaring & Griffith, 2013), fight off predators by giving alarm calls or aggressive flights (Regelmann & Curio, 1986), join forces to compete over food resources or nest sites (Black & Owen, 1989; Black, 2001), and alternate vigilance and foraging (McGowan & Woolfenden, 1989; Sedinger & Raveling, 1990).

Regardless of whether conflict or coordination between breeding partners is occurring, the mechanisms allowing pairs to reach the adjustment of parental workload is an important but largely unstudied question. Previous research on the division of labour during biparental care has experimentally altered the workload of one partner by either handicapping it (wing clip, weight) (Schwagmeyer, Mock & Parker, 2002) or by modifying offspring begging calls (Hinde, 2006) and then measured how each partner adjusts its own workload as a consequence. However, we do not know how partners estimate each other's effort, and whether they somehow communicate with each other to reach a given level of parental investment.

If communication between partners is involved in parental care adjustment, acoustic communication may play a key role in this process. Birds produce a wide variety of vocalizations, especially during the breeding period. Male vocal behaviour is very well studied in birds, although much less is known about female vocalizations (Riebel, Hall & Langmore, 2005) and interactive communication between male and female, with the exception of acoustic duets (Faraabaugh, 1982; Hall, 2004, 2009; Benedict, 2008; Dahlin & Benedict, 2013). Avian duets are joint acoustic displays between two birds that make temporally coordinated vocal or nonvocal sounds. Among them, the highly coordinated song duets of tropical songbirds are the most studied. These duets have been hypothesized to fulfil several functions, such as pair-bond maintenance, mate guarding, territory defence or synchronization of reproductive effort. However, the possibility that duets could play a role in parental care has never been explored.

Although song duetting is rare (approximately 4% of bird species), interactive communication between mates involving simpler and less conspicuous vocalizations is likely to be more widespread (Todt, Hultsch & Duvall, 1981; Lamprecht *et al.*, 1985; Morton & Derrickson, 1996; Wright & Dahlin, 2007). In particular, the sounds produced inside the nest by females and used in interactive communication between mates may be more widespread than previously assumed (Ritchison, 1983; Beletsky & Orians, 1985; Yasukawa, 1989; McDonald & Greenberg, 1991; Halkin, 1997; Halfwerk *et al.*, 2011; Halfwerk, Bot & Slabbekoorn, 2012). We recently described a simple and quiet form of call duets at the nest in wild zebra finches *Taeniopygia guttata* (Elie *et al.*, 2010). Each time partners meet at the nest, they perform simple coordinated mutual vocal displays that can be described as call duets (Fig. 1A; see also Supporting information, File S1) (Elie *et al.*, 2010). These duets involve calls that are softer than many others in this species (Zann, 1996) and may therefore represent a private communication between mates at the nest that could be involved in parental care adjustment.

Zebra finches maintain life-long pair bonds and mates show high coordination of activities during reproduction (Mariette & Griffith, 2015). Both parents contribute to nest building, incubation, and the provisioning of chicks (Zann, 1996). The male and female start incubation on the same day (Gilby, Mainwaring & Griffith, 2013) and multiple studies have found partners share incubation time equally, both in the wild and in captivity (El-Wailly, 1966; Delesalle, 1986; Zann & Rossetto, 1991; Gorman, Arnold & Nager, 2005; Gilby *et al.*, 2013). Typically, the pair takes turns incubating and foraging. The call duets (thereafter referred to as 'duets' rather than 'call duets' for simplicity) occur during the transition where the foraging partner relieves the incubating partner: a nest-relief (Elie *et al.*, 2010). Which partner controls the length of an incubation bout and whether incubation sharing involves any communication between partners remains to be determined. In addition, zebra finch mates are highly coordinated during the nestling period; in the wild, partners visit the nest and foraging patches together as a pair rather than independently of each other (Mariette & Griffith, 2012, 2015). Pairs increase visit coordination when brood size is experimentally increased, and better-coordinated pairs produce heavier nestlings (Mariette & Griffith, 2015). Similarity in the personality traits of partners might contribute to this effect if more similar partners have heavier nestlings as suggested in domestic zebra finches (Schuett, Godin & Dall, 2011; but see also Schielzeth *et al.*, 2011). Coordination of breeding

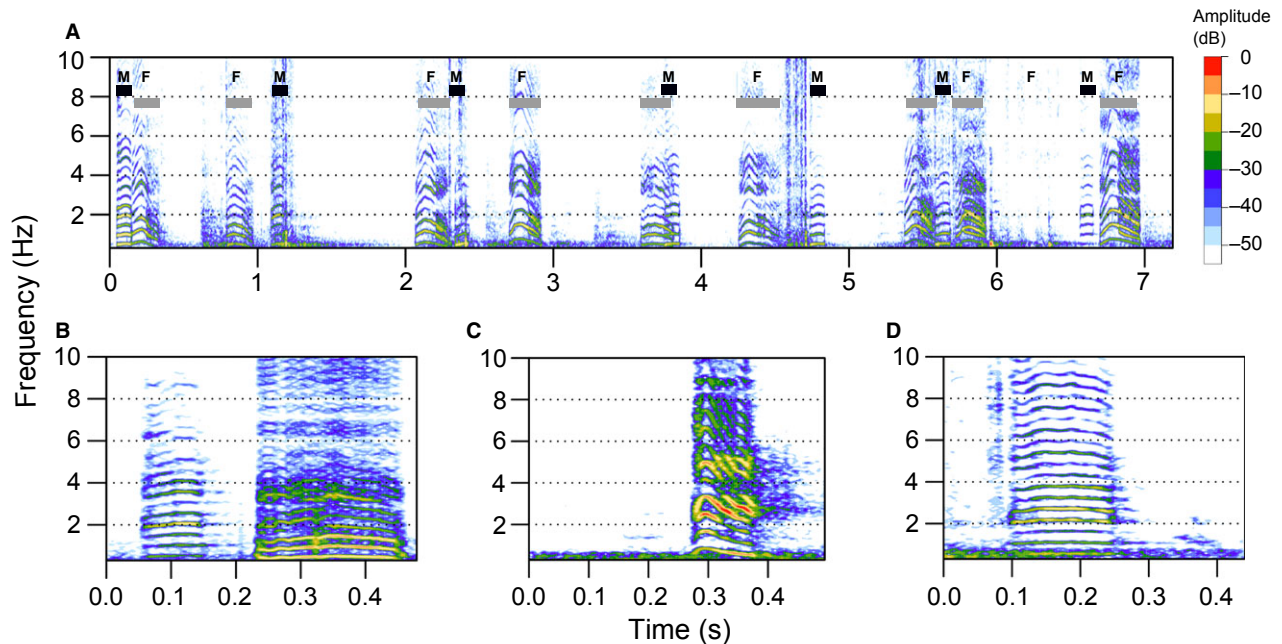


Figure 1. A, duet performed by zebra finch mates when they take turns incubating (M, male vocalization; F, female vocalization). Mates perform only one duet per incubation nest relief (see Supporting information, File S1). B–D, examples of call types used during these sequences, (B) one Tet (Short Call) followed by a Whine (see Supporting information, File S2), (C) one male Distance Call (Short Call) (see Supporting information, File S3), and (D) one female Distance Call (Short Call) (see Supporting information, File S4). Spectrograms were prepared using SEEWAVE (Sueur *et al.*, 2008) in R (R Development Core Team, 2014).

activities between partners could be reached by communication, with duets being part of the process.

In the present study, we aimed to investigate whether duets at the nest could play a role in the adjustment of incubation shifts between zebra finch partners. Using domesticated birds breeding in a large aviary, we disrupted the usual nest-relief pattern of a pair by delaying male return to the nest, and investigated whether duetting between mates was affected, and how birds responded to these modifications. We delayed the male's return to relieve its partner by trapping the male in an acoustically and visually isolated feeder. To control for the contact opportunities between partners in a second experimental condition, we again closed the feeder but without trapping the male inside. This again delayed male return to the nest because he postponed his visit to the feeder until after it was re-opened but did not affect a pair's ability to communicate.

MATERIAL AND METHODS

HOUSING CONDITIONS

The present study was conducted in spring 2011 at the University of Saint-Etienne, France. We banded 54 males and 54 females with a unique combination of two plastic colour bands and a transponder tag.

Birds were allowed to breed freely in a large indoor aviary ($6.5 \times 5.5 \times 3.5$ m; temperature: 20–30 °C, daylight: 07.30–20.30 h) and were provided with 50 nest-boxes (dimensions $13 \times 12 \times 17$ cm). To simulate the separation of the partners that occurs in the wild when one partner incubates and the other one is foraging, all food and water in the aviary were provided in a separate room (thereafter 'feeder', dimensions: $3.2 \times 1 \times 1.30$ m). This feeder was visually separated from the breeding area and acoustically insulated using acoustic foam (the intensity of a white noise broadcasted in the breeding area at 2 m from the feeder was 19 dB SPL lower inside than outside the feeder at the same distance). Moreover, birds entered the feeder using two small entrances (diameter 14 cm) oriented in the direction opposite to the breeding area. Birds were fed with finch seed mix, cuttlefish bones and water *ad libitum* and supplemented with salad and boiled eggs twice a week. The feeder was also equipped with perches and baths. Dried grass was provided as nest material *ad libitum* and cotton wool three times a week.

RECORDING AND EXPERIMENTAL APPROACH

Out of the 108 birds, 32 pairs bred during the experiment and, among them, 12 pairs were successfully recorded in all experimental conditions (see below).

Breeding pairs were recorded in the morning (between 09.00 and 14.00 h), during incubation. The day before recording, a tie microphone (C417; AKG) was installed inside the nest-box and connected to a digital recorder (PMD-671; Marantz). During the recording session an observer, sitting either in a hide inside the aviary or behind a one-way mirror outside the aviary, recorded the behaviour of partners during nest relief (presence of partners in the nest area and movements in and out of the nest-box). We used a within pair design to limit the number of possible confounding factors between our two experimental conditions. Each pair was recorded on 2 days (interval of 0–6 days). On each recording day, the pair was recorded under the control (i.e. non-manipulated) condition, as well as under one of the two different experimental conditions (i.e. male inside the feeder or outside; see below). The order of experimental days was randomized across pairs. We successfully recorded 12 pairs in all four conditions, and so our sample size was 48 recordings. Our sample size is limited because incubation only last 10 days and most nests started at the same time so we could not record all the nests. In addition, monitoring individuals outside the nest to trap the male inside the feeder was challenging given the size of the aviary and the large number of birds.

On each recording day, the nest was observed and recorded under undisturbed conditions until the female returned to the nest and the male went out (except for two nests showing the reverse). This nest-relief represents the ‘control’ (i.e. non-manipulated) condition. Then the feeder was closed for 1 h to obtain one of two experimental situations: (1) the male was trapped inside the feeder (‘IN’) when the female was in the nest or (2) both the male and the female remained outside the feeder (‘OUT’). In the second situation, mates continued to carry out nest reliefs and were not separated for the duration of the feeder closure, although they were both unable to forage for 1 h. In both IN and OUT conditions, we analyzed the first nest-relief after re-opening the feeder (referred to as ‘experimental duets’), which corresponded to the male returning to the nest to relieve the female in 23 out of 24 nest-reliefs. In summary, duets were obtained for three conditions:

1. Control: last duet before closing the feeder (one duet per pair per day, $N = 24$ duets; female returning in 22 duets, male in two).
2. IN: first duet after re-opening the feeder when the male had been trapped inside it (one duet per pair, $N = 12$ duets; male returning in all 12 duets).
3. OUT: first duet after re-opening the feeder when the male had remained outside (one duet per pair, $N = 12$ duets; male returning in 11 duets, female in one).

In most cases, the sex of the returning bird differed between control and experimental conditions. However, in a different dataset ($N = 18$ pairs), the sex of the returning bird had no effect on the parameters of the duet analyzed here (see Supporting information, Data S1). To test the effect of our manipulations on duet characteristics, all 48 duets were therefore included and classified on the basis of the experimental condition rather than on the basis of the sex of the bird returning to the nest. However, for simplicity, in analyses based on experimental duets only (see below), the one duet with the female returning was excluded because these analyses were specifically linking each partner calling pattern with its subsequent incubation behaviour. Including the duet with a female returning did not change any of the results.

DUET ANALYSIS

When zebra finch mates take turns incubating, they perform a duet (i.e. a sequence of male and female calls that either alternate or partly overlap). There is typically only one duet per nest-relief, according to certain criteria: a duet started with the first call of one mate answered by its partner within 10 s, and lasted until one bird left or both birds stopped calling for at least 10 s. We measured the duration of three phases of the duet:

1. Arriving phase: the duet begins when the returning mate is still outside the nest (usually < 2 m from the nest entrance) whereas its incubating partner is inside.
2. Transitioning phase: the returning bird meets its partner either inside the nest or just outside. In most cases, the returning bird enters the box before the incubating partner gets out; however, in six out of 48 cases, the incubating bird met its partner at the nest’s entrance. In these cases, the two birds vocalize outside the nest during this phase.
3. Departure phase: if the transitioning phase took place inside the nest, the departure phase starts when the incubating bird goes out of the nest; if the transitioning phase took place outside the nest, the departure phase starts when the returning bird goes inside the nest. During this phase, mates continue interacting vocally until the duet ends when the previously incubating bird leaves the nest area (or when both birds stop calling for more than 10 s).

The duration of these three phases was measured manually on the acoustic recordings (44.1 kHz, 16 bit) using PRAAT (<http://www.fon.hum.uva.nl/praat/>),

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). Birds make characteristic noises when entering or exiting the boxes, allowing us to precisely detect these events.

To analyze the temporal structure of the duet, we used a semi-automatic detection of the calls. Using SEEWAVE (Sueur, Aubin & Simonis, 2008) in R (R Development Core Team, 2014), we segmented the recording according to an amplitude threshold to obtain a list of start and end times of each detected call. In a second step, all recordings were checked manually using PRAAT to add any call missed by the automatic detection or separate overlapping calls wrongly counted as one call.

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 instead on the bird's position inside or outside the nest (Elie *et al.*, 2010). In the present study, we distinguished three types of vocalizations:

1. **Short Calls:** these are harmonic stacks generally shorter than 100 ms. Zebra finches show a continuum of soft short calls used in close social context (Zann, 1996) (tets, cackles, arks) (Fig. 1B; see also Supporting information, File S2) as well as louder distance calls (Zann, 1996) (Fig. 1C, D; see also Supporting information, Files S3, S4; approximately 100 ms for males and 200 ms for females). The acoustic conditions of the nest-boxes (creating attenuation and reverberation of the sound) in the aviary (with partly overlapping vocalizations from other birds) did not allow us to accurately discriminate between these different calls, and so we grouped them into the single call type 'Short Call'.
2. **Whines:** these are soft, long (around 300 ms, with high variation) and high-pitched moans. This 'pleading' sound is a vocalization specifically uttered inside the nest (Zann, 1996) (Fig. 1B; see also Supporting information, File S2).
3. **Song:** males sang in only five out of the 48 duets analyzed. Each song syllable was counted as a call.

The identity of the caller was determined by visual observation of the birds' behaviours (described above) and the characteristics of the recordings. During arriving and departure phases, 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. During the transitioning

phase, we managed to attribute calls to individuals using the individual signature of the calls.

From the list of calls, we measured call duration, as well as temporal parameters of the duet sequence: the total duration, the average call rate (number of calls per minute defined as the total number of calls divided by the time spent calling), and, for each sex: the total number of calls, the time spent calling (i.e. the duration between the first and the last calls), and the average call rate. To describe the repertoire used, because Song was rare (see above) and birds used only two call types, we measured Whine proportion, as the percentage of Whines among all calls in the duet.

RECORDING OF BIRDS' ACTIVITIES

Each bird was identified by a PIT-tag (Passive Integrated Transponder tag; Trovan ID100A) glued on one band. Antennas (Dorset Identification BV, The Netherlands) were installed in the nest-boxes around the nest built by the birds with dried grass and cotton, and at the entrance of the feeder. In this way, time spent in the nest as well as exits and entrances at the feeder were recorded for each bird (unless technical issue, see below).

The time spent away from the nest by one partner was equivalent to the time spent in the nest by its partner because, during our observations, parents never ended their incubation bout before their partner returned to the nest. To estimate incubation effort, we measured 'incubation bout' duration as the time spent inside the nest by one bird before (or after) the analyzed duets. In addition, we quantified the 'contribution to incubation' between partners by measuring the relative participation of each partner to incubation using the percentage of time the female incubated over the total incubation time. This female contribution to incubation was measured on an equal number of incubation bouts for the male and the female, corresponding to ~2 h of PIT-tag recordings before the analyzed duets (and after in the case of experimental duets).

By closing the feeder, birds were unable to eat during 1 h. To estimate females' motivation to feed at the time of the experimental duet (after re-opening the feeder), we measured the time between their exit from the nest box (i.e. the last detection in the nest) and their entrance into the feeder (i.e. first detection at the feeder door). To estimate the readiness of males to come back to the nest after the treatment, we measured the difference between their last detection at the feeder door and their first detection in the nest. We then compared these times with those in the last relief before closing the feeder when the male was returning to the nest and the female was

leaving (the experimental duet in which the female rather than the male was returning to the nest was removed from this analysis). Here, we took care to compare reliefs with the same sex returning because it is possible that the time to return to the nest and to join the feeder is individual specific. Lastly, because of technical problems (saturation of the PIT-tag data loggers as a result of intense bird activity), pit-tag data at the feeder entrance were available for 39 out of 48 relieves for the females and 36 out of 48 relieves for the males.

ETHICAL NOTE

Experiments were performed under the authorization number 42-218-0901-38 SV 09 (ENES Lab, Direction Départementale des Services Vétérinaires de la Loire) and were in agreement with the French and European legislations regarding experiments on animals.

STATISTICAL ANALYSIS

Overview

The purpose of our experiment was, in a first step, to delay male return to the nest (IN and OUT), at the same time as controlling for mate separation effects (OUT), and to investigate the effect on mate communication at the nest. In a second step, we tested whether mate communication or incubation share, which were both affected by our experiment, best predicted subsequent incubation behaviour. For the first step, we checked that our manipulation had the intended effect on birds' incubation behaviour, and tested whether it directly affected duet characteristics. Even though both experimental conditions delayed male return, there was a lot of overlap between conditions, and so we also tested whether duet characteristics responded linearly to the duration of the preceding incubation bout (the condition and the duration of the incubation bout could not be included in the same model as they were collinear). In an attempt to reduce the number of parameters tested, and still performing a thorough analysis given the absence of a priori knowledge, we grouped duet characteristics under (1) overall temporal structure (duration of the duet, duration of the different phases and call rate) and (2) detailed vocal repertoire (type and duration of calls given by each partner). Because the latter did not differ between experimental conditions, we did not include it further when investigating the linear effect of incubation bout duration on the prediction of post-manipulation incubation behaviour. Lastly, to improve our interpretation of the effect of our manipulation on birds' incubation behaviour, we also investigated the effect of the manipulation on birds' visits to the feeder.

All statistical tests were performed using R (R Development Core Team, 2014). Normality of the data was tested using Shapiro–Wilk test. Some parameters were transformed to reach normality (male time to return to the nest was log-transformed and female time to enter the feeder was square-root-transformed). In addition, all models were checked for normality and homogeneity by visual inspection of plots of residuals against fitted values. The analysis of variance function of the car package was used to obtain *P*-values on models. $P < 0.05$ was considered statistically significant. All post-hoc tests were performed using multiple comparisons tests (glht function of the multcomp package, with Tukey contrasts). All linear mixed models (LMM) used restricted maximum likelihood estimation, except for the model comparison approach, which was instead based on maximum likelihood. Estimates and SEs were calculated using the lsmeans function.

Principal component analysis (PCA)

All three PCA were performed using the function `dudi.pca` of the `ade4` package, which performs a normed PCA (i.e. a PCA on correlation matrix). Principal component with Eigen value above one (Kaiser criterion) were selected. Two PCA were performed to test the effect of delaying males' return to the nest on first (1) the overall temporal structure of the duet and then (2) its detailed call composition for each partner. Lastly, (3) a third PCA, identical to the first but using only experimental duets, was used to test the effect of experimental duets' characteristics on subsequent incubation behaviour. Control duets, which occurred just before closing the feeder, were omitted from this third PCA because the feeder manipulation was specifically designed to interfere with usual incubating schedule.

1. The first PCA summarized four temporal parameters of the duets: call rate, duet total duration, duration of arriving phase, and duration of transitioning phase. These four parameters were chosen to avoid linear dependencies (e.g. as duet total duration = duration of arriving phase + duration of transitioning phase + duration of departure phase, we chose only duet total duration, duration of arriving phase, duration of transitioning phase). The first principal component PC1 explained 50.16% of the variance and was described by the equation: $-0.81 \text{ call rate} + 0.87 \text{ duet duration} + 0.64 \text{ arriving phase duration} + 0.44 \text{ transitioning phase duration}$. PC2 explained 28.70% of the variance and was described by the equation: $-0.11 \text{ call rate} - 0.03 \text{ duet duration} - 0.67 \text{ arriving phase duration} + 0.83 \text{ transitioning phase duration}$.

2. The second PCA describing the vocal repertoire of each partner in the duet included the duration of Whines and Short Calls for each sex, and the proportion of Whine. Because of missing data when one of the two partners did not produce one of the two call types (and therefore no duration for that call type was available), the sample size was 41 (instead of 48) duets. Considering the proportion of Whines in all 48 duets or the duration of each call type singly ($44 < N < 48$) gave the same results (i.e. all nonsignificant; data not shown). PC1 explained 39.98% of the variance and was described by the equation: 0.77 Whine proportion + 0.62 male Short Calls duration + 0.68 female Short Calls duration + 0.52 male Whines duration + 0.53 female Whines duration. PC2 explained 24.24% of the variance and was described by the equation: -0.21 Whine proportion - 0.25 male Short Calls duration + 0.42 female Short Calls duration - 0.66 male Whines duration + 0.70 female Whines duration.
3. The third PCA on experimental duets only, had similar loadings to the first PCA on all duets. Indeed, PC1 explained 50.78% of the variance and was described by the equation: -0.82 call rate + 0.86 duet duration + 0.31 arriving phase duration + 0.72 transitioning phase duration. PC2 explained 25.51% of the variance and was described by the equation: 0.12 call rate + 0.08 duet duration - 0.91 arriving phase duration + 0.42 transitioning phase duration.

Statistical models

For the first step, to test the effect of our experimental treatments on (1) incubation behaviour, (2) birds' movements from and to the feeder, and (3) duets' overall and detailed characteristics (first and second PCA), we used LMM (lmer function of the lmerTest package). All had the experimental condition (three levels: control, IN, OUT) as a fixed factor and the recording day (two levels: first day and second day) nested within the pair identity (12 levels) as random factors. In addition, we tested for a linear effect of incubation duration on duet's overall temporal structure in another model using the same random factors but with the duration of the incubation bout as a covariate instead of the three-level experimental condition.

In a second step, to test the effect of experimental duets' characteristics on subsequent incubation behaviour, we first investigated whether duet overall temporal structure (third PCA) predicted incubation behaviour, and we then tested which duet characteristic or previous incubation behaviour best explained subsequent incubation, using a model

comparison approach. First, we performed two LMMs, using, respectively, PC1 or PC2 from the third PCA as a covariate and the pair identity (12 levels) as a random factor (recording day was not a random factor in this model because the dataset limited to experimental duets had only one recording per day for each pair). Second, to test which parameter best explained subsequent incubation behaviour, we built three LMM model sets to test three response variables: (1) the duration of male's incubation bout (immediately following the experimental duet), (2) the duration of female's incubation bout (when she returned from her off-nest bout after the experimental duet), and (3) female contribution to incubation over the 2 h following the experimental duet. Each model set used eight fixed factors: six acoustic parameters of the experimental duet (for each sex: number of calls, call rate, time spent calling) and two incubation parameters (duration of females' last incubation bout before the experimental duet, or females' contribution to incubation in the 2 h prior to the experimental duet). The pair identity (12 levels) was used as a random factor. Collinearity was checked for all fixed factors using the variance inflating factor (vif function of the car package). Time spent calling was excluded from the analysis because it had a $vif > 10$, indicating high collinearity with the other predictors (other parameters all had $vif < 5.3$). The correlation between call rates from the male and the female was high ($r = 0.81$, Spearman correlation), although this factor was not correlated with other parameters; other correlations between parameters never exceeded $r = 0.5$. A model selection was then performed on the six remaining parameters using the dredge function from the MuMIn package, which compares all possible models built using subsets of the initial factors of the complete model, including null model. Models were compared using Akaike information criteria corrected for small sample size (AIC_c). When more than one model had some support (i.e. $\Delta AIC_c < 2$; Burnham & Anderson, 2002), the importance of explanatory terms was evaluated by calculating the predictor weight for each term (i.e. the sum of the Akaike weights for each model that contained that variable).

RESULTS

EFFECT OF CLOSING THE FEEDER ON THE DURATION OF INCUBATION BOUTS AND ON FEMALES' CONTRIBUTION TO INCUBATION

By closing the feeder for 1 h with the male either inside or outside, we obtained three different

conditions with differences in the duration of incubation bout (i.e. time spent in the nest between two nest reliefs) and the proportion of incubation time carried out by females (Table 1). The duration of incubation bout just prior to the relief was significantly increased by trapping the male in the feeder (IN condition) and, to a lesser extent, by preventing access to the feeder for both partners (OUT condition) (Fig. 2A, Table 1). In the control condition, mates shared incubation time equally (Fig. 2B, Table 1). In the OUT condition, birds were still able to perform nest relief normally, with a nest relief every 20–40 min, although they were unable to forage because the feeder was closed. In this condition, the duration of the incubation bouts just before the experimental duet (and therefore females' contribution to incubation) increased (Fig. 2B, Table 1) because the male, which was off the nest when the feeder re-opened, went to eat before returning to the nest (100% of the nine males with PIT-tag data were detected in the feeder before returning to the nest; the female returning to the nest in this condition was not detected). Finally, by trapping the male in the feeder (IN condition), we forced the female to carry out most of the incubation time (Fig. 2B, Table 1). In sum,

for both types of experimental duets, the female had not eaten for over 1 h and the male was late coming back from the feeder.

EFFECT OF DELAYING MALE'S RETURN ON BIRDS' MOVEMENT TIMING

When males had been trapped inside the feeder, males were significantly faster to return to the nest after exiting the feeder (i.e. seven out of nine males with PIT-tag data) (Fig. 3A, Table 1) and females tended to be faster to go to the feeder after the nest relief, although this was not statistically significant (seven out of 10 females) (Fig. 3B, Table 1).

ACOUSTIC STRUCTURE OF THE DUETS

During nest-reliefs, calls were always emitted, normally by both birds thereby producing a duet (96% of the nest-reliefs observed) or, more rarely, only by the bird inside the nest (4% of the reliefs).

Duet temporal structure (PC1 of the first PCA) was significantly affected by the experimental condition: when the male had been trapped inside the feeder (IN condition), PC1 was significantly lower (shorter duets, shorter arriving and transitioning phases,

Table 1. Statistical analysis of the effect of delaying male's return on nest-relief and birds' movement timing

	d.f.	χ^2 or Z value (post-hoc)	P value	Estimate \pm SE control condition	Estimate \pm SE OUT condition	Estimate \pm SE IN condition
Female contribution to incubation (%)						
	2	50.34	< 0.001	51 \pm 3 N = 24	64 \pm 4 N = 12	74 \pm 4 N = 12
OUT-Control		3.98	< 0.001			
IN-Control		6.86	< 0.001			
IN-OUT		2.50	0.033			
Incubation bout duration (min)						
	2	56.84	< 0.001	38 \pm 4 N = 24	55 \pm 6 N = 12	85 \pm 6 N = 12
OUT-Control		2.79	0.015			
IN-Control		7.53	< 0.001			
IN-OUT		4.11	< 0.001			
Female time to go to the feeder (min; log transformed)						
	2	0.35	0.842	0.77 \pm 0.11 N = 19	0.74 \pm 0.17 N = 9	0.66 \pm 0.15 N = 11
Male time to go to the nest (min; square-root transformed)						
	2	9.85	0.007	28 \pm 3 N = 17	27 \pm 4 N = 9	14 \pm 4 N = 10
OUT-Control		-0.22	0.974			
IN-Control		-3.00	0.007			
IN-OUT		-2.41	0.042			

Significant P-values are shown in bold. N values below the full sample size of 48 (12 pairs with four duets each: two duets in control condition, one duet in IN condition, and one duet in OUT condition) are a result of missing values.

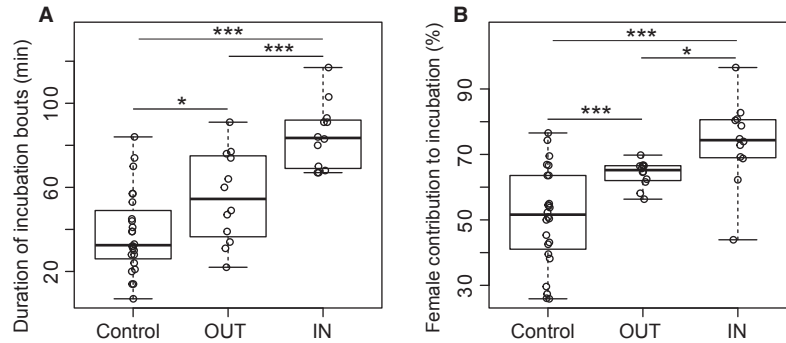


Figure 2. Duration of incubation bouts (time spent in the nest between two nest-reliefs) (A) and female contribution to incubation (B) in the three experimental conditions. Boxes are the first to third quartiles, lines are medians, whiskers are extreme values, and each point represents one duet (control: $N = 24$; OUT: $N = 12$; IN: $N = 12$; linear mixed model: *** $P < 0.001$; * $P < 0.05$).

higher call rate) compared to control (PC1 reduced in 75% of the pairs) (Fig. 4A, Table 2). The second principal component was not affected by the conditions (Table 2). Similarly, across treatment groups, PC1 significantly decreased when the duration of the incubation bout increased (LMM, $\chi^2 = 8.83$, d.f. = 1, $P = 0.003$, $N = 48$) (Fig 4B), whereas the second principal component was not affected (LMM, $\chi^2 = 0.12$, d.f. = 1, $P = 0.720$, $N = 48$). Therefore, the longer the incubation bout, the shorter and more accelerated the duet.

VOCAL REPERTOIRE FOR EACH PARTNER

The first and second principal components (PC1 and PC2 of the second PCA) were not affected by the conditions (LMM, PC1: LMM, $\chi^2 = 0.76$, d.f. = 2, $P = 0.684$, $N = 41$; PC2: $\chi^2 = 1.62$, d.f. = 2, $P = 0.444$, $N = 41$). Therefore, delaying the male's return had no effect on the proportion of Whine versus Short Calls and the duration of the calls of either partner.

PREDICTORS OF THE CONTRIBUTION OF PARTNERS TO INCUBATION AFTER EXPERIMENTAL DUETS

Pairs did not appear to compensate for the additional female incubation time caused by male's delay in OUT and IN conditions because the females' contributions to incubation before and after the experimental duets were not negatively correlated (LMM, $\chi^2 = 1.37$, d.f. = 1, $P = 0.242$, $N = 23$) (Fig. 5A). Instead, the incubation behaviour of pairs varied with the characteristics of their duet under experimental conditions. Indeed, females' contribution to incubation decreased when the previous duet had a lower PC1 for the third PCA (i.e. was shorter and more accelerated; LMM, $\chi^2 = 14.97$, d.f. = 1, $P < 0.001$, $N = 23$) (Fig. 5B). Female's contribution to incubation was not affected by PC2 (LMM, $\chi^2 = 0.37$, d.f. = 1, $P = 0.540$, $N = 23$).

The parameter that best explained subsequent incubation behaviour was the number of male calls: the more the male called, the shorter his following incubation bout (Fig. 5C, Table 3). Including the

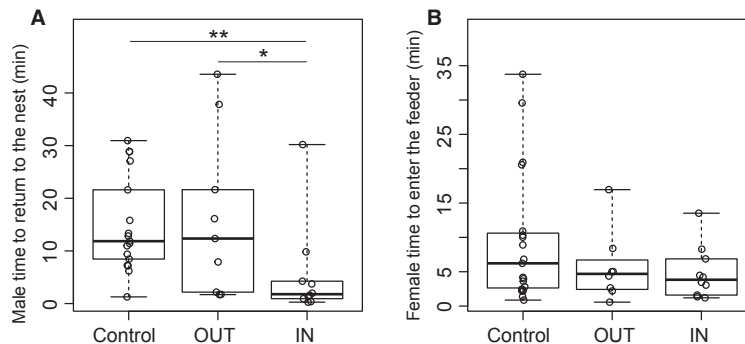


Figure 3. Time to return to the nest for the male (A) and time to enter the feeder for the female (B) in the three experimental conditions. Boxes are the first to third quartiles, lines are medians, whiskers are extreme values, and each point represents a duet (control: $N = 24$; OUT: $N = 12$; IN: $N = 12$; linear mixed model: ** $P < 0.01$; * $P < 0.05$).

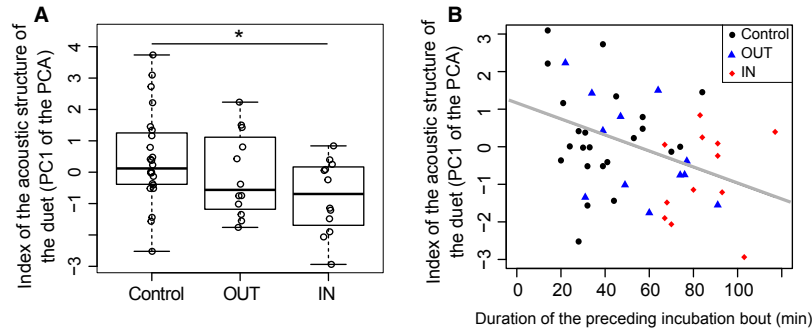


Figure 4. Effects of delaying male return to the nest on duet structure. Principal component (PC)1 is the first principal component of a principal component analysis, and low values of PC1 indicate shorter duets with higher call rate, and, to a lesser extent, shorter arriving and transitioning phases. In (A), boxes are the first to third quartiles, lines are medians, whiskers are extreme values, and each point represents a duet. In (B), the regression line of PC1 is shown as a function of the duration of the preceding incubation bout.

Table 2. Statistical analysis of the effect of delaying male’s return on duet characteristics

	d.f.	χ^2 or Z value (post-hoc)	P value	Estimate \pm SE control condition	Estimate \pm SE OUT condition	Estimate \pm SE IN condition
Index of acoustic structure of the duet (PC1 of the PCA)						
	2	6.63	0.036	0.44 \pm 0.28 N = 24	-0.10 \pm 0.39 N = 12	-0.78 \pm 0.39 N = 12
OUT-Control		-1.12	0.498			
IN-Control		-2.56	0.028			
IN-OUT		-1.24	0.428			
Index of acoustic structure of the duet (PC2 of the PCA)						
	2	0.71	0.702	-0.13 \pm 0.22	0.10 \pm 0.32	0.16 \pm 0.32

Significant *P* values are shown in bold. PC, principal component; PCA, principal component analysis.

female contribution to incubation before the experimental duet did not improve the model because the model with both predictors was equivalent to that with male call number only ($\Delta AIC < 2$). Moreover, the sum of the Akaike weights for each model that contained male call number is higher (0.605) than those of female incubation bout before the experimental duet (0.468) (Fig. 5D). Similarly, females’ call rate was the best predictor of female’s first incubation bout when she returned to the nest after being off-nest following the experimental duet (Table 3). The higher the female’s call rate, the shorter her incubation bout. Finally, females’ vocal behaviour (call rate, sum of the Akaike weights: 0.819), as well as males’ vocal behaviour (number of call and call rate, respectively, 1.764 and 0.573), best explained female contribution to incubation in the 2 h following the experimental duet (Table 3). In agreement with the analysis of the third PCA above, female contribution to incubation decreased with duets with fewer male’s calls and higher call rate from both the male and the female.

DISCUSSION

We found that the duration of the incubation bout was mostly determined by the returning partner because, under our experimental conditions, parents never ended their incubation bout before their partner returned to the nest. Delaying males’ return to the nest increased females’ contribution to incubation, and also modified the vocal exchange of partners, which was shorter with a higher call rate, corresponding to an accelerated duet. Furthermore, the incubation behaviour of pairs after that accelerated experimental duet varied with the characteristics of that duet rather than with their previous incubation effort. Indeed, the shorter and more accelerated the experimental duet, the less females subsequently contributed to incubation. It was difficult to separate male and female contributions to duets, especially features such as call rate, as a result of the high level of contribution of both partners. Nevertheless, the vocal behaviour of each mate was the best predictor of its subsequent incubation bout duration. Our results

therefore support the hypothesis that the vocal exchange of partners at the nest plays a role in incubation shift coordination, in addition to the experimental conditions that had altered this duet.

The male appeared to communicate his willingness to spend time incubating by calling less during the duet and the female indicated that she will decrease her subsequent incubation duration by increasing her call rate. Importantly, because the duration of an incubation bout depends on when the returning partner is coming back, this suggests that birds responded to their partner's demand by coming back and relieving them early or late depending on the information they received during the relief. Each partner may thus use the vocal behaviour of its mate during the duet to predict its future behaviour and adjust its own behaviour pre-emptively. This is consistent with a vocal negotiation process where each partner signals its capacity to invest in parental care and its mate adjusts its own contribution in

response to this information (McNamara *et al.*, 1999; Johnstone & Roulin, 2003; Johnstone & Hinde, 2006; Bell *et al.*, 2010). Our results therefore suggest that duets are used to adjust incubation duties between partners and may function as vocal negotiation processes. In the present study, we manipulated male's time to return to the nest during the female's incubation shift, and we thus studied the impact of a male delay on the process of negotiation over parental care. This process might be different in the case of a female delay, and it would be very interesting to design the reverse experiment by delaying the female during the male's incubation shift.

The decrease in duration of the arriving phase and the transitioning phase indicated that birds did the physical relief faster after delaying male return to the nest: the returning male did not spend as much time vocalizing outside the nest but instead went quickly inside. The transitioning phase inside the nest was also shorter and females left quickly. It appears that

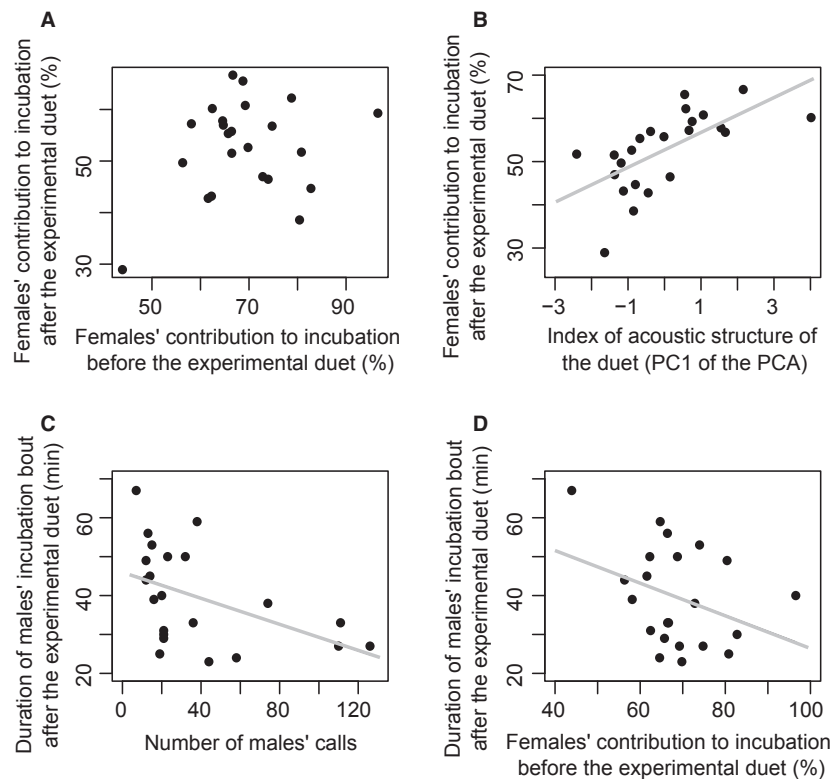


Figure 5. Predictors of the contribution of partners to incubation after experimental duet (11 pairs in OUT and 12 pairs in IN conditions: $N = 23$). A, female contribution to incubation before the experimental duet does not predict female contribution to incubation after the experimental duet. B, principal component (PC)1 is the first principal component of a principal component analysis, and low values of PC1 (shorter duets with higher call rate, and, to a lesser extent, shorter arriving and transitioning phases) predict a decrease in female contribution to incubation after the experimental duet. C, fewer male calls predict an increase in male contribution to incubation after the experimental duet. Male call number is a better predictor of male contribution to incubation after the experimental duet than female contribution to incubation before the experimental duet (D).

Table 3. Model comparison to test which of the correlated acoustic and behavioural parameters best explained incubation behaviour after the experimental duet: duration of male's incubation bout, duration of female's incubation bout, and females' contribution to incubation

Model number	(Intercept)	Female call number	Male call number	Female call rate	Male call rate	Female incubation bout before the experimental duet	Female contribution to incubation before the experimental duet	d.f.	Log likelihood	AIC _c	ΔAIC _c	Weight
Duration of male's incubation bout												
1	46.12		-0.1692					4	-83.682	177.7	0.00	0.166
2	70.26		-0.1576				-0.3584	5	-82.303	178.4	0.64	0.120
3	46.66		-0.2166					4	-84.770	179.9	2.18	0.056
6	39.64							3	-86.489	180.3	2.59	0.045
Duration of female's incubation bout												
1	50.76			-0.1717				4	-96.175	202.7	0.00	0.218
2	83.56			-0.1870				5	-95.476	204.7	2.00	0.080
3	63.88			-0.1485		-0.2186		5	-95.531	204.8	2.11	0.076
4	38.77							3	-98.858	205.0	2.35	0.067
5	61.18					-0.3324		4	-97.550	205.5	2.75	0.055
6	48.26				-0.1293			4	-97.607	205.6	2.86	0.052
Females' contribution to incubation												
1	54.60		0.1037		-0.0863			5	-71.911	157.6	0.00	0.200
2	58.72			-0.0927				4	-73.920	158.2	0.62	0.147
3	55.24		0.0657	-0.0790				5	-72.843	159.4	1.87	0.079
4	58.92		0.1123		-0.0844	-0.0710		6	-71.266	160.1	2.56	0.056
5	58.91				-0.0908			4	-74.940	160.2	2.66	0.053
32	52.24							3	-79.157	165.6	8.08	0.004

Only models with weight > 0.05, as well as null models, are presented. Significant models are shown in bold.

both birds were accelerating the relief. This is confirmed by the transponders data, showing a significantly shorter time for the male to return from the feeder to the nest compared to the control condition. The haste of both partners could be explained by the motivation of the female to eat after her extended nest attendance and of the male to return to the nest after an extended absence (Dearborn, 2001; Cresswell *et al.*, 2003; but see also Bulla *et al.*, 2014). Nevertheless, the experimental extension of the female's nest attendance remains within the range of bout duration for the species and it is possible that greater disruptions (e.g. a longer absence of the male) would cause some females to terminate their incubation bout before their mate returns (Chaurand & Weimerskirch, 1994).

Our results showed clear patterns even though the sample size was only moderate, with 12 pairs per experimental group, possibly because the within-pair design partly compensated for that limitation. The effects that we report were followed by the large majority of individuals in our sample, although it is possible that more subtle differences were missed. Moreover, future studies could directly manipulate pair communication by using playback to artificially increase calling rate, although achieving convincing conditions to birds may be technically challenging. In addition, it remains to be investigated whether more information is encoded in the acoustic characteristics of the calls themselves because the recording conditions in the present study did not allow for the analysis of calls' spectral structure. In particular, if the stress level of individuals increases as they are forced to incubate for long periods, it is possible that the spectrum of their calls shift to higher frequency bands (Perez *et al.*, 2012) and that their partner is sensitive to such modulations (Perez *et al.*, In press). Nevertheless, vocal repertoire (calls duration and proportion of Whines) was maintained in accelerated experimental duets. This suggests that the pace of the duet could be sufficient to cause functional changes in the behaviour of individuals, and thus be a relevant signal for pair coordination.

The present study found that duets in domesticated zebra finches are similar to those in wild birds (Elie *et al.*, 2010). Insights that we learn regarding the structure and function of duets in a captive environment may thus be applicable to wild birds. Because females of many bird species vocalize at the nest (Ritchison, 1983; Beletsky & Orians, 1985; Yasukawa, 1989; McDonald & Greenberg, 1991; Halkin, 1997; Halfwerk *et al.*, 2011, 2012), call duets between partners at the nest are likely to be widespread. The coordination of parental care via call duets at the nest is therefore likely to also occur in some other species. Although many functions have

been attributed to duets in a range of species (Faraugh, 1982; Hall, 2004, 2009; Benedict, 2008; Dahlin & Benedict, 2013), their role in parental care negotiation had not been considered previously.

Overall, we have demonstrated that partners modify their vocal exchange when their incubation routine is experimentally altered by delaying male return, and they also adjust their time off-nest according to their calling behaviour in the previous duet. Taken together, these results suggest that acoustic communication may play a role in the negotiation of parental care between breeding partners.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s website:

Data S1. Analysis of the effect of the sex of the returning partner on the structure of the duet.

File S1. Wave file of a call duet.

File S2. Wave file of a Tet (Short Call) followed by a Whine.

File S3. Wave file of a male Distance Call (Short Call).

File S4. Wave file of a female Distance Call (Short Call).