



Incubating females signal their needs during intrapair vocal communication at the nest: a feeding experiment in great tits



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Parental care is a key factor of breeding success and parents face evolutionary trade-offs between investment in current offspring and future reproduction and survival. Incubation in birds is energetically costly and the balance between parental and offspring's energetic needs is especially challenging when only one sex incubates, generally the female. In that case, males can contribute indirectly to incubation effort by feeding their mate and females may use begging behaviours to signal their needs to their visiting partner. The great tit, *Parus major*, is a good model species to test whether females use acoustic communication from the nest to signal their needs to their mate outside because females interact vocally with their mate during incubation. To test whether females use these vocal exchanges to communicate how hungry they are, great tit pairs were recorded on 2 days during incubation: 1 day with a feeder of mealworms in the nestbox and 1 day with an empty feeder. First, food supplementation increased females' nest attentiveness, revealing a decrease in foraging activity and consequently in females' needs. Second, females signalled their need for food both during their male's visits inside the nest but also during the vocal exchange immediately preceding the male's entrance by calling more and by modifying the frequency spectrum of their calls. So females' calling behaviour is an honest signal of need not only during their male's visits, but also before his entrance in the nest.

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Biparental care requires that parents work as a team. Many theoretical and empirical studies have investigated how each parent adjusts its behaviour to an increase or a decrease in the parental effort of its partner (Houston & Davies, 1985; Houston, Szekely, & McNamara, 2005; Lessells, 2012; McNamara, Gasson, & Houston, 1999; McNamara, Houston, Barta, & Osorno, 2003; Westneat & Sargent, 1996). However, few studies have explored the mechanisms allowing this adjustment (Boucaud, Mariette, Villain, & Vignal, 2016; Johnstone et al., 2014; Meade, Nam, Lee, & Hatchwell, 2011). In birds, parents may use acoustic communication to organize parental care. Indeed, several bird species use vocalizations around the nest. In some species, females have been reported to call when leaving the nest and these vocalizations may increase their mate's nest defence against predators (Yasukawa, 1989), signal female identity (Collias, 1963; McDonald & Greenberg, 1991), or inform their mate about their activities and reproductive state (Beletsky & Orians, 1985). Unlike male vocal

behaviours, however, female vocalizations have been little studied (Riebel, 2003, 2016; Riebel, Hall, & Langmore, 2005) and their role during communication between mates rarely described (Benedict, 2008; Dahlin & Benedict, 2013; Elie et al., 2010; Gill, Goymann, Ter Maat, & Gahr, 2015; Hall, 2004, 2009; Perez, Fernandez, Griffith, Vignal, & Soula, 2015; Ter Maat, Trost, Sagunsky, Seltsmann, & Gahr, 2014; Villain, Fernandez, Bouchut, Soula, & Vignal, 2016). Here we tested whether incubating female birds signal their needs to their partner during intrapair acoustic communication.

Parental care represents an evolutionary trade-off between current reproductive investment and future reproduction and survival (Clutton-Brock, 1991). Incubation in birds is an interesting model to study scaling of parental effort because it is energetically costly (Thomson, Monaghan, & Furness, 1998; Williams, 1996) and incubating parents must balance the thermal needs of the eggs with their own energetic needs. Moreover, this trade-off can be exacerbated by low food supply, which further limits the amount of energy an individual can obtain during a foraging bout (Chalfoun & Martin, 2007). This energetic trade-off might be especially challenging in species with single-sex incubation, because the eggs are left unattended when the incubating parent, generally the female,

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needs to forage (Deeming, 2002). In many species of birds with female-only incubation, males feed their mate during incubation and this might offset the trade-off between eggs' development and female's condition (Kendeigh, 1952; Lyon & Montgomerie, 1985; Silver, Andrews, & Ball, 1985). Males have been shown to adjust their workload to the needs of their partner in experimental studies: they increased their feeding rate when their female's foraging ability was experimentally impaired by wing clipping, and decreased it when their female received supplementary food (Cantarero, López-Arrabé, Palma, Redondo, & Moreno, 2014; Pearse, Cavitt, & Cully, 2004; Smith, Källander, Hultman, & Sanzén, 1989). Thus, male incubation feeding responds at least partially to the female's needs, but how the male gets information about the female's state and whether communication within a pair mediates this adjustment remain poorly understood.

During male incubation feeding, the female may use begging behaviours to signal her needs. While nestlings' begging has been well studied (Horn & Leonard, 2005) and is considered as an honest signal of need (Kilner & Johnstone, 1997), fewer studies have considered the role of female begging. In black-capped chickadees, *Poecile atricapillus*, begging call rate decreases in females supplemented with food during the egg-laying period (Otter, Atherton, & van Oort, 2007). In the European robin, *Erithacus rubecula*, females that are well fed by their male during the fertile period have larger clutches and lower begging call rates (Tobias & Seddon, 2002). Begging intensity increases when females have not been fed by their mate for a long period (yellow warbler, *Setophaga petechia*; Moore & Rohwer, 2012) or have been experimentally handicapped (pied flycatcher, *Ficedula hypoleuca*; Cantarero et al., 2014), and males responded by increasing feeding rates accordingly. All these results suggest that females signal their needs using begging behaviours during their male's visits. But females may also signal their needs before their mate enters the nest, for example using interactive vocal communication with him outside the nest. In northern cardinals, *Cardinalis cardinalis*, males visited the nest with food more often after their female answered their vocalizations by singing from the nest (Halkin, 1997).

The great tit, *Parus major*, is a good model species to test whether females signal their needs vocally during interactive acoustic communication with their mate. The female incubates the eggs alone and regularly leaves the nest to forage (Cramp & Perrins, 1993). The male often feeds the female and mate feeding starts at egg laying, increases during incubation and lasts until the young leaves the nest (Hinde, 1952; Royama, 1966). The incubating female answers her mate singing outside the nest (Gorissen & Eens, 2004; Halfwerk et al., 2011; Halfwerk, Bot, & Slabbekoorn, 2012). Moreover, in a previous study (Boucaud, Valère, et al., 2016), we observed vocal exchanges between the female inside the nest and her mate outside. These vocal exchanges consisted of vocalization bouts alternated at the same tempo between mates. We observed three contexts of vocal exchanges which differed in their outcome: (1) the female flew out of the nest; (2) the male entered the box with food, and the female started a begging display; and (3) the female stayed in and the male stayed out of the nest. Because birds vocalized more and at higher tempo during exchanges that ended in the male feeding the female inside the nest, we hypothesized that females could signal their need for food to their mate during intrapair vocal exchanges (Boucaud, Valère, et al., 2016).

In the present study, we tested whether females signal their needs for food (1) during the vocal exchange with their mate outside the nest and (2) during the begging display produced during the male feeding that may immediately follow a vocal exchange. To do so, we experimentally manipulated females' needs during incubation using food supplementation. We recorded great tit pairs on 2 days: 1 day with a feeder of mealworms inside the

nestbox and 1 day with an empty feeder. If females' acoustic communication at the nest is an honest signal of need, females' calling activity should decrease with food supplementation. For example, we expected that females would decrease their call rate and/or their number of calls.

METHODS

Study Site and Species

Our study was conducted in spring 2014 in wooded areas close to the campus of Université de St-Etienne, in France (45°25'N, 4°25'E). We installed 54 nestboxes (wood, 150 × 150 mm and 250 mm high, with an entrance hole of 32 mm diameter) between winter 2012 and winter 2014. To record occupation by a breeding pair, we checked the nestboxes once a week starting at the end of March, and when occupied, three times a week to monitor breeding.

Experimental Procedure

Data were collected in April–May 2014 on 12 great tit pairs. The acoustic activity of each pair was recorded during incubation on 2 successive days, on which two separate experimental conditions were performed (order balanced between conditions). In both conditions, a cardboard feeder (30 × 40 mm and 20 mm high) was installed inside the nestbox (see [Supplementary Material](#)). It was located on the balcony so it did not disturb birds' movement in and out of the nestbox. The two conditions differed with respect to the presence or absence of food in the feeder: control condition: the feeder was empty; food condition: the feeder contained 10 g of mealworms. At the end of the recording, the remaining mealworms were weighed to measure how much was eaten by the female. Eleven of 12 females ate the mealworms. Thus our final sample size was 11 pairs. Females ate on average 6.7 ± 2.3 g (mean \pm SD), and only one female ate all the mealworms, so the quantity provided represented ad libitum food. In our population, females weighed on average 16.7 ± 0.7 g, thus eating on average 40% of their body mass in mealworms.

The feeder and the recorder were installed on the afternoon before the recording day. Then, the recording automatically started at 0530 hours and ended at 1400 hours, avoiding any disturbance for the birds at the beginning of the experiment. Preliminary observations showed that birds did not hesitate to enter the nestbox after the installation of the set-up. Moreover, we observed an average of nine feeding events (male entrances in the nestbox) per recording which is close to the total number of feeding events in an entire day in another study on the same species (Royama, 1966). Furthermore, if the equipment had disturbed the birds, we would predict that some birds would have habituated and the number of feeding events would have increased between days 1 and 2 but we did not observe any such change.

In the food condition, freshly killed mealworms were put into the feeder after sunset. Preliminary observations using video cameras in nestboxes showed that birds' behaviour was not disturbed by the presence of the mealworms inside the nest, and that the females ate the mealworms available in the feeder.

The recorder (SongMeters SM2+, 16-bit, 44 kHz sampling rate; Wildlife Acoustics Inc., Concord, MA, U.S.A.) was positioned near the nestbox on the tree trunk, connected to a microphone (SMX-II, Wildlife Acoustics Inc.; omnidirectional, flat frequency response 20 Hz–20 kHz, sensitivity -36 ± 4 dB, 0 dB = 1 V/pa at 1 kHz) inside the nestbox just below the ceiling (inbuilt pre-amplifier gain set at +24 dB) and a microphone outside, fixed on the tree trunk at the height of the nestbox (inbuilt pre-amplifier gain set at +42 dB).

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