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Songbird mates change their call structure and intrapair communication at the nest in response to environmental noise

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The coordination of behaviours between mates is a central aspect of the biology of the monogamous pair bonding in birds. This coordination may rely on intrapair acoustic communication, which is surprisingly poorly understood. Here we examined the impact of an increased level of background noise on intrapair acoustic communication at the nest in the zebra finch, *Taeniopygia guttata*. We monitored how partners adapted their acoustic interactions in response to a playback of wind noise inside the nestbox during incubation. Both zebra finch parents incubate and use coordinated call duets when they meet at the nest. The incubating parent can vocalize to its partner either outside the nestbox (sentinel duets) or inside the nestbox (relief and visit duets), depending on the context of the meeting. Pairs use these duets to communicate on predation threats (sentinel duets), incubation duties (relief) and other nesting activities (visit duets). Each of these duets probably represents a critical component of pair coordination. In response to the noise playback, partners called less and more rapidly during visit and relief duets. Female and male calls were more regularly and precisely alternated during relief duets. Mates increased the number of visit duets and their spatial proximity during sentinel duets. Furthermore, both females and males produced louder, higher-frequency and less broadband calls. Taken together our results show that birds use several strategies to adjust to noise during incubation, underlining the importance of effective intrapair communication for breeding pairs.

Monogamy in birds represents a partnership in which the female and male adjust their behaviour to each other and synchronize many of their activities (Black, 1996). Many long-term monogamous species show an increase in reproductive success with pair bond duration, which may be due to the improvement in partners' coordination over time (mate familiarity effect, Black, 2001; Coulson, 1966; Forslund & Pärt, 1995). In some species, partners synchronize their foraging trips or their nest visits to feed the chicks (Lee, Kim, & Hatchwell, 2010; Van Rooij & Griffith, 2013), and their degree of synchrony can correlate with their reproductive success (Mariette & Griffith, 2012, 2015). In species in which both partners incubate, hatching success may be increased when parents better coordinate incubation bouts (Spoon, Millam, & Owings, 2006). Partners' coordination during parental care may reflect their coordination in other situations: mates may defend their resources as a team by alarm calling for danger (Krams, Krama, & Igaune, 2006), repelling predators or intruders on their territory (Black, 2001; Regelmann & Curio, 1986) or alternating vigilance periods (McGowan & Woolfenden, 1989).

Communication and especially acoustic communication may play a key role in mate coordination. Whereas birdsong has been studied in the context of mate choice extensively in males (Catchpole & Slater, 2008) and more rarely in females (Cooney & Cockburn, 1995; Langmore, 1998; Odom, Hall, Riebel, Omland, & Langmore, 2014; Riebel, 2003; Riebel, Hall, & Langmore, 2005), much less is known about vocal interactions after pair formation between the female and male of a breeding pair (Gorissen, Eens, & Nelson, 2004) with the exception of acoustic duets. Duets are joint acoustic displays of partners that alternate or partly overlap vocal or nonvocal sounds (Dahlin & Wright, 2009; Farabaugh, 1982; Hall, 2004, 2009). Although rare (ca. 4% of bird species), they have attracted much interest, and the highly coordinated

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and conspicuous song duets of tropical bird species have been particularly well studied (Hall, 2004, 2009). But intrapair communication may be more widespread and involve simpler or low-amplitude vocalizations such as calls (Lamprecht, Kaiser, Peters, & Kirchgessner, 1985; Morton & Derrickson, 1996; Todt, Hultch, & Duvall, 1981; Wright & Dahlin, 2007). Females can produce sounds at the nest (Beletsky & Orians, 1985; McDonald & Greenberg, 1991; Yasukawa, 1989) that may be used in interactive communication with their mate (Gorissen et al., 2004). Such vocal interactions can facilitate a pair's coordination during breeding (Halkin, 1997; Ritchison, 1983). For instance, nest relief and greeting ceremonies have been described in several bird species but their functions remain unclear (Wachtmeister, 2001).

If vocal interactions around the nest allow coordination of behaviours between mates, they must remain efficient despite environmental constraints on acoustic communication. Noise is a common constraint on acoustic communication. By decreasing signal to noise ratio, background noise makes the signal harder to extract for the receiver (Brenowitz, 1982; Wiley & Richards, 1982). Noise particularly constrains acoustic communication if spectral components of the noise and the signal partly overlap (Barber, Crooks, & Fristrup, 2010; Francis & Barber, 2013; Halfwerk & Slabbekoorn, 2015; Slabbekoorn, 2004). Birds have evolved many adaptive strategies to cope with background noise and to increase signal reception efficacy (Brumm & Slabbekoorn, 2005). Senders can use different frequencies to avoid spectral overlap between signal and noise (Slabbekoorn & Peet, 2003). They can increase signal amplitude (the ‘Lombard effect’; Brumm & Todt, 2002; Cynx, Lewis, Tavel, & Tse, 1998; Potash, 1972) or signal redundancy (Brumm & Slater, 2006; Lengagne, Aubin, Lauga, & Jouventin, 1999), as well as change the timing of their vocalizations to avoid noise (Brumm, 2006b; Dreiss, Ruppli, Faller, & Roulin, 2015; Gil, Honarmand, Pascual, Pérez-Mena, & Garcia, 2014). Senders and receivers can also adjust their location during communication, such as moving closer to each other (Halfwerk, Bot, & Slabbekoorn, 2012) or stay outside/inside the nest cavity (Blumenrath, Dabelsteen, & Pederson, 2004). The effects of background noise have been primarily studied on songs and other long-range vocalizations, and thus little is understood about the effects of background noise on private, short-range vocalizations (Leonard & Horn, 2005, 2008). Importantly, short-range vocalizations are less affected by degradation during sound propagation and thus probably require very different adjustment strategies from long-range vocalizations. Noise probably hinders intrapair communication around the nest during breeding, which could explain the observed impairment of reproductive success by noise (Barber et al., 2010; Slabbekoorn & Ripmeester, 2008).

The zebra finch, *Taeniopygia guttata*, provides an excellent study system to test whether partners adapt short-range intrapair communication to noise constraints. Zebra finches form lifelong pair bonds and are highly coordinated partners, starting incubation on the same day (Gilby, Mainwaring, & Griffith, 2013), sharing incubation time equally (Delesalle, 1986; Gilby et al., 2013; Gorman, Arnold, & Nager, 2005; Zann & Rossetto, 1991), and synchronizing visits to the nest and to foraging patches during the nestling period (Mariette & Griffith, 2012, 2015). Each time they meet around the nest during incubation or the nestling period, mates perform a call duet that probably aids coordination (Boucaud, Mariette, Villain, & Vignal, 2016; Elie et al., 2010). Zebra finches live in semiarid zones of Australia, an unpredictable environment in which windy conditions are highly variable on an hourly basis. Because zebra finch calls, and particularly nest calls, have a spectrum in the low range (Elie et al., 2010; Elie & Theunissen, 2015; Zann, 1996), they are very likely to overlap in frequency with wind noise. To our knowledge no experiment testing this effect has been conducted in zebra finches.

In the present study, we exposed incubating zebra finch pairs to a natural wind noise playback inside their nestbox. Because the female and male take turns incubating, both partners were exposed to the noise. After 15 h of noise, intrapair communication and partners' behaviour were monitored and compared to the control condition. Because call duets are thought to aid partners' coordination during incubation, we expected birds to show strategies to maintain signal efficacy in response to the noise playback. We monitored three duet types, incubation relief/nest visit/sentinel, and we studied four aspects of this intrapair communication: (1) the temporal structure of duets; (2) the female–male dynamic during the duet; (3) the number of vocal interactions between partners and the spatial proximity of partners during interactions; and finally (4) the acoustic structure of the calls used during interactions. In response to this experimental increase in noise, we expected the partners either to avoid communicating or to display strategies to cope with it, for example by increasing signal redundancy (longer duets and/or duets composed of longer calls), increasing partners' proximity during vocal interactions and/or changing signal structure (frequency range and/or amplitude).

METHODS

Subjects and Housing Conditions

Eighteen pairs of zebra finches were used in this study, from October 2013 to December 2013. All birds came from our breeding colony (ENES laboratory, University of Saint-Etienne). They were all the same age (between 24 and 28 months at the start of the experiment) and the experiment was conducted on the third reproductive event of their lifetime for every pair. Before the experiment, pairs were housed separately in cages (40 × 40 × 40 cm) equipped with perches and a pool for environmental enrichment. All birds were kept under the same environmental conditions (temperature between 24 and 26 °C, light conditions 14:10 h light:dark). Birds were fed with finch seed cocktail, egg paste, water and cuttlefish bones ad libitum and supplemented with salad once a week. For the experiment, pairs were transferred to an indoor breeding aviary (6.5 × 5.5 m and 3.5 m high, temperature between 19 and 24 °C, light conditions 14:10 h light:dark). Twenty-seven nestboxes were installed (13 × 12 cm and 17 cm high).

During the experiment, all 18 pairs were allowed to breed freely in the aviary. Pairs were provided with dry grass and cotton ad libitum. Birds were identified with two plastic colour bands.

As the experiment was performed during incubation, pairs were captured a few days after hatching (from day 1 to 5 post hatching) and put back in their initial home cage with their nestbox containing the chicks. Other pairs were released in the aviary to replace the outgoing ones, so that the aviary always contained 12 breeding pairs, keeping the conspecific background noise at a stable level.

Ethical Note

Experiments were performed under the authorization no. 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 legislation regarding experiments on animals.