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Articles

Vocal communication at the nest between mates in wild zebra finches: a private vocal duet?

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Bird vocal duets are joint displays where two individuals, generally a mated pair, produce temporally coordinated vocalizations. Duets may contribute to pair bond maintenance, mate guarding or collaborative defence of resources. The degree of coordination between mates and the variety of vocalizations, however, vary considerably. Although only 3–4.3% of bird species have been reported to duet, this may be because studies have generally focused on conspicuous duets, and more private forms of duet might have been overlooked. We investigated private vocal communication between mates in wild zebra finches, *Taeniopygia guttata*, a gregarious Australian songbird that forms life-long pair bonds. The partners are inseparable unless nest building, incubating or brooding. Using microphones inside nestboxes, we monitored interactive communication between partners at the nest and its variation during different stages of breeding. After periods of separation, partners performed coordinated mutual vocal displays involving specific soft vocal elements that fulfilled all the criteria used to define duets. In addition, using playback experiments, we obtained preliminary results suggesting that these soft calls could allow mate recognition. Thus, we propose that mutual displays at the nest in zebra finches represent private vocal duets and may function to mediate pair bond maintenance.

Mutual displays associated with partner choice have been extensively studied (Andersson 1994). In contrast, display behaviours that continue beyond pair formation in monogamous pairs remain poorly understood (Wachtmeister 2001), with the notable exception of acoustic duets performed by mated pairs in birds and primates (Farabaugh 1982; Hall 2004, 2009).

Avian duets are mutual acoustic displays between two birds, generally a mated pair, that make temporally coordinated vocal or nonvocal sounds (Farabaugh 1982; Hall 2004). Duetting may function in defence of resources and territory and thus represents a collaborative display (Thorpe 1972; Todt et al. 1981; Hall 2000; Marshall Ball & Slater 2004; Hall & Magrath 2007; Hall & Peters 2008). Vocal duets may also contribute to pair bond maintenance by maintaining contact between partners, synchronizing or stimulating reproduction, and advertising mated status (Thorpe 1972; Wickler 1980; Hall 2000; Todt & Naguib 2000). It has also been hypothesized that duets may reflect a conflict between the sexes and could thus serve a function in mate guarding or mate manipulation (Levin 1996a, b; Wachtmeister 2001; Seddon & Tobias 2006). Taken together, these studies suggest that duets may play a role in most aspects of the monogamous pair bond (reviewed in Hall 2004, 2009) and a growing number of studies suggest that the function of such duets may vary with context or species and that duets may have multiple roles (Grafe et al. 2004; Hall 2004, 2009; Marshall Ball et al. 2006; Logue 2007; Mennill & Vehrencamp 2008).

Duetting is commonly associated with long-term monogamy in oscine as well as in nonoscine groups, such as the 'triumph ceremonies' of Anseriformes (Farabaugh 1982; Malacarne et al. 1991; Benedict 2008). There is no indication that the ecological correlates and life history traits of duetting species differ from those of

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nonduetting monogamous species (Hall 2009); however, duetting seems to be more common in the tropics (Mann et al. 2009), and duetting species therefore often have life history traits typical of low latitudes. None the less, the majority of tropical monogamous species do not duet, including species in which both male and female sing (Hall 2009). In fact only 3–4.3% of bird species have been reported to duet, even though duetting occurs across as many as 40% of bird families, including passerines and nonpasserines (Farabaugh 1982; Hall 2009). Moreover, the variety of duetting displays between species remains puzzling. Even in closely related species, duets may vary from loosely overlapping bouts of vocalizations to remarkably complex, coordinated performances (Mann et al. 2009).

Therefore, considering the importance for monogamous species of the many functions that duetting fulfils and the phylogenetic dispersion of duetting, the rarity of duetting is surprising. It is possible that one reason for the low level is that duetting might actually occur in many more species than is currently acknowledged. This might be because most studies on vocal duets have focused on songbird species showing complex and conspicuous duets with high temporal precision (Morton 1996; Langmore 1998) whereas studies on duets involving simpler vocalizations such as calls (Lamprecht et al. 1985; Wright & Dahlin 2007) or low-amplitude vocalizations (Todt et al. 1981; Morton & Derrickson 1996) remain rare. Discrete or private forms of signals have previously been described in communication networks (Dabelsteen 2005). Because of the difficulty of monitoring or even detecting them, such quiet signals have long been overlooked, but their contexts of occurrence and their physical structure have started to be studied (Dabelsteen et al. 1998).

Here we suggest that subtle, private forms of duet may exist as part of the display behaviours of monogamous birds. Using tie-microphones inside nestboxes, we monitored the vocal communication that occurs between mates at the nest in wild zebra finches, *Taeniopygia guttata*, and its variation through the different stages of a reproductive attempt. Zebra finches are gregarious songbirds that form life-long pair bonds (Zann 1996). Only male zebra finches sing, but both sexes utter a full repertoire of single-syllable calls used in pair communication (Zann 1996; Vignal et al. 2004, 2008). We recorded vocal interactions that occur at the nest and asked whether these sequences could be considered as duets. Sounds produced inside the nest by females and used in communication between mates have been described in some bird species (Ritchison 1983; Beletsky & Orians 1985; Yasukawa 1989; McDonald & Greenberg 1991; Halkin 1997), but to the best of our knowledge, the use of quiet vocalizations has been reported in very few studies (Gorissen & Eens 2004, 2005) and never been examined as possible vocal duets. Several essential characteristics can be used to define vocal duets (reviewed in Hall 2004). The bouts of vocalizations between mated birds that compose duets show a high temporal coordination (Farabaugh 1982). Second, male and female sound elements in a duet are not randomly ordered, but show a high level of alternation (Farabaugh 1982). Third, duet initiation, relative participation and the sound elements used in duets can be sex specific (Wickler & Seibt 1982). In the present study, we investigated whether these characteristics occur in the vocal interactions that take place at the nest between mates of wild zebra finches. Using preliminary playback experiments, we also explored whether these vocal interactions could be involved in mate recognition.

METHODS

Study Site and Species

The zebra finch is a small, sexually dichromatic passerine that inhabits open habitat in most of the arid and semiarid zone of Australia. They maintain life-long pair bonds and both parents contribute to nest building, incubation and the provisioning of the nestlings (Zann 1996). Extrapair paternity in the wild is rare relative to that in other socially monogamous passerines (2.4% of offspring, Griffith et al. 2010). Both parents are thought to stay together throughout the year, and throughout the day, except in periods when the nest has to be attended continuously (i.e. incubation and brooding) so that the duration of separation varies across the reproductive stages (see below; Zann 1996).

We studied a population of wild zebra finches in November 2008 at the University of New South Wales Arid Zone Research Station at Fowlers Gap, 112 km north of Broken Hill in far western New South Wales, Australia (31°05′S, 142°42′E). The study site at Gap Hills (30°57′S, 141°46′E) had 200 nestboxes erected on individual stakes next to a tree or a bush and located within a 1 km radius of a permanent water source. Birds entered the nestbox through a round hole 30 mm in diameter, with a perch, 90 mm long, 30 mm below the entrance hole (see Griffith et al. 2008 for further site and nestbox description).

This work was conducted under the authorities of the Animal Ethics Committees at the University of New South Wales and Macquarie University, a Scientific Research Permit from the New South Wales Parks and Wildlife Service and a banding Authority of the Australian Bird and Bat Banding Scheme.

Sound Recording and Behavioural Observations

The study focused on behaviours and vocalizations given by mates in the vicinity of the nest. We did not record the pairs outside this area. Each studied nestbox ($N = 15$) was monitored every 2–4 days throughout the breeding season (September to December). In November, we recorded pair vocal interactions at different reproductive stages defined as follows: stage 1: nest building and egg laying; stage 2: incubation; stage 3: young nestlings 0–5 days old (unable to thermoregulate); stage 4: old nestlings 6–12 days old (capable of thermoregulation). We obtained 6.9 ± 1.5 (mean $\pm$ SE) recordings per pair ($N = 15$), and a total of 103 vocal sequences. Some pairs ($N = 5$) were recorded at more than one stage. Before the recording period, adults were caught using a nestbox trap and banded with a numbered metal band (provided by the Australian Bird and Bat Banding Scheme) and a unique combination of two colour bands for identification. Even though half of the birds in the recorded nests remained unbanded, no pair or individual could have been recorded at two different nests because all recordings took place in a short time window (3 weeks) relative to the length of a breeding attempt, and there has been no evidence of social polygyny in this population (Griffith et al. 2008, 2010).

To monitor private communication between partners at the nest, we observed bird behaviour at the nest and recorded vocal sequences from breeding pairs using omnidirectional tie-microphones (AKG C417) placed inside nestboxes and connected to a Marantz PMD670 recorder (D&M Holdings Inc., Kanagawa, Japan). The observer sat quietly at 15–20 m from the nestbox partly hidden in the vegetation, and observed the nestbox using binoculars. Upon arrival at the nest, a bird usually sat in the tree or sometimes on the perch while its partner was inside the nestbox. When both parents arrived together at the nest, they generally took turns to enter the nestbox one at a time. Partners interacted vocally when they were together (in visual contact) but also when one partner was inside the nestbox and its partner was in the tree. During observations, we recorded the arrival and departure time of each partner and its position during vocal interactions (either in the tree or in the nestbox).