



## Impact of group size and social composition on group vocal activity and acoustic network in a social songbird



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In social species individuals living in the same group may synchronize activities such as movements, foraging or antipredator vigilance. Synchronization of activities can also be observed between partners especially during breeding and can be crucial for breeding success. Vocalizations are behaviours that can be coordinated between individuals, but simultaneous vocalizations in groups have mostly been considered as noise that does not bear any information. Indeed, little is known about the structure and function of vocal communications involving a network of individuals. How individual vocal activity forms part of the communal sound and how the group influences individual vocal activity are questions that remain to be studied. Zebra finches, *Taeniopygia guttata*, are social, monogamous songbirds that form lifelong pair bonds. In the wild, they are typically found in small groups, with the pair as the primary social unit, and they gather in 'social' trees where both females and males produce vocalizations. Here we investigated in the laboratory the influence of group size and composition on general vocal activity and synchrony, as well as the influence of pair bond and spatial location on the finer characteristics of dyads' vocal interactions. We used a set-up that locked the birds at fixed spatial positions of our choosing to control the proximity network and allowed us to match most of the vocalizations with specific individuals. We used an in-house software suite that automatically detects vocalizations from hours of passive recording. We found that zebra finch groups synchronized their general vocal activity with waves of collective vocalizations, which depended on both the size and the composition of the group. The acoustic network was shaped by pair bonds at different timescales. Birds preferentially vocalized close in time to (synchrony) or directly after (turn taking) their partner when it was present and the nearest neighbour when the partner was not available.

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In social species, many activities are synchronized between individuals living in the same group. Group members maintain group cohesion during movements and foraging (Agetsuma, 1995; Beauchamp, 1992; Blanc & Thériez, 1998; Blanc, Thériez, & Brelurut, 1999; Boyd & Bandi, 2002; Chivers, 1974; Conradt, 1998; Côte, Schaefer, & Messier, 1997; Daan & Slopssema, 1978; Gillingham & Klein, 1992; Linnane, Brereton, & Giller, 2001; McMahon & Evans, 1992; Rasmussen, 1985; Rook & Huckle, 1995; Ruckstuhl, 1998, 1999; Ruckstuhl & Neuhaus, 2001; Saino, Fasola, & Waiyaki, 1995; Schenkeveld & Ydenberg, 1985; Tayler, 1953; Tremblay & Chérel, 1999; Wilson, Wilson, & McQuaid, 1986).

Individuals may also coordinate activities such as antipredator vigilance and feeding (Gerkema & Verhulst, 1990; Kavanagh, 1978; Rook & Penning, 1991). Activities can also be synchronized between partners of a pair. Pairs in many long-term monogamous species show an increase in their breeding success over time, and this could be attributed to a better coordination of partners (Black & Hulme, 1996; Forslund & Pärt, 1995). Partners can also coordinate foraging activities, and can synchronize their nest visits to feed the chicks (Bebbington & Hatchwell, 2015; Lee, Kim, & Hatchwell, 2010; Mariette & Griffith, 2012, 2015; Van Rooij & Griffith, 2013). When both partners incubate, their hatching success can increase by synchronizing foraging trips (Coulson, 1966; Davis, 1988) or coordinating incubation bouts (Spoon, Millam, & Owings, 2006).

Vocalizations can also be coordinated between individuals. Territorial songbirds compete vocally by answering each other, sometimes matching their song types and overlapping songs as a

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signal of escalation (Langemann, Tavares, Peake, & McGregor, 2000). Some monogamous birds use coordinated vocal duets for territory defence, mate guarding, pair bond maintenance (Farabaugh, 1982; Hall, 2004) or parental care (Boucaud, Mariette, Villain, & Vignal, 2015; Elie et al., 2010). Some group vocal productions have also been identified as organized signals bearing messages, like the communal vocalizations of some social mammals that communicate on spacing (Bornean gibbons, *Hylobates muelleri*, Mitani, 1984; wolves, *Canis lupus*, Harrington & Mech, 1979; Frommolt, 1999) or group size (female lions, *Panthera leo*, McComb, Packer, & Pusey, 1994). Most of the time, however, group vocal productions have been considered as by-products of individuals' simultaneous but not necessarily coordinated vocalizations. For example, this noisy sound can result from the activity of up to thousands of individuals in choruses of birds (Burt & Vehrencamp, 2005), insects (Greenfield, 1994) and frogs (Bates, Cropp, Gonchar, & Knowles, 2010; Jones, Jones, & Ratman, 2009; Marshall, 2003; Simmons, Bates, & Knowles, 2009), as well as in fish communities (D'spain & Berger, 2004; Locascio, 2004; Locascio & Mann, 2005; Mann, 2003), colonies of nesting birds (Adret-Hausberger, 1982; Mathevon, 1997) or breeding marine mammals (Schusterman, 1978; Southall, Schusterman, & Kastak, 2003). This sound resulting from a group of individuals vocalizing simultaneously has mainly been viewed as a source of noise pollution constraining pairwise communications (Aubin & Jouventin, 1998; Gerhardt & Klump, 1988), but this group sound with no clear identifiable message might contain information on the structure of the underlying social network (McGregor & Horn, 2014).

Not much is known about the structures and functions of vocal communications involving a network of individuals. More specifically, little is known about the dynamics of pairs and group vocal exchanges at an individual level resolution. How individual vocal activity forms part of a communal sound and how the group influences individual vocal activity are questions that remain to be studied. Yet, we know that the group, as a communication network, is composed of several signallers and receivers sharing the same active signalling space, which implies that it can interfere with pairwise vocal exchanges. Eavesdropping is defined as extracting information from signalling interactions while not being the main recipient, and seems to occur in many species (McGregor & Dabelsteen, 1996). In birds, for example, it has been shown that eavesdroppers can respond to vocal exchanges even if they were not part of it initially (Mennill, Ratcliffe, & Boag, 2002). Audience effects show that the presence of other conspecifics can influence a sender's behaviour (Doutrelant, McGregor, & Oliveira, 2001; Evans & Marler, 1994; Hector, Seyfarth, & Raleigh, 1989; Matos & McGregor, 2002; Plath, Blum, Schlupp, & Tiedemann, 2008). The communication behaviour of male zebra finches, *Taeniopygia guttata*, can be modified by the individuals that are listening, and by the nature of the social relationships between them (Vignal, Mathevon, & Mottin, 2004).

The zebra finch is a social species native to Australia and is monogamous. This songbird forms lifelong pair bonds (Zann, 1996), and partners are inseparable even outside the breeding season. In the wild, zebra finches are usually found in small groups, and the pair is the primary social unit (McCowan, Mariette, & Griffith, 2015). This species extensively uses acoustic communication during social interactions: groups gather in 'social' trees near watering points or feeding areas (Zann, 1996) in which they produce a background sound composed of calls and songs. Some studies have started to focus on vocal dynamics in this species (Elie, Soula, Mathevon, & Vignal, 2011; Fernandez, Mariette, Vignal, & Soula, 2016; Gill, Goymann, Ter Maat, & Gahr, 2015; Perez, Fernandez, Griffith, Vignal, & Soula, 2015; Villain, Fernandez, Bouchut, Soula, & Vignal, 2016). Because of the amount of accumulated

knowledge on both behavioural and neurobiological aspects of its acoustic communication, the zebra finch is an interesting model to study communal vocalization and its relation to the social structure of the group.

Here we hypothesized that the organization of group vocal activity might reveal some aspects of group structure, such as size and composition. Using the zebra finch as a study species, we investigated the impact of group size and composition on proxies of the group vocal activity and synchrony. We also tested the influence of pair bonds and spatial location on the finer characteristics of dyads' vocal interactions. One common difficulty encountered when studying an acoustic network is to determine the identity of the caller and thus to match vocalizations with individuals. Also, in assessing the acoustic network it might be relevant to control the spatial proximity between individuals. To overcome both these issues we used a set-up that first locked the birds in a fixed spatial network of our choosing and allowed us to match vocalizations with individuals. We used an in-house software suite that automatically detects vocalizations from hours of passive recording. Our set-up also allowed automatic removal of nonvocalizations (wings or cage noise) using classification.

We built groups of identical sex ratio but that varied in group size and social structure (percentage of paired/unpaired birds). We recorded these groups' vocal activity during several hours on several days, and analysed the vocal sequences resulting from these recordings.

## METHODS

### *Subjects and Housing Conditions*

We used 88 adult zebra finches: 44 males and 44 females. All birds came from our breeding colony. Before the experiment, unpaired males and unpaired females were housed with individuals of the same sex, and female–male 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: 24–26 °C, 14:10 h light:dark, water, seeds and cuttlefish bones ad libitum and supplemented with salad once a week. As zebra finches are opportunistic breeders, all conditions were suitable for them to breed (water restriction is needed to keep them in nonbreeding condition, Prior, Heimovics, & Soma, 2013). However, they did not have access to nest material so they were not breeding at the time of the recording.

### *Recording Protocol*

The experiment took place from March to May 2014 and from January to February 2015. The day before the experiment, each bird was moved from the rearing room to the experimental room (sound-attenuating chamber, 1.76 × 2.28 m and 2.22 m high, Silence Box model B, Tip Top Wood, France) and was placed in a cage (40 × 40 cm and 25 cm high). Microphones (Audio Technica AT803), connected to a recorder (zoom R16), were placed on top of each cage, above the head of the bird and facing downwards, which is the best position to minimize the variability in vocalization amplitude due to the orientation of the bird's head, and thus maximize vocalization detection (Brumm & Zollinger, 2011). On each recording day, we recorded vocal exchanges for 3–6 h between 1000 and 1600 hours.

### *Group Composition*

We recorded 35 groups of different sizes (two, four or eight individuals) and different social compositions (0%, 50% or 100% of

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