



## Male and female Steere's liocichlas respond differently to solo and stereo duet playback

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Duets are a form of poorly understood signal created by two individuals temporally coordinating their vocalizations. It has been hypothesized that duetting functions in (1) joint resource defence, (2) avoiding usurpation from a partnership, (3) preventing a partner from being usurped, and (4) signalling commitment to a partner. To distinguish between these hypotheses, we need to determine the intended receiver of the duets and whether duetting is a collaborative act. Steere's liocichla (Timaliidae: *Liocichla steerii*) is an endemic passerine bird found in the forest edge habitat of mountains in Taiwan. Mated pairs engage in duetting typically initiated by males. We conducted a stereo duet playback experiment, controlled for position effects, to examine the function of duetting in Steere's liocichla. Playback stimuli included conspecific stranger female solo song, stranger male solo song, stranger duet song and neighbour duet song. During the playbacks, males initiated nearly all vocalizations. The propensity for males to sing was not significantly different between the stranger treatments but was lower in neighbour duet playback. However, females responded more to their partner's song, thus creating the duet, after stranger female solo and stranger duet playbacks. Pair members tended to approach the playback source together rather than move separately towards different speakers. When pair members did approach different speakers, however, the birds approached the speaker singing their sex-specific song. Our findings indicate that in addition to joint resource defence, duets in Steere's liocichla also serve a mate-guarding function to avoid being usurped.

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Duetting, in which vocalizations of two individuals occur in a temporally linked fashion, is found in many species including birds, insects, frogs and primates (Farabaugh 1982; Tobias et al. 1998; Geissmann 2002; Bailey 2003). While research on avian duets has been especially productive recently, this form of acoustic communication remains poorly understood. Our knowledge of birdsong nowadays comes mainly from male birds, but females also sing, particularly in tropical and subtropical species, and can duet with males (Farabaugh 1982). Furthermore, a recent phylogenetic study suggests that the reason for male-biased singing in many temperate species is not the increase in male song but the repeated loss of female song in association with movements from tropical to temperate areas (Price et al. 2009), so we cannot fully understand the evolution of birdsong until we know more about duetting and the females' role in singing.

Various hypotheses have been proposed to explain the functional significance of duetting and evidence so far suggests that

duetting serves multiple functions (reviewed in Hall 2004; Brumm & Slater 2007; Topp & Mennill 2008). The joint resource defence hypothesis states that duetting functions as a collaborative display to advertise territory and resource ownership to outsiders (Seibt & Wickler 1977). In the mate-guarding hypothesis, an individual joins its partner's song to advertise their mated status and therefore avoid being usurped (Stokes & Williams 1968) or prevent its partner from being usurped (Appleby et al. 1999). Duetting may also signal commitment to a partner if it requires considerable effort to achieve coordination (Wickler 1980). The aforementioned hypotheses can be classified into four major categories according to the intended receivers of the signals: (1) outsiders irrespective of sex, (2) outsiders of the same sex, (3) outsiders of the opposite sex and (4) partners (Hall 2004). Determining the social context in which duetting occurs, particularly in relation to sex, as well as the associated behaviour that accompanies duets is critical to distinguish between these hypotheses. Countersinging interactions between territorial holders are contexts in which duetting occurs. Studies on male song used in this context found a common phenomenon that territorial holders reduce aggression towards neighbours compared to strangers (Stoddard 1996). Strangers are

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more likely to engage in attempts to usurp territory holders than neighbours from established territories. Males can defend their territory more efficiently by recognizing neighbours' song and direct their energy towards strangers. Some duetting birds have also been reported to recognize neighbours by their duets (Wiley & Wiley 1977; Hall 2000; Grafe & Bitz 2004). However, to show that duetting has a territorial function, further evidence about the increased effort put into duetting when facing strangers is needed. Such behavioural change includes increased duetting rate, increased precision or type matching. It has been hypothesized that the need to interact with neighbours, including facilitating inter- or intrapair recognition, is responsible for pair-specific 'duet types' observed in some species (Rogers et al. 2006; Logue 2007). The joint resource defence hypothesis is supported by considerable observational and experimental evidence (Logue 2005) and it is likely that the 'dear enemy effect' is a widespread phenomenon among duetting species (Temeles 1994; Hall 2000). Studying the duetting behaviour in response to neighbours versus strangers will broaden our knowledge of the recognition ability of females and the significance of duet features that discriminate duets from solo songs.

Recently, stereo duet playback has been shown to be an effective approach to test competing duetting hypotheses. By broadcasting male and female vocalizations separately through two speakers, stereo duet playback makes it possible to distinguish between sex-specific and coordinated targets of focal pairs (Logue & Gammon 2004; Rogers et al. 2004; Mennill 2006). Experimental designs incorporating neighbour and stranger song and those from males versus females can be incorporated into a stereo playback protocol allowing the investigator to tease apart the social dynamics of duetting behaviour.

Steere's liocichla (Timaliidae: *Liocichla steerii*) is an endemic passerine species found predominantly in the forest edge habitat of mountains on the island of Taiwan. The breeding season is typically March–September, and double or multiple clutching is common. Socially monogamous pairs defend a territory in which they build cup nests mostly in shrubs or herbaceous layers and share parental care (H. L. Mays & C.-T. Yao, personal communication). The average territory size is  $1455 \pm 863 \text{ m}^2$  (Hsieh 2005). Pairs engage in duets characterized by a tonal 'chi-chu' of males followed by females with a series of buzzy 'ji-ji-ji' elements. Female Steere's liocichlas rarely sing spontaneously, and almost all duets (96%) are created by females joining their partners' song (Weng 2007). Previous playback experiments showed that territorial females were more likely to join their partners' song in response to simulated intrusion (Hsieh 2005). However, because these playbacks were conducted with a single speaker, it is not clear whether the approaching pairs were defending collaboratively or sex-specifically in response to duet playback. Although duetting is a joint display given by two birds, individual interests may differ and need to be examined.

In this study, we aimed to address three questions regarding the intended receivers of duets in Steere's liocichla by conducting stereo playbacks. Playback treatments included a repertoire of songs heard under natural conditions including stranger female solos, stranger male solos, stranger duets and neighbour duets. First, we needed to know whether the duets in Steere's liocichla are targeted at conspecific outsiders. If duets function in communicating with conspecific outsiders, duet rate will increase in the context of simulated intrusion. Otherwise, if duets function solely in communicating with a partner, playback will have little effect on duetting behaviour. Second, we investigated whether duetting female Steere's liocichlas show sex-specific aggression in territory defence. If the targeted receivers are outsiders regardless of sex, females will respond equally to speakers broadcasting male or female vocalizations. If duets are targeted at outsiders of a specific sex to prevent

them or their partners from being usurped, females will show bias towards the speaker broadcasting vocalizations of a specific sex. Finally, we investigated whether Steere's liocichlas discriminate between neighbour and stranger by their duets. If they are able to do so, they should respond more strongly to stranger duet playbacks.

## METHODS

We conducted a two-round, stereo playback experiment using 12 mated pairs from 21 April to 4 July in 2006 at Meifeng Highland Experimental Farm (elevation approximately 2100 m) of National Taiwan University in Nantou County, Taiwan. The approximately 30 ha core study area consisted of a mosaic of agricultural and natural forest in various stages of succession (Lin 2006). As two pairs showed no apparent responses to playback in two of three treatments and we were not sure whether the subjects were present, we used only data from 10 pairs.

Both members of six pairs and one member of three pairs were captured with mist nets and banded; the other three individuals were identified by their vocalizations. Each captured individual was banded with a unique combination of three coloured plastic rings and a numbered metal ring. We collected 50  $\mu\text{l}$  of blood per bird via the brachial vein. Blood was transferred to 500  $\mu\text{l}$  of Lysis buffer (0.01 M Tris, 0.01 M NaCl, 0.01 M EDTA, 1% n-lauroylsarcosine, pH 7.5; Seutin et al. 1991). Sex was determined by polymerase chain reaction (PCR) amplification of an intron in the sex-linked chromobox-helicase-DNA-binding gene (CHD; Griffiths et al. 1998). In another descriptive study, we built our spectrogram database for each individual with recordings done while colour bands were also noted (Weng 2007). We found that each individual has its distinctive version of the song, so we could distinguish individuals by the frequency and temporal characteristics of the song. The songs of the unbanded individuals in this playback study were recorded before playback trials to be used as identification marks.

### Playback Stimuli

We gave four playback treatments to each pair of birds: stranger male solos, stranger female solos, stranger duets and neighbour duets. Stimuli used in the playback were selected from recordings obtained under natural conditions and processed using Avisoft-SASLab Pro 4.23b (Avisoft Bioacoustics, Berlin, Germany). The recordings were made within 20 m of the singers and those with high signal-to-noise ratio were chosen for stimuli. For a duet playback, the chosen duet was split into male and female song components so that each could be played back on a separate channel while retaining the original temporal features. Male and female songs were assigned at random to each channel during playback. The stereo duet was replicated 24 times and interspersed randomly between blanks to form a 4 min file. The duet rate used in playback is higher than averaged natural duetting rates, but still within the range of duetting rates in Steere's liocichla (Mays et al. 2006a; Weng 2007; mean  $\pm$  SD =  $0.11 \pm 0.19$ , range 0–1). For a solo playback, all procedures were the same except that the second channel contained a blank element instead of a song element of the other sex. The WAV song files were adjusted to the maximum volume and then burned on to an audio CD for playback using iTunes software (Apple, Cupertino, CA, U.S.A.). Playback amplitude was 60 dB measured at 10 m from the speaker. Songs used in the playback treatments of stranger female solos, stranger male solos and stranger duets were recorded from strangers whose territories were at least five territories away from the focal pair in Meifeng. In the playback treatment of neighbour duets, songs from one of the immediate neighbours were used. A song from the same individual was used only once as stranger and/or as neighbour to avoid pseudoreplication.

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