



## Strong ungraded responses to playback of solos, duets and choruses in a cooperatively breeding Neotropical songbird

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Coordinated vocal displays of cooperatively breeding animals provide a compelling model for investigating the opposing motivations for engaging in conflict versus cooperative behaviours. Hypotheses for the function of coordinated vocal displays differ with respect to these motivations and have been traditionally investigated by using playback to simulate varying degrees of threat to individuals and groups. We evaluated the function of coordinated vocal displays by presenting territorial groups of cooperatively breeding rufous-naped wrens, *Campylorhynchus rufinucha*, with three playback stimuli: solos, duets and choruses. We found that all groups responded strongly to playback by approaching the loudspeaker together, vocalizing, and performing visual displays. A composite playback response measure showed significantly more aggressive reactions to all playback treatments compared to a pre-playback control period, yet did not vary across solo, duet and chorus treatments. This suggests that the playback stimuli represented equally strong threats despite the varying numbers of contributors to each stimulus, and does not support the hypothesis that coordinated vocalizations are graded signals of threat in this species. Our findings stand in contrast to previous playback studies that have reported an increase in aggression with an increasing number of simulated intruders, or an increase in coordinated vocalizations in response to solo playback. We interpret the results of our study as evidence that coordinated vocalizations function in the cooperative behaviour of joint territory defence in the rufous-naped wren. © 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Cooperation and conflict are opposing motivations that govern social interactions in animals. Much research has investigated the degree of individual motivation for engaging in cooperative versus conflict-based behaviours as an evolutionary consequence of the resulting fitness benefits. The cooperative behaviour of aiding a breeding partner in rearing offspring has direct fitness benefits (Maynard Smith 1977), while cooperating to assist related individuals to rear their offspring has indirect benefits in the form of kin selection (Hamilton 1964). In contrast, conflict can arise when partners have opposing motivations for parental investment, or when related individuals queue for breeding opportunities in social groups, and this can lead to aggressive signalling contests or outright physical fights (Wiley & Rabenold 1984).

Cooperatively breeding animals often produce coordinated territorial displays, and this has been suggested as a way in which nonbreeding helpers cooperate with breeders (e.g. Cockburn 1998),

but has also been argued to reflect the conflicting interests of the members of the group (e.g. Reyer & Schmidl 1988). Decisions to cooperate or act in conflict may be influenced by assessing acoustic signals produced by members of an animal's own social group, or by assessing acoustic signals produced by competing groups during territorial encounters. Assessment of group size may be especially important in social animals because group size may outweigh interindividual differences in determining resource holding potential between contestants (Parker 1974; McComb 1992; McComb et al. 1994; Seddon & Tobias 2003; Radford 2003). Consequently, the advertisement of group size and the assessment of rival group size through coordinated vocal displays may mediate social interactions in group-living animals. The degree to which animals participate in coordinated vocalizations presents an excellent opportunity to investigate cooperative and conflict-based behaviours.

Few studies have tested the function of group vocalizations in animals using playback to simulate varying degrees of threat. McComb et al. (1994) compared the response to playback of single female lions, *Panthera leo*, to playback of both solo and group vocalizations. Females were less likely to approach groups than to approach single individuals. Similarly, Radford (2003) broadcast playbacks representing varying numbers of intruders to territorial

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groups of green woodhoopoes, *Phoeniculus purpureus*. Individuals and groups responded more aggressively to playback of larger groups than to playback of smaller groups by increasing the length of their vocal response. Seddon & Tobias (2003) performed playbacks of varying group sizes to territorial groups of subdesert mesites, *Monias benschi*. The number of simulated intruders significantly influenced group responses, where resident birds approached more cautiously and produced a more prolonged and communal response to playback simulating increasing numbers of intruders. Taken together, these studies have shown that animal behaviour can be influenced by the composition of the defending focal group and the rival group, and that this influence reflects the possibility of recruiting additional group members (McComb et al. 1994), or attaining reproductive opportunities (Radford 2003; Seddon & Tobias 2003).

Bird species provide good study systems for investigating coordinated vocal signalling because they are conspicuous, show a variety of social mating systems, and vary dramatically in their modes of signal production and in the functional significance of their signals. The form and adaptive significance of bird song has generated much scientific interest, leading to numerous hypotheses for its function. The primary functions of bird song in many taxa are mate attraction and territory defence (Catchpole & Slater 2008). While this is true for species in which only males sing, more complex forms of acoustic signalling, such as the coordinated vocalizations produced by both males and females in many tropical birds, have been hypothesized to function in a variety of additional ways that reflect the motivation of each individual. The coordinated production of vocalizations by two birds, known as a duet, has been studied in increasing detail in recent years (reviewed in Hall 2004). This increase in research has led to many hypotheses that explain the adaptive significance of the behaviour from the perspective of both individuals. In particular, these hypotheses investigate the degree to which duetting is a cooperative behaviour benefiting both birds, or alternatively representing conflict between the birds, benefiting only one of the duet partners. As a cooperative behaviour, duetting functions in joint territory defence (e.g. rufous-and-white wrens, *Thryothorus rufalbus*: Mennill 2006; magpie larks, *Grallina cyanoleuca*: Rogers et al. 2004), in achieving reproductive synchrony (white-browed robin-chat, *Cossypha heuglini*: Todt & Hultsch 1982) and in maintaining acoustic contact (rufous-and-white wrens: Mennill & Vehrencamp 2008). Alternatively, duetting has been suggested to play a conflicting role between members of a pair, in mate guarding (e.g. bay wren, *Thryothorus nigricapillus*: Levin 1996) and paternity guarding (e.g. slate-coloured boubou, *Laniarius funebris*: Sonnenschein & Reyer 1983).

Birds that breed cooperatively also produce group vocalizations where more than two birds combine their vocalizations into a coordinated vocal display known as a chorus. Chorusing is especially interesting from an evolutionary perspective, because the motivation of extrapair group members requires consideration. Hypotheses explaining the adaptive significance of chorusing are similar to those of duetting, and can be classified based on whether they propose conflict or cooperation among the group. There is strong evidence that chorusing functions as a cooperative behaviour in collaborative territory defence (e.g. laughing kookaburras, *Dacelo novaeguineae*: Reyer & Schmidl 1988; Baker 2004; Australian magpies, *Gymnorhina tibicen*: Brown & Farabaugh 1991; white-browed sparrow-weavers, *Plocepasser mahali*: Wingfield & Lewis 1993; subdesert mesites: Seddon 2002; black-breasted wood-quail, *Odontophorus leucolaemus*: Hale 2006) and in maintaining social bonds within the group (Australian magpies: Brown et al. 1988). Chorusing has also been suggested to function as a form of conflict between group members by mediating social hierarchies (e.g. laughing kookaburras: Reyer & Schmidl 1988).

We investigated the function of duetting and chorusing behaviour in a cooperatively breeding bird, the rufous-naped wren, *Campylorhynchus rufinucha*. This species is a widespread and common songbird inhabiting the dry forests of western Central America from southwest Mexico to northwest Costa Rica. Birds live in groups of two or more individuals and produce duets and choruses composed of simultaneous contributions of repeated syllable phrases (Bradley & Mennill, in press). We used audio playback of solos, duets and choruses to simulate varying levels of threat to resident territorial birds. If duets and choruses provide groups with information with which to assess the ability of rival groups to defend resources, we predicted that territorial birds would show increased aggression in response to increasing numbers of simulated intruders, because threat to the defended territory should increase with the size of the rival group. Alternatively, if duets and choruses are important for pair or group cohesion (Thorpe 1972), we predicted that territorial birds would show higher aggression towards solo playback than towards duet or chorus playback, because lone individuals probably represent rival individuals prospecting for new breeding opportunities. By assessing responses of territorial groups to varying degrees of threat to individuals and groups in this way, we investigated the functional significance of coordinated vocal behaviour in a complex social context.

## METHODS

### *Study Population and Study Site*

We presented a series of playback trials to 18 territorial groups of free-living rufous-naped wrens in sector Santa Rosa, Area Conservación Guanacaste, Costa Rica (10°40'N, 85°30'W). Sixteen territories were occupied by a breeding pair, while the remaining two territories were occupied by a breeding pair and one additional adult. The study site was predominantly regenerating deciduous dry forest with isolated remnant patches of mature evergreen forest. All 18 territorial groups were located along minor access roads, within second-growth forest with a canopy height of 15–20 m and an understory dominated by bull horn acacia (*Acacia collinsii*), the preferred nesting tree of the rufous-naped wren (Joyce 1993). We conducted the experiments from 28 July to 13 August 2007 after all pairs had commenced breeding activities, approximately 75 days after the start of the rainy season. During the experiment, we observed recently fledged, nonsinging, dependent juveniles in nine of the 18 territories; the remaining nine groups were assumed to have had a failed first breeding attempt. We did not conduct playback experiments on groups that were known to be incubating eggs because a pilot study showed that incubating females seldom respond to playback, whereas females in prenesting and fledgling periods regularly respond to playback. We conducted all playback trials during periods with low wind and without rain, when background noise was low.

### *Playback Stimuli*

To simulate territorial intrusion by one, two or three rival conspecifics, we presented each territorial group with three different playback treatments: solos, duets and choruses. We created playback stimuli using songs recorded from birds within the study population that were strangers to the playback subjects. To generate stimuli, we first isolated songs from field recordings collected in natural contexts, each with a high signal-to-noise ratio. We then selectively filtered background noise from the recordings by using the lasso selection tool followed by a frequency bandpass filter between 250 Hz and 21 000 Hz using

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