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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.

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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

Audition (Adobe, San Jose, CA, U.S.A.). All recordings were then normalized to -1 dB using Audition. We created solo song playback stimuli (Fig. 1a) by looping a single song phrase six times in immediate succession, which is similar in structure to that of naturally occurring songs (Bradley & Mennill, *in press*). We created duet playback stimuli (Fig. 1b) by combining the same solo song phrase type recorded from each member of a mated pair, such that the second bird's contribution started after the first bird's initial phrase, with an additional 0.15 s offset. This offset realistically simulates the asynchrony of contributions to naturally occurring duets. We created chorus playback stimuli (Fig. 1c) using the above duet in addition to the same solo phrase type recorded from a bird neighbouring the pair that contributed the duet, incorporating an additional offset of 0.15 s. For all three types of stimulus, the six-phrase playback stimulus was repeated four times at a rate of once every 30 s, so that all playback stimuli were the same length. The three playback stimuli produced in this way represented a 'stimulus set'. In total, we created four different stimulus sets from recordings obtained from four different groups. This reduced the amount of pseudoreplication in our experimental design by decreasing repeated sampling of responses to the same stimulus set (Kroodsma 1989). One of the four treatment sets was presented to each test group according to a factorial design where two of the stimulus sets were presented to five groups and two sets were presented to four groups. None of the 18 test groups received playback produced from birds closer than three territories distant (approximately 0.5 km).

Playback Trials

We broadcast single-channel playback stimuli (16-bit WAV files) from an iPod (Apple, Cupertino, CA, U.S.A.) connected to a Minivox PB-25 loudspeaker (Anchor Audio, Torrance, CA, U.S.A.). The speaker was mounted on a pole 1.5 m above the ground, facing upwards, and positioned near the edge of the subject group's territory (approximately 20 m from territory boundary, roughly one-half the distance from the territory edge to the territory centre). In this study population, territories were very densely packed within the Neotropical dry forest habitat, with little or no undefended space between territories. In pilot trials, where we presented playback at territory boundaries, neighbouring groups routinely responded to playback, and the subject group typically began interacting with neighbours. Presenting playback within the territory eliminated this confounding interaction. We held the volume of the speaker constant across all playback trials at a natural sound pressure level (80 dB at 1 m horizontal distance from the forward-oriented speaker using a Realistic

sound level meter model 33-4050). Prior to broadcasting any playback stimuli, we monitored the focal group for 30 min to obtain baseline data to compare against behaviours observed following playback. The order of presentation of the three playback stimuli was chosen using a block factorial design, whereby each of the six possible orders of presentation was given to three different groups. Each stimulus presentation was followed by a 20 min silent period to allow the group to respond and then return to normal behaviour. In a separate study of the same population (Bradley & Mennill, *in press*), we found that the natural song rates ($\bar{x} \pm \text{SE}$) peaked after dawn between 0500 and 0600 hours (solos = 12.2 ± 1.7 songs/h; duets = 15.9 ± 2.1 songs/h; choruses = 3.7 ± 1.32), yet were produced at consistently lower levels between 0600 and 1100 hours (solos = 6.0 ± 0.9 songs/h; duets = 8.9 ± 0.3 songs/h; choruses = 4.0 ± 1.8). Based on this pattern, we conducted all playback trials between 0600 and 1030 hours.

During each playback trial we made observations and recordings of the resident group from a partially concealed location 20 m from the speaker. All vocal responses were recorded with a directional microphone (Sennheiser ME66) and a solid-state digital recorder (Marantz PMD-660). To quantify the response to each treatment we measured the following response variables: (1) latency to first vocalization; (2) the percentage of songs produced by more than one bird (i.e. duets and/or choruses); (3) closeness of approach to loudspeaker; and (4) the proportion of the trial that any member of the subject group was within 10 m of the speaker. Because the majority of our playback groups were mated pairs, and only two subject groups included adult extrapair birds (see Bradley & Mennill, *in press*), we did not assess chorus rate as a separate response variable, although we describe the chorusing behaviour of the two groups-of-three anecdotally. We measured latency to first vocalization from the start of the first playback stimulus; for the preplayback control period, we measured latency from the arbitrary time of the start of our recording (20 min before the first playback stimulus), which provided us with a background comparison rate for each response measure. We considered the following signal variants to be consistent with aggressive responses: short latencies of response, high solo song rates, high duet rates, small distances of closest approach and high proportions of the trial spent within 10 m of the speaker. We did not attempt to track responses of individuals, because of the thick vegetation at our study site, the rapid and often secretive movements of the playback subjects, and the fact that birds tended to stay in very close proximity to their groupmates; instead, we evaluated the responses of the entire territorial group as a unit. We collated all vocal responses to playback trials by visualizing the sounds as spectrograms and annotating them using SYRINX-PC (J. Burt, Seattle, WA, U.S.A.).

Statistical Analysis

To compare the behaviour of territorial rufous-naped wrens during the preplayback control period and following the three playback treatments, we performed a principal components analysis to reduce the variables to a single composite response measure. Principal components analysis was conducted on all five response variables using Varimax rotation, and generated one principal component (PC1) with an eigenvalue greater than 1.0. PC1 explained 53.6% of the variance in the five response variables and showed strong positive loading from solo song rate, duet song rate and the proportion of the trial that any member of the subject group was within 10 m of the speaker, and negative loading from latency to response and closeness of approach to the speaker. As such, we refer to PC1 as 'intensity of response' where high PC1 scores are consistent with strong aggressive responses. We tested

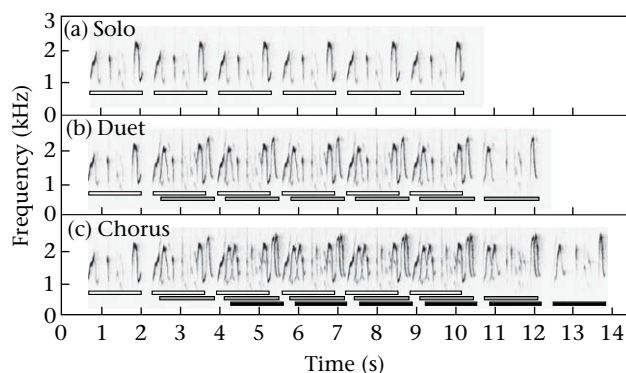


Figure 1. Sound spectrograms of one example set of playback stimuli used to simulate (a) solos, (b) duets and (c) choruses of rufous-naped wrens. Four different stimulus sets were used according to a factorial design. Bars underscore the vocal contributions of different individuals.

for differences in the responses of rufous-naped wrens to different playback treatments using ANOVA, modelling the effects of a within-subject factor (the type of playback treatment), and two between-subject factors (the order of presentation of playback stimuli, and the presence or absence of dependent, nonsinging fledglings), on the response variable (the PC1 'intensity of response' measure). Principal components analysis was performed using JMP 6.0 (SAS Institute, Cary, NC, U.S.A.) and ANOVA was performed using SPSS 16.0 (SPSS Inc., Chicago, IL, U.S.A.). We present all values as means \pm SE.

To determine whether our analysis was adequate to detect an effect of playback treatment, if in fact one existed, we performed retrospective power analysis in GPower 13.0 (Franz Faul, Universität Kiel, Germany). Following the advice of Thomas & Juanes (1996), we calculated power based on the effect size of an independent investigation by Seddon & Tobias (2003), which involved playback of solos, duets and choruses to territorial birds. We calculated the effect sizes of Seddon & Tobias (2003) to vary between 0.86 and 0.24, and used the mean effect size, 0.48, to calculate statistical power in our study.

Ethical Note

Presentation of song playback in this study elicited aggression in the study subjects. However, these levels of aggression were commonplace during naturally occurring territorial contests, and care was taken to minimize stress to the birds by avoiding playback beyond normal levels. After playback trials, birds readily returned to foraging and social behaviour with group members. This study was performed in compliance with regulations of the Animal Care Committee of the University of Windsor and the Government of Costa Rica.

RESULTS

In all 18 trials, playback elicited strong aggressive responses from territorial rufous-naped wren groups. In response to playback, birds vocalized, approached the speaker and produced visual displays that are normally associated with aggressive interactions in this species, including fanning tail feathers and erecting chest feathers. Overall, birds showed a significant response to playback; the principal component summarizing aggressive behaviour (PC1) showed a significant effect of treatment ($F_{3,24} = 6.33$, $P = 0.001$; Fig. 2), but no effect of playback order ($F_{5,8} = 1.13$, $P = 0.4$), or the presence of fledglings in the responding group ($F_{1,8} = 0.97$, $P = 0.35$). A post hoc Tukey test showed a significant difference between the aggressive behaviour PC1 score for birds during the silent preplayback period (-0.73 ± 0.29) compared to their responses to playback of solos (0.19 ± 0.22), duets (0.26 ± 0.20) and choruses (0.28 ± 0.13), but no significant difference between responses to the three playback treatments. Retrospective power analysis revealed that our experimental design had a high power (0.88) to detect an effect of playback treatment, if one existed.

To examine variation in each of the individual response measures included in the multivariate response, we compared our four univariate measures across the three treatments. Rufous-naped wrens showed very similar levels of response to all three playback treatments for the percentage of songs that they sang as duets or choruses, for the latency of their responses to the three treatments, for their proximity to the loudspeaker, and for the proportion of the trial that they spent near the loudspeaker (Fig. 3).

Two of the 18 groups consisted of a breeding pair plus an extrapair individual. These groups-of-three rarely gave three-part

choruses during the preplayback silent period (1.0 ± 1.0 songs/h) but often produced three-part choruses in response to playback of solos (60.0 ± 30.0 songs/h), duets (90.0 ± 30.0 songs/h) and choruses (54.0 ± 6.0 songs/h); the small number of groups with three individuals precluded statistical comparison across treatments.

DISCUSSION

We found that rufous-naped wren groups reacted aggressively to playback simulating territorial intrusion of rival birds singing solos, duets and choruses. Resident birds showed elevated aggressive responses to the playback treatments, including a combination of vocal and physical behaviours. Compared to the natural, passive context represented by the preplayback period, groups produced solos and duets at a higher rate following playback. Interestingly, we found that playback subjects responded with equal intensity across each of the playback treatments, suggesting that all three treatments were perceived as similar levels of threat.

A strong reaction to playback simulating the vocalizations of a conspecific rival is not unexpected. Many previous playback studies have shown that males use song to defend territories and that animals react strongly to territorial intrusions represented by playback (McGregor 1992). Some studies have also shown that birds increase their rate of duetting in response to playback (e.g. Levin 1996; Hall 2000; Mennill 2006), indicating that duets may function in joint territorial defence (Seibt & Wickler 1977). Alternatively, duets may function as a form of acoustic mate guarding to deter intruding birds from usurping a partner (Stokes & Williams 1968), or as a paternity guard to deter males from seeking to copulate with the female (Sonnenschein & Reyer 1983). We found that rufous-naped wrens produced more solos and duets in response to all three playback treatments compared to the preplayback control period, suggesting that both solos and duets are used in territorial defence. However, we cannot be sure whether the responding birds produced duets to advertise that they were a united defensive unit, or whether they produced duets as a mate- or paternity-guarding signal to advertise their partner's paired status.

We found that rufous-naped wrens did not produce graded responses to different simulated threats levels. To evaluate this result, we considered the relative threat that each of the playback stimuli might represent to the territorial groups. Solo playback is likely to be more of a threat to the pair bond than to the territory, and probably simulates a single individual that is prospecting to form a new partnership, to fill a vacant position on a territory, or to seek extrapair mating opportunities. In contrast, duet and chorus playbacks are likely to pose more of a threat to the territorial tenure of the resident group than they are to a pair bond, and probably simulate a rival pair or trio attempting to defend or obtain a new territory. The results of our playback experiment do not suggest that communal vocalizations function in pair or group cohesion; under this hypothesis we would predict that duet rate should be higher in response to solo playback compared to duet or chorus playback. Additionally, given that we found no clear difference in the level of aggression in response to the different playback treatments, we infer that communal vocalizations are not used to assess the ability of rival groups to defend resources. Choruses are somewhat rare in this species, and the rarity of choruses, compared to solos and duets, may also explain why groups do not use choruses as a means to assess rival group size.

The findings of this study stand in contrast to some other playback studies involving duetting and chorusing birds. Hall

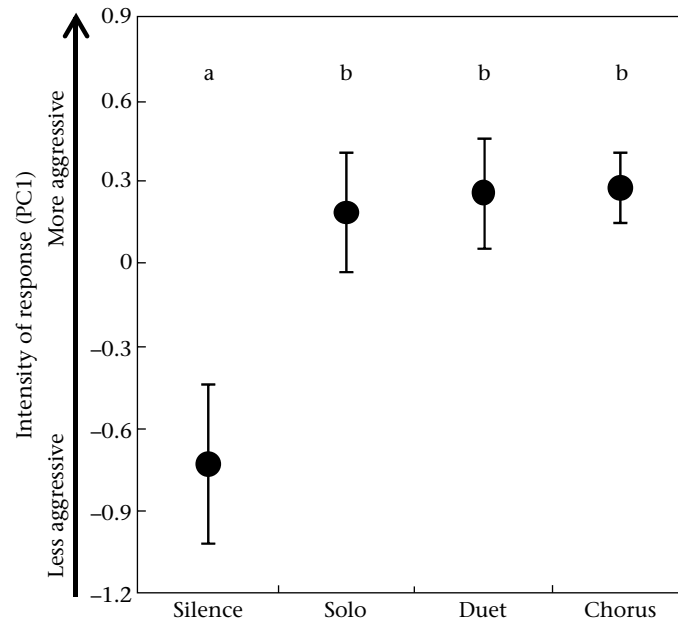


Figure 2. Responses of rufous-naped wrens to playback of solos, duets and choruses ($N = 18$). Intensity of response is a composite variable summarized through principal components analysis where positive values are consistent with aggressive responses (short latencies of response, high percentage of songs coordinated, small distances of closest approach to speaker and high proportions of the trial spent within 10 m of the speaker). Letters above error bars denote significance, whereby treatments that share letters were not significantly different.

(2000) gave solo and duet playback to magpie larks, and found that birds sang proportionately more duets in response to playback of duets compared to solos. We found no significant difference in the percentage of songs that were produced as duets or

choruses across different treatments, indicating that the production of coordinated song in this species is not influenced by the number of intruders into a territory. However, Seddon & Tobias (2003) found that the number of intruders presented to subdesert

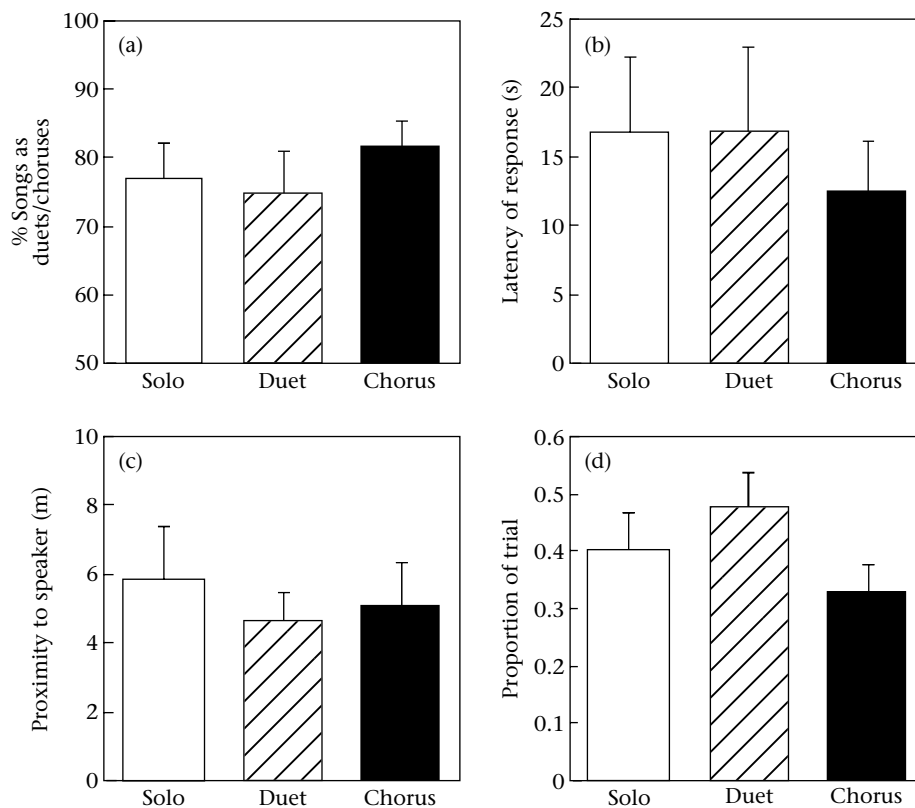


Figure 3. Individual response measures of rufous-naped wrens to conspecific solo, duet and chorus song playback ($N = 18$). Response measures assessed were (a) the percentage of all vocal responses produced as a duet/chorus, (b) the latency of vocal response to playback, (c) the closest approach to the speaker and (d) the proportion of the playback trial that at least one bird spent within 10 m of the speaker.

mesites strongly influenced the strength of response to playback. As the number of vocal contributors in the playback increased, vocal responses became more protracted, groups became less likely to approach, and the number of vocal contributors increased (Seddon & Tobias 2003). These authors concluded that groups respond more collectively and with greater caution to threats from two or more intruders compared to single intruders. Radford (2003) investigated the effect of the number of simulated intruders on group responses in the green woodhoopoe. He found that focal groups spent more time vocalizing in response to playback representing a group larger than they did to a smaller playback group. These studies show that coordinated vocalizations increase in aggression as more members of the focal group participate.

Our predictions of a graded response to the varying threat levels represented by our three playback treatments were not met. To our knowledge, only two studies to date have reported similar results. Fedy & Stutchbury (2005) found that white-bellied antbirds, *Myrmeciza longipennis*, respond equally to male solo, female solo and duet playback. From these findings, Fedy & Stutchbury (2005) concluded that duetting does not serve a mate-guarding function in white-bellied antbirds, and when viewed together with other data indicating that duetting rates do not vary seasonally, these authors also excluded a territory function for duetting. Mennill & Vehrencamp (2008) similarly found a lack of a graded response to playback of male solos, female solos and duets by rufous-and-white wrens of both sexes. In combination with physical response data from subject pairs, the authors concluded that duetting is a multifunctional signal, functioning in acoustic contact, cooperative territorial defence and intrasexual aggression (Mennill & Vehrencamp 2008).

Both resource demand and territorial aggression are often higher during breeding periods compared to nonbreeding periods, because individuals must defend access to resources in order to feed developing nestlings and fledged juveniles. The contrast between the lack of graded response levels in the present study and the findings reported in others studies may be attributed to a variation in resource demand. For example, Hall (2000) conducted playback experiments on magpie larks in the nonbreeding and prebreeding seasons, and Radford (2003) studied green woodhoopoes after all breeding was complete. Both of these studies found an increase in response measures with an increasing number of simulated territorial intruders. In contrast, we presented playback while groups either had very recently fledged young or had failed an initial breeding attempt and were probably preparing to reneat. As a result of the potentially elevated resource demand during this period, aggression levels may have been sufficiently high to produce a strong response to all playback treatments, regardless of the number of simulated intruders the treatment represented. Future studies of this species could perform a similar experimental procedure in the prebreeding period (between September and March in our study population) and would provide an interesting point of comparison.

In this study we presented playback to subject groups from 20 m inside the territory to minimize interactions with neighbours. In a study of the cooperatively breeding, congeneric stripe-backed wren, *Campylorhynchus nuchalis* (Price 1999), playback of all non-group vocalizations were viewed as equally threatening by subject groups when presented at the territory centre. In the present study, the location of the stimulus presentation could therefore potentially explain the observed ungraded responses across treatment types. Future experiments involving playback presented at territory boundaries may provide further insight into the functions of coordinated singing.

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