Function of duet coordination in a territorial socially monogamous bird

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Acknowledgements

We thank Vicky and Gary Dowling for logistical support at Fowlers Gap Arid Zone Research Station as well as Robin Thibault and Melissa Ardila Villamizar for help during data collection.

Abstract

Duetting, a cooperative vocal behaviour performed by mated pairs, is a distinctive vocal behaviour among many species in specifically primates and birds. The exact features of duets that may make them a stronger territorial signal is still inconclusive. One hypothesis is that the precision of duet coordination can indicate the quality or dedication of a pair, and thus the degree of threat posed to a rival pair. To address the implications of duetting precision in a territorial context, we determined to what extend the duetting behaviour in the chirruping wedgebill (*Psophodes cristatus*), a territorial, socially monogamous passerine, is affected by the precision of duet coordination. We tested this with playback experiments where we broadcast coordinated and uncoordinated duets at mated pairs, predicting that pairs would exhibit stronger responses to coordinated duets than to uncoordinated ones and sing more coordinated after the simulated intrusion. We found that neither response intensity nor coordination of either sex differed between coordinated and uncoordinated duets. Since chirruping wedgebills did respond consistently to playback, we suggest that either (1) coordination of duetting does not hold a function in joint resource defence in this species, (2) playback stimuli were too threatening for them to adjust their coordination on a level we could detect or (3) they do not discriminate between our coordinated and uncoordinated playback treatments. We highlight the

notion that there may be variety in functions of duetting at play within and across avian species, and that different aspects of duets such as coordination and intensity may hold different functions.

Keywords: Antiphonal duet, female song, cooperation, pair quality, chirruping wedgebill, playback

Introduction

Duetting is a form of communication where two individuals contribute to a vocal signal, which has been observed in primates (De Gregorio et al., 2022), birds (Hall, 2009), and insects (Bailey, 2003). Duetting behaviour typically involves coordinated vocalizations between mated pairs and serves multiple functions within and outside the pair bond (Dahlin & Benedict, 2014; Hall, 2004, 2009; Todt & Naguib, 2000). Historically, studies regarded duetting as a form of sexual conflict, where an attempt to attract mates with vocalisations is barred by an individual that inserts their vocalisation in their partners' display (Levin, 1996; Sonnenschein & Reyer, 1983). However, more recent work confirmed that duetting is a form of cooperation rather than conflict in the pair, where both pair-bonded mates benefit from participating in duetting (Dahlin & Benedict, 2014; Templeton et al., 2011).

Cooperative functions of duets include joint territorial defence (Hall & Peters, 2008; Logue, 2005), maintaining the pair bond and contact with the mate (Logue, 2007; Mennill & Vehrencamp, 2008), and ensuring reproductive synchrony (Schwabl & Sonnenschein, 1992; Todt & Hultsch, 1982). Of these hypotheses, joint resource defence is considered as both the most prevalent and primary function of duetting in birds (Dahlin & Benedict, 2014; Hall, 2009). The joint resource defence hypothesis suggests that the duetting is used as a mechanism to protect a duetting pair's territory. Duets not only announce the presence of multiple signallers but also indicate their preparedness or ability to defend the territory (Dahlin & Benedict, 2014; Diniz et al., 2019; Hall, 2009). Duetting can be used to share an individuals' position and identity with their partner, even in noisy and dense habitats. In this setting, it can be more efficient than contact calls (Hall, 2009; Mentesana et al., 2020). However, we still know little about what features of duets make them a stronger signal.

Duets have major structural differences, both within and across species, which may explain their versatility in functions across a wide range of settings (Hall, 2009). One major component of these differences is variation in duet coordination, including how precisely two duetting partners time their vocalisations. When duetting, individuals need to be attentive, anticipate, and respond immediately to parts sung by their duetting companion. For instance, in the black-bellied wren (*Pheugopedius fasciatoventris)* duet timing is based on the preceding notes of the mate's song (Logue et al., 2008). This attention is required not only when the partner starts singing, but also to adjustments in tempo and phrase types during the rest of the duet. Higher attentiveness can result in more precisely coordinated duets, which may require changes by both the initiator and responder (Diniz et al., 2021; Hall, 2009).

Coordination within duets may be a signal for competitiveness of pairs. For example, in an experimental study on magpie-larks (*Grallina cyanoleuca*) where pairs were exposed to playbacks of

highly coordinated and uncoordinated duets as simulated territory intrusions, males responded more aggressively to coordinated duets than uncoordinated duets (Hall & Magrath, 2007). Here, coordination was defined relatively coarsely as general overlap in time of song by the pair members. To date, studies on duet coordination have varied definitions on coordination, and tend to use very temporally coarse measures such as overall song overlap (Hall & Magrath, 2007), song gap length (Logue et al., 2008), and phrase rhythm (Diniz et al., 2021). However, birds can perceive temporal differences in vocalisations on extremely fine scales (e.g. Dooling et al., 2002; Lohr et al., 2006) meaning that small temporal differences in coordination may be perceived and assessed as striking signals of competitiveness by duetting birds. Additionally, a duet can arguably still be coordinated if the degree of overlap and/or gaps is high, if the timing of vocalisations remains consistent throughout the duet. Temporal coordination is likely affected by pair-bond tenure, whereby newly established pairs are less coordinated (Hall & Magrath, 2007), and may become particularly relevant on a finer temporal level where coordination becomes more challenging. Thus, this may be perceived as a signal of the stability of the partnership and effectiveness at defending a resource such as a territory. Thereby, coordination of male and female song exemplifies pair quality in the context of cooperative territorial defence (Hall, 2000).

Here, we experimentally test whether vocal coordination within territorial pairs functions as a cooperative resource defence signal in the chirruping wedgebill (*Psophodes cristatus*), a socially monogamous passerine endemic to the Australian arid zone. We measured vocal coordination on both a coarse level (total song overlap) and fine-scale level (note-by-note). Chirruping wedgebills produce sex-specific vocalisations, where the male produces a tri-syllable phrase and the female a mono-syllable phrase (Austin et al., 2019). This species has a very high song rate during early morning, which is often found to function in territory defence (e.g. Amrhein *et al.* 2004; Kacelnik & Krebs 1983; Trillo & Vehrencamp 2005). As the arid zone is exemplified by scarce and patchy resource availability, effective territory defence is likely crucial for survival and reproductive success. Altogether, these factors make the chirruping wedgebill an ideal species to test whether high coordination in duetting increases perceived threat within a territorial context. Here, we expose territorial pairs to playback of coordinated and uncoordinated duets and measure their vocal response, specifically the intensity of response and duetting coordination to their partner. We predict that wedgebills perceive duet coordination as a territorial signal and will respond more intensely and coordinated to playback with high duet coordination.

Methods

a. Study species and data collection

We studied Chirruping wedgebills at Fowlers Gap Arid Zone Research station (31°05' S, 142°42' E), New South Wales, Australia in Oct 2023 and Sept 2024. Chirruping wedgebills are sedentary socially monogamous passerines that occupy distinct territories and have home ranges of ca. 1.5ha (Speelman et al., in prep). Chirruping wedgebills produce antiphonal duets, whereby the female typically inserts her mono-syllabic phrase in the recess between the male tri-syllabic phrases, but either sex also produce solo vocalisations (Figure 1, after Austin *et al.* 2019). We identified and monitored territorial pairs by visiting the territory at least twice and confirming pairs were duetting from the same location. Pairs were monitored outside the breeding period.

b. Playback stimuli

The experiment consisted of two different stimuli: a coordinated and uncoordinated playback of conspecific duets. We recorded non-playback induced duets from 8 local pairs that were more than 500m away from the experimental subjects during Sept and Oct 2023 using a directional microphone (Sennheiser ME66/K6) and a digital audio recorder (ZOOM H4n Handy Recorder). Stimuli were created by manipulating the timing of the start of the female syllable in relation to the ending of the last male syllable using Audacity 3.4.2. We first prepared the playback files by high-pass filtering background noise (200Hz, 48dB per octave roll-off) and normalizing the maximum amplitude of each signal (to -1dB). To produce the coordinated duet (Figure S1A), the female syllable was inserted directly after every third last male syllable. Interval duration between male phrases was standardized per duet by calculating the average interval duration between male and female elements of the focal duet. The coordinated duet was then used to create the uncoordinated duet (Figure S1B) by varying every female syllable using randomly generated values with σ = 0.3s. Coordination of the playback and the responses during the experiment was measured as the standard deviation of all note-by-note gaps between partners, i.e. the time between the end of the partner's vocalisation and the start of the focal individual's vocalisation. The playback treatments differed in coordination after manipulating the recordings for both the female (Wilcoxon signed-ranks test: Z=-2.66, p=0.008, mean coordinated ± σ = 0.02 ± 0.02, mean uncoordinated ± σ = 0.23 ± 0.11; Figure S2A) and male vocalisations (Wilcoxon signed-ranks test: Z=-2.42, p=0.016, mean coordinated ± σ = 0.06 ± 0.07, mean uncoordinated ± σ = 0.20 ± 0.08; Figure S2B).

c. Playback experiments

A total of 24 pairs received the treatments on two separate trial days, with a recess period of 1-5 days between trial days. Playback experiments were conducted between 6:00 and 11:00am, from mid to late Oct 2023 and early to late Sept 2024. All trials consisted of a single duet type (coordinated/uncoordinated) with (i) 5min silence, (ii) 45s of playback (ii) 30s silent period, (iv) 45s of playback, and (v) 5min silence. Stimuli were broadcast from a cell phone using the VLC WAVE player connected with an AUX cable to an Ultimate Ears Megaboom loudspeaker placed at 1m from the ground in vegetation (e.g. a shrub) inside the territory of the focal pair where they have been observed to vocalise before. Playback volume was standardized for all trials to be ca. 52dB (A-weighted) in silent conditions 30m away, verified with a sound pressure level meter (Voltcraft SL-300). 1-2 observers were seated between 15-20m away from the loudspeaker hidden behind vegetation and recorded vocal responses of the focal pair using a directional microphone and audio recorder of the same type as mentioned above. After the playback, closest distance between the loudspeaker and the male and the female (based on observations during the trial) were measured using a tape measure.

d. Statistical analysis

All analyses were conducted using R 4.4.0 (R Core Team, 2024), and used linear mixed models (LMMs) using *lme4* 1.1.35.3 (Bates et al., 2015) to test whether responses to coordinated and uncoordinated trials differed. Responses of chirruping wedgebills included five measures: closest distance to speaker during the trial (m), latency to vocalise since start of playback (sec), number of vocalisations during trial (*N* vocalisations), vocalisation duration (time between first and last vocalisation in sec), and coordination (Table 1). Coordination was measured using two metrics: a fine-scale measure (note-by-note, see Methods section *Playback stimuli*) and a coarse measure (fraction of all time spent vocalising that overlaps with vocalisations of the other sex). Vocalisations made during the two 45s playback sequences were emitted from the analyses to ensure they were not confused with the playback itself. Due to the large number of response measures, we ran a principal component analysis (PCA) on these measures per sex. We excluded coordination to their partner as a measure in the PCA, as we were specifically interested in the coordination of duets by trial pairs responding to playback. For both sexes, we used the first principal component (PC1) which explained 90.7% of the variance in males (eigenvalue=1.75) and 96.6% in females (eigenvalue=2.08) as a measure of response intensity for further analysis. Based on the PC1 loadings, a high PC1 score indicates a strong response intensity for both sexes (Table 1).

We ran separate LMMs for both response intensity and coordination as response variables for both sexes since male chirruping wedgebills have consistently higher vocalisation rates than females (Austin et al., 2019), and we expect the coordination measures to be inherently different among the sexes due

to the structure of the duet. As predictor variables, we added playback treatment (coordinated/uncoordinated), trial order (1/2), minutes since sunrise (mean centred and divided by 1σ), and year (2023/2024). As random factors, we included focal pair identity and source playback pair (i.e. the recording used for creating playbacks). We found that all model assumptions (normality of residuals and random effects, homogeneity of variance, variance inflation factor <3) were met using *performance* 0.13.0 (Lüdecke et al., 2021). Significance of playback treatment was determined using a likelihood-ratio-test (LRT) by comparing a model with and without playback treatment as a fixed effect (using ANOVA).

Results

Of all 24 pairs exposed to the two treatments, in 18 pairs both the male and female responded during both treatments, whereas in the remaining 6 pairs only the male responded at least during one treatment. Since we were specifically interested in the response of both partners, we excluded these 6 pairs from further analyses. All values mentioned below are mean ± σ.

Response intensity measured as scores on the first principal component was unaffected by playback treatment in both males (LRT=0.601, coordinated: 0.19 ± 1.72, uncoordinated: -0.17 ± 1.54) and females (LRT = 0.883, coordinated: -0.017 ± 0.69, uncoordinated: 0.61±0.38; Table 2, Figure 2). All other effects were also not significant, except for year of playback in males (β = 1.694, SE = 0.539, p = 0.007; Table 2), indicating that males tested in 2024 responded more intensively than males tested in 2023. Fine-scale coordination of the syllables during duetting was also unaffected by playback treatment for males (LRT = 0.160, coordinated: 0.33 ± 0.09; uncoordinated: 0.38 ± 0.13) and females (LRT = 0.255, coordinated: 0.38 ± 0.10; uncoordinated: 0.36 ± 0.11; Figure 3), as well as all other predictor variables (Table 3). The coarse metric of coordination as fraction of the vocalisations overlapping with the partner was consistent with fine-scale coordination: there was no effect of playback treatment for males (LRT = 0.917, coordinated: 0.05 ± 0.04, uncoordinated: 0.04 ± 0.04) and females (LRT = 0.386, coordinated: 0.27 ± 0.23; uncoordinated: 0.21 ± 0.16; Table 4, Figure 4). There was a treatment order effect in males where they had less overlap with their partner during the second trial (β = -0.023, SE = 0.007, p = 0.003), and a year effect in females where they had more overlap with their partner during 2024 than 2023 (β = 0.157, SE = 0.070, p = 0.040).

Discussion

We found chirruping wedgebills did not respond more intensively or more coordinated to playback of coordinated compared to uncoordinated duets of unfamiliar pairs. Thus, our findings are not in line with the hypothesis that vocal coordination in both a coarse and a fine note-to-note level in duets

functions as a cooperative resource defence signal where coordinated duets represent a more threatening display. This expands on limited previous studies that have tested duet coordination in a territorial context. While magpie-larks appeared to perceive coordinated duets as more threatening (Hall & Magrath, 2007), Neotropical wrens (*Henicorhina leucophrys*) seemed indifferent to such differences in duet coordination (Dingle & Slabbekoorn, 2018) and three other wren species (rufous-and-white wrens, *Thryophilus rufalbus*; rufous-and-white wrens, *Thryophilus rufalbus*, plain wrens, *Cantorchilus modestus*) did not respond differently to coordinated versus uncoordinated duets (Kovach et al., 2014).

Our results could be explained by three alternative explanations. First, it may be the case that in chirruping wedgebills, coordination within duets does not function as a more threatening territorial display. This may indicate that chirruping wedgebills regard all intruding pairs as equally threatening. Alternatively, they may they still perceive some pairs more threatening during territorial displays than others depending on other aspects of duetting, such as the rate of vocalisations by the initiator (e.g. Catchpole & Slater 2008), the answering rate by the partner (e.g. Schwabl & Sonnenschein 1992), and the degree of song overlap between the male and the female (e.g. Naguib & Todt 1997; Trainer & McDonald 1995). It may even be that non-vocal aspects during duetting are more important, such as proximity to the partner (Hultsch & Todt, 1984), synchronised movements (Tingay, 1974; Todt & Fiebelkorn, 1980), and visual displays (Kraaijeveld & Mulder, 2002). Coordination may still be functionally important, but in different contexts such as for pair-bond maintenance (Wickler, 1980).

Second, it may be that exposure to playback elicits a very strong response to territorial pairs, leading them to a highly aroused internal state (Hall, 2009; Todt et al., 1981). In this case, it may be difficult for these pairs to still produce highly coordinated duets in response to the stimuli. However, if this would be the case, we could expect chirruping wedgebills to still respond more intensively to coordinated rather than uncoordinated duets, which we did not find. Our playback experiments were conducted at locations where territorial pairs have been observed to vocalise consistently, indicating this may be their preferred vocalising spot or even the centre of a territory. If this is the case, the presence of an unfamiliar pair duetting in this location may be a highly threatening display leading to them responding either without temporal precision or with maximum temporal precision (these are not distinguishable in this case), regardless of whether the duet stimulus is coordinated or not.

Third, it may be that the differences in the coordinated and uncoordinated playback treatments were not meaningful for chirruping wedgebills in a territorial context. The differences in playback treatments in our case indeed might have been potentially too subtle to elicit a differential response in a highly aroused territorial conflict. Other studies tended to define coordination on a coarser level, i.e., when

male and female songs were generally overlapping in time (e.g. Dingle & Slabbekoorn, 2018; Diniz et al., 2021; Hall & Magrath, 2007; Keenan et al., 2020; Logue et al., 2008; but see Ręk & Magrath, 2023). Thus, overall it appears that the exact level (i.e. scale of measurement) of coordination may matter and may have different functions. The existence of duetting per se already implies some levels of coordination (Hall & Peters, 2008), and the fine temporal adjustment within a duet then might have more specific, potentially within-pair, functions that do not trigger differential responses in territorial conflicts. The natural variability of the female to the male phrase in duets (σ=0.26; Austin *et al.* 2019) is comparable to the variability in our uncoordinated treatment (σ=0.23), whereas the coordinated treatment is seemingly much less variable (σ=0.02). This suggests that the coordinated treatment may be too precise for chirruping wedgebills to produce and potentially even to perceive. However, numerous studies suggests that avian species that produce duets can time vocalisations precisely and perceive small temporal differences (Hall, 2006; Logue et al., 2008; Voigt et al., 2006). For example, black-bellied wrens respond to their partner within less than 0.08s during duets (Logue et al., 2008), suggesting that they anticipate their partner's vocalisations on small temporal scales and are able to rapidly adjust their vocalisation timing according to their partner. Whether chirruping wedgebills discriminate between small differences in temporal coordination in other non-territorial contexts remains to be investigated.

Our study contrasts the hypothesis that very fine-scale and coarse duet coordination functions as a threatening territorial display. We highlight there may be a variety of functions at play within and across avian species and that the precise level of coordination may matter. The exact functions and implications of variation in duetting may depend on the ecological and social contexts of the environment that individuals reside in, as well as life history traits of species that duet. Additionally, within duets, different aspects of the behaviour such as coordination and intensity may hold different functions. Since duetting is a jointly expressed trait within a dyad, it should be regarded within the context of individuals as well as the pair-bond, and characteristics of both sexes are likely to play a role in the execution of the duet. To test whether duet coordination holds functional significance in species, we suggest that studies should examine multiple hypotheses in the experimental approach that are relevant in the context of the species.

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381 Tables

382 Table 1. Response measures of vocal pairs to playback during the trial, how they were measured, and
383 PCA loadings per sex.

Response measure	Description	PCA loadings male	PCA loadings female
Distance to speaker	The closest distance between individual and speaker in meters during the trial	-0.489	-0.496
Latency to vocalise	Seconds taken until first vocalisation is produced since start of playback after the end of the first 45s playback sequence	-0.498	-0.452
Number of vocalisations	Number of vocalisations produced during trial	0.488	0.493
Vocalisation duration	Seconds between the start of the first and end of the last vocalisation after the end of the first 45s playback sequence	0.524	0.554
Fine-scale coordination	Standard deviation of the time between the end of the partner's vocalisation and the start of the focal individual's vocalisation	NA	NA
Coarse coordination	Fraction of all time spent vocalising that overlaps with vocalisations of the partner	NA	NA

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Table 2. Linear mixed model output of male and female response intensity (PC1). Reference levels of fixed effects are coordinated = yes, trial number = 1, year = 2023. Pair identity is the pair exposed to playback, and source playback is the identity of the pair used to create the playback files. Significant effects are indicated in bold.

	Males				***Females***			
Fixed effects	***β***	***SE***	***t***	***p***	***β***	***SE***	***t***	***p***
Intercept	-0.455	0.495	-0.921	0.368	0.045	0.240	0.188	0.855
Coordinated (no)	-0.186	0.384	-0.485	0.634	-0.025	0.207	-0.127	0.900
Year (2024)	**1.694**	**0.539**	**3.144**	**0.007**	-0.070	0.244	-0.286	0.779
Minutes since sunrise	-0.344	0.243	-1.417	0.167	-0.132	0.121	-1.091	0.287
Trial (2)	-0.769	0.411	-1.869	0.078	0.018	0.221	0.081	0.936
Random effects	***σ***	***N***			***σ***	***N***		
Pair identity	0.797	18			0.263	18		
Source playback pair	0.223	8			0.137	8		
Residual	1.107				0.601			

Table 3. Linear mixed model output of male and female fine-scale response coordination (σ focal to partner response latency). Reference levels of fixed effects are coordinated = yes, trial number = 1, year = 2023. Pair identity is the pair exposed to playback, and source playback is the identity of the pair used to create the playback files. Significant effects are indicated in bold.

	Males				***Females***			
Fixed effects	***β***	***SE***	***t***	***p***	***β***	***SE***	***t***	***p***
Intercept	-0.694	0.351	-1.780	0.091	-0.450	0.391	-0.155	0.909
Coordinated (no)	0.402	0.302	1.329	0.201	-0.349	0.315	-1.111	0.278
Year (2024)	0.476	0.366	1.300	0.212	0.207	0.360	0.575	0.569
Minutes since sunrise	0.189	0.180	1.049	0.303	0.051	0.173	0.292	0.773
Trial (2)	0.295	0.323	0.913	0.373	0.172	0.329	0.524	0.605
Random effects	***σ***	***N***			**σ**	***N***		
Pair identity	0.455	18			<0.001	18		
Source playback pair	0.029	8			0.547	8		
Residual	0.879				0.892			

Table 4. Linear mixed model output of male and female coarse response coordination (fraction of overlap with partner vocalisations). Reference levels of fixed effects are coordinated = yes, trial number = 1, year = 2023. Pair identity is the pair exposed to playback, and source playback is the identity of the pair used to create the playback files. Significant effects are indicated in bold.

	Males				***Females***			
Fixed effects	***β***	***SE***	***t***	***p***	***β***	***SE***	***t***	***p***
Intercept	0.062	0.015	4.207	0.001	0.182	0.066	2.779	0.010
Coordinated (no)	-0.001	0.006	-0.093	0.927	-0.045	0.055	-0.814	0.427
Year (2024)	-0.004	0.015	-0.246	0.811	**0.157**	**0.070**	**2.247**	**0.040**
Minutes since sunrise	-0.002	0.004	-0.460	0.650	0.004	0.033	0.144	0.887
Trial (2)	-0.023	0.007	-3.473	0.003	-0.023	0.059	-0.389	0.702
Random effects	***σ***	***N***			**σ**	***N***		
Pair identity	0.023	18			0.094	18		
Source playback pair	0.027	8			<0.001	8		
Residual	0.017				0.025			

Figure legends

Figure 1: Spectrograms of chirruping wedgebill vocalisations: (a) the tri-syllabic male trill song (syllables I, II, III); (b) the mono-syllabic female song; and (c) a male and female duet, with male and female contributions indicated by a and b, respectively (Austin et al., 2019).

Figure 2. Violin plots of response intensity (PC1) of females and males to coordinated and uncoordinated playback treatments. Black dots and lines represent individual responses.

Figure 3. Violin plots of fine-scale response coordination (σ focal to partner response latency) of females and males to coordinated and uncoordinated playback treatments. Black dots and lines represent individual responses.

Figure 4. Violin plots of coarse response coordination (fraction of time vocalising that overlaps with partner vocalisations) of females and males to coordinated and uncoordinated playback treatments. Black dots and lines represent individual responses.