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ORIGINAL ARTICLE

Solos, duets and choruses: vocal behaviour of the Rufous-naped Wren (*Campylorhynchus rufinucha*), a cooperatively breeding neotropical songbird

David W. Bradley · Daniel J. Mennill

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Abstract Vocal communication in duetting and chorusing birds is a growing area of study in avian ecology, yet much remains unknown about temporal and population-level variation in these complex vocal signals. In this study, we describe the acoustic structure and temporal variation in solos, duets, and choruses in the Rufous-naped Wren (*Campylorhynchus rufinucha*), a cooperatively breeding neotropical passerine. We collected focal recordings of 19 groups to assess both diel and seasonal variation in vocal output, as well as population-wide sharing of vocal signals. We found that birds produce a complex array of vocalisations, including tonal, frequency-modulated syllables grouped into phrases, as well as stereotyped, atonal sounds. Songs are produced as solos or combined into duets and choruses. Solo and duet songs show a dawn chorus effect. Solo song rate, but not duet or chorus rate, varied across breeding stages. The majority of phrases are shared amongst groups, significantly more amongst groups in nearby territories. We suggest that chorus songs may be an important indicator of group identity and may play a role in maintaining group territories, but do not play a role in relation to the breeding cycle. The degree of population-wide phrase-sharing suggests either short-distance dispersal or delayed song learning. This paper is the first fine-scale description of vocal behaviour in this species and enhances our understanding of group-singing in a complex social environment.

Keywords Rufous-naped Wren · *Campylorhynchus rufinucha* · Duet · Chorus · Cooperative breeding

Introduction

Avian vocal duets are coordinated acoustic signals produced by two individuals, usually a mated pair in a long-term pair bond (Farabaugh 1982). Several non-mutually exclusive hypotheses have been proposed for the function of duetting, the most widely supported of which concern joint resource defence, mate defence, paternity defence and as a signal of partner commitment (Hall 2004). These hypothesised functions represent varying levels of cooperation and conflict between the sexes and help explain the adaptive value of coordinated singing from the perspective of both the male and the female. Although avian duetting has received modest attention, we know less about the adaptive value of avian chorusing. This complex, coordinated behaviour occurs when more than two birds combine their vocalisations into an acoustic display (e.g. Seddon 2002; Baker 2004; Hale 2006). Choruses are necessarily more complex than duets because more individuals are involved, each with differing degrees of motivation for conflict or cooperation. It has been suggested that choruses may function similarly to duets, either cooperatively in joint resource defence (Reyer and Schmidl 1988; Brown and Farabaugh 1991; Wingfield and Lewis 1993; Seddon 2002; Baker 2004; Hale 2006) and in maintaining social bonds within the group (Brown et al. 1988), or in conflict

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D. W. Bradley · D. J. Mennill
Department of Biological Sciences, University of Windsor,
401 Sunset Avenue, Windsor, ON N9B3P4, Canada

Present Address:
D. W. Bradley (✉)
Department of Biological Sciences, University of Waikato,
Gate 1 Knighton Road, Private Bag 3105,
Hamilton 3240, New Zealand
e-mail: db63@waikato.ac.nz

between group members by mediating social hierarchies (Reyer and Schmidl 1988). Despite these findings, much remains unknown about avian choruses, in particular the relationship between mating systems and the structure and function of both duetting and chorusing.

We studied solos, duets and choruses in the Rufous-naped Wren (*Campylorhynchus rufinucha*), a neotropical passerine that lives in groups of two or more (Skutch 1935, 1960). One of the more controversial aspects of this species' behaviour is the extent to which non-reproducing individuals assist in rearing other birds' offspring. In his seminal work on Central American birds, Skutch (1960) described family groups together outside the breeding season and extra-pair individuals aiding in the provisioning of other birds' offspring. Although Selander (1964) and Wiley (1983) concluded that cooperative breeding did not occur in this species, the more comprehensive study by Joyce (1993) clearly documented examples of cooperative breeding, although this occurred in fewer than 10% of nests.

Long-term territory tenure and the convergence of gender roles are common characteristics of tropical birds (Stutchbury and Morton 2001). As a result, communication between tropical songbirds is necessarily different than in temperate regions where, in general, males sing to defend territories and attract mates whilst females do not sing (Langmore 1998). The genus *Campylorhynchus* is a particularly interesting taxon in this regard, because it is commonplace for both males and females to sing, for mated pairs to perform duets, and for groups to sing choruses whilst cooperating to rear a single brood of young (reviewed in Barker 1999). Despite this, little research has been conducted on the role of vocal communication in mediating territoriality and maintaining social bonds within groups in this genus, including those of Rufous-naped Wrens. Although their vocalisations have been anecdotally characterised in several onomatopoeic descriptions (Skutch 1935, 1940, 1960; Selander 1964), little attempt has been made to quantify their vocal behaviour in a rigorous way. In particular, no studies to date have quantified fine-scale structural features of Rufous-naped Wren vocalisations, or attempted to quantify song output as a function of daily or seasonal rhythms. Additionally, no studies have assessed the diversity of vocalisations on an individual or population-level.

In this study, we present the first formal fine-scale description of the complex vocal behaviour of Rufous-naped Wrens based on recordings collected in the seasonal dry forests of Guanacaste, Costa Rica. We analyse temporal structure of vocal behaviour in the context of daily and seasonal rhythms in this species. We also assess population-level variation in the acoustic structure of vocalisations, and the degree to which vocal characteristics are shared within the population. We discuss our findings in light of the functional significance of duetting and chorusing, and the process of song learning in this species.

Methods

Field techniques

Rufous-naped Wrens inhabit the tropical dry forest of western Central America from the Mexican states of Colima and Michoacan, to San José Province in Costa Rica (Howell and Webb 1995; Stiles and Skutch 1989). We conducted this study in the deciduous tropical dry forest of sector Santa Rosa of the Area de Conservación Guanacaste, Costa Rica (10°40′N, 85°30′W). In early May 2007, we located and mapped 20 contiguous Rufous-naped Wren territories by following birds within their territory. When birds began to construct their bulky, domed nests in mid-May, nest locations were recorded with a global positioning system and monitored every 2–4 days. Rufous-naped Wrens are sexually monomorphic in plumage yet dimorphic in body measurements. We attempted to capture birds using mist nets using song playback, but capturing this species proved to be extremely difficult due to their behaviour of remaining high in the canopy above the loudspeakers and mist nets. Over a 3-week period of intensive netting, we were successful in capturing only four individuals in 2 of the 20 territories, to which we applied unique combinations of coloured and metal rings. However, observations of the ringed birds, as well as of other colour-ringed birds that were not part of the present study, confirmed that birds remained within the same space throughout the study period, and showed season-long territory tenure. Consequently, we are confident that we could reliably return to the same individuals in the same territories for the unringed birds that constituted the rest of our study population.

We collected focal audio recordings of birds in 19 of the 20 territories between 5 May 2007 and 20 July 2007 (one territory was abandoned part way through the study after being recorded only twice and was not included in our analyses of vocal behaviour). We used a directional microphone (Sennheiser ME66) and a solid state digital recorder (Marantz PMD 660) and saved digital recordings as uncompressed monoaural WAV files (16-bit, 44 kHz). Recording sessions lasted approximately 2 h and were collected in one of two time periods; between 0500 and 0700 hours CST (early morning) or between 0730 and 1030 hours (late morning). Whenever possible, we recorded each territorial group during two early morning sessions and two late morning sessions. During recordings, we classified the breeding stage of the focal group into one of the following categories: pre-egg laying stage (before the female laid eggs and the pair were nest building); incubation stage (when the female was seen visiting and incubating eggs in the nest); nestling stage (after eggs had hatched and parents were either brooding or chick feeding); or fledgling stage (when chicks had left the nest and were accompanying the pair around the territory). In total we collected 153 h of recordings from 19 groups. On average, we recorded each group for a total of 8.06 ± 0.31 h.

Analysis of vocalisations

We analysed audio recordings by visualising sounds as spectrograms using SYRINX-PC (J. Burt, Seattle, WA, USA). We characterised all vocalisations based on the number of contributors as either a solo (one bird vocalising), a duet (two birds vocalising), or a chorus (more than two birds vocalising). Each vocalisation was deemed distinct when separated from other vocalisations by at least 1 s. We subdivided vocalisations into two categories based on the type of sound being produced: (1) those consisting of lengthy, repeated phrases of tonal syllables which showed a high degree of variability and most resemble song; and (2) several shorter, stereotyped, atonal vocalisations that most resemble calls (sensu Catchpole and Slater 2008). We characterised duets based on the combination of these vocalisation categories (i.e. whether the two birds were producing tonal or atonal vocalisations). Choruses were considerably harder to separate into different vocal parts and so were termed choruses whenever three birds took part in the vocalisation. We categorised and numbered each of the distinct vocalisations and stored them as separate sound files in a population-level phrase dictionary.

To describe the fine-scale structure of the songs, we performed detailed measurements of frequency and temporal characteristics of the component song phrases. We determined the ten most commonly produced phrases in the population and isolated ten examples of each from ten different individuals. On each of the resulting 100 phrases, we performed fine-scale measurements using the time and frequency cursors in SYRINX-PC. We measured the number of distinct syllables in each phrase, the length of the entire phrase, and the maximum and minimum frequencies produced in each phrase. Spectrograms were generated with an FFT length of 1,024 points and viewed as a Blackman window, allowing a frequency resolution of 4.8 Hz and a temporal resolution of 1.6×10^{-3} s. When comparing male and female phrases, we measured the maximum and minimum frequencies, and the frequency of maximum amplitude (FMA) of each syllable in each phrase using AUDITION (Adobe Systems, San Jose, CA, USA).

We determined song output in relation to time of day by assessing the number of times each type of vocalisation (solo, duet and chorus) was produced in each of the hourly periods after sunrise (sunrise occurred consistently at approximately 0500 hours). Solo song rates and duet song rates were calculated for all groups, and chorus song rates were only calculated for groups of more than two birds. We performed a similar analysis to determine song output across the four breeding stages outlined above.

We examined phrase-sharing by comparing repertoires amongst groups. We categorised tonal phrases into different phrase types by visually comparing the sound spectrograms. We considered two phrases to be of the same phrase type when they shared at least half of the component syllables (following Hill et al. 1999; Burt et al. 2001). For each territory, we calculated group repertoire size as the number of different phrase types produced by any bird in the group. When possible, we determined the individual phrase repertoires of both male and female birds in a mated pair ($n = 2$ pairs where one or both of the pair was colour-ringed). To assess whether our sampling of phrase repertoires was complete, we plotted the cumulative number of novel phrase types detected against the cumulative number of phrases songs. We report phrase repertoires of Rufous-naped Wren groups where sampling was deemed complete based on whether this curve reached an asymptote. Consistent with other studies (e.g. Byers 1996; Hill et al. 1999; Molles and Vehrencamp 1999; Wilson et al. 2000; Molles et al. 2006; Nicholson et al. 2007), we determined the proportion of shared phrase types between groups in the population using the formula developed by McGregor and Krebs (1982) account for comparisons between groups with different repertoire sizes: $2N_s/(R_1 + R_2)$, where N_s is the number of shared phrases, and R_1 and R_2 are the repertoire sizes of the two groups. We then related the proportion of shared repertoires between each of the groups to the physical separation of their territories, measured in terms of the number of intervening territories.

Statistical analysis

We analysed song output in relation to breeding stage and time of day by performing mixed-model ANOVA. We used this analysis because including both random and fixed factors allowed us to account for non-independence of data collected from the same group (random factor) whilst assessing variation in the dependent variables (fixed factors). In these models, we estimated variance in the random factor using the residual maximum likelihood technique and in the fixed factors using standard least squares. We assessed phrase-sharing in the population using a Mantel test, by creating two matrices: one matrix represented the number of shared phrases of all the groups in relation to each other; the second matrix represented the number of intervening territories between each territory as a proxy of physical separation. We used POPTOOLS 3.0 (G. Hood, Canberra, Australia), performing 999 iterations of random matrices per run to compare correlations with the observed matrices. Additionally, to assess how phrase-sharing between groups varied as a function of the distance between groups, we calculated pairwise comparisons of phrase-sharing between all different territories, and ran a linear regression on these values against distances-of-separation between territories (expressed as number of intervening territories), using JMP 5.0 (SAS Institute, Cary, NC, USA). All tests are two-tailed and all values are reported as mean ± SE.

Results

Amongst 20 Rufous-naped Wren territories in the neotropical dry forest of Costa Rica, we found that 18 territories (90%) were occupied by a breeding pair, and 2 territories (10%) were occupied by a breeding pair plus an additional individual. The groups of three birds regularly moved around their territories and foraged together, often counter-singing with neighbouring groups by performing three-part choruses. Observations of the groups of three around the nest suggested that all three birds were involved in bringing food to the nestlings, although as the birds were not ringed this could not be definitively confirmed.

Solo vocalisations

Rufous-naped Wrens produce melodic, frequency-modulated syllables that they combine into distinctive tonal phrases (Fig. 1a). On average, phrases are 1.70 ± 0.07 s long, are composed of 4.7 ± 0.5 syllables, and range in frequency from a minimum of 861 ± 31 Hz to a maximum of 2,635 ± 85 Hz. Both sexes produce tonal phrases, with both members of a mated pair often capable of producing the same phrase type (Fig. 1a). Rufous-naped Wrens also produce a variety of stereotyped, atonal vocalisations in various contexts (Fig. 1b): waahs are comprised of loosely spaced harmonic stacks; barks are comprised of harsh bursts of broadband noise; nasal snarls consist of tightly spaced harmonic stacks; and rattles are longer vocalisations comprised of a series of chattering broadband notes.

In addition to isolated tonal phrases and atonal vocalisations, Rufous-naped Wrens often produce solo songs by repeating phrases several times in succession (Fig. 1c). Birds most often repeat the same phrase type in succession during these solo songs (92.7 ± 0.6% of recorded solo songs), although they occasionally switch phrase type at least once part way through the song (7.3 ± 2.0% of recorded solo songs).

Duet and chorus vocalisations

Rufous-naped Wrens create duets when members of a pair simultaneously vocalise: either when both produce tonal phrases (“two-tonal duets”), one bird produces tonal phrases and a second bird produces atonal vocalisations (“one-tonal duets”), or when both birds produce atonal vocalisations (“atonal duets”). When producing two-tonal duets, mated pairs often match their phrase types (Fig. 2a; 51.4 ± 1.7% of recorded two-tonal duets), and sometimes do not match their phrase types (Fig. 2b; 48.6 ± 1.8% of recorded two-tonal duets). Because we could assign phrase repertoires only to territories, and not to individuals, we cannot calculate a specific chance level of phrase-type matching in two-tonal duets. However, since we know that individual birds possess moderately large phrase repertoires (see below), the observed level of phrase matching must be substantially higher than chance. In the groups of three birds, we found that tonal phrases and atonal vocalisations are combined in different ways to produce choruses, including all three birds singing tonal phrases (Fig. 2c), some birds singing tonal and others singing atonal phrases, or all three birds producing atonal phrases.

When producing coordinated vocalisations, Rufous-naped Wrens perform intricate visual displays. In the early stages of a duet, pairs often alight on the same perch and make short-distance movements towards each other. Whilst vocalising, pairs make purposeful postures, such as spreading their tail feathers, raising their beaks into a vertical position, and erecting the feathers on their chests. We only observed visual displays in association with the production of tonal phrases, and not of atonal vocalisations, and only whilst producing duets or choruses.

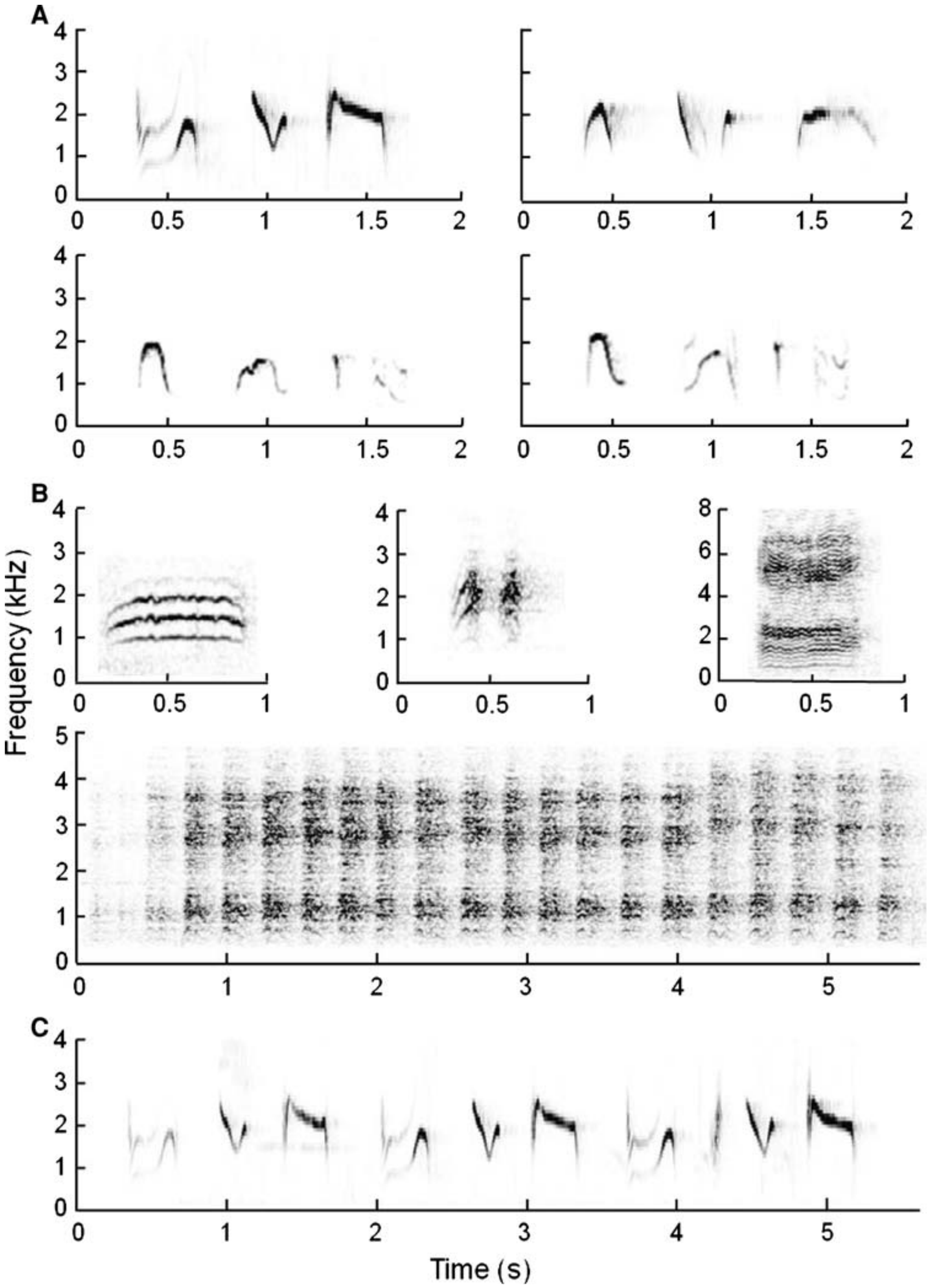
Male versus female vocalisations

Frequency components of Rufous-naped Wren songs varied with sex. Males sing phrases with significantly lower FMA (1,380 ± 35 Hz) than females (1,770 ± 55 kHz; ANOVA $F_{1,2} = 35.8$, $P = 0.03$), and with a significantly lower maximum frequency (2,190 ± 55 kHz) than females (2,900 ± 55 kHz; ANOVA $F_{1,2} = 82.6$, $P = 0.01$). Our repertoire sampling of individuals of known sex was complete for males and incomplete for females (Fig. 3a), yet suggests that males and females possess similarly sized repertoires.

Song output

Solo song output varied with time of day for tonal phrases, but not for atonal phrases. Solo tonal vocalisation rates

Fig. 1 Sound spectrograms of Rufous-naped Wren (*Campylorhynchus rufinucha*) solos. **a** Examples of tonal syllable phrases, produced by males (*left*) and females (*right*). **b** Examples of atonal vocalisations; waah (*top left*), bark (*top centre*), snarl (*top right*) and rattle (*bottom*). **c** A typical solo song comprised of repeated phrases of tonal syllables. Note different scale of vertical and horizontal axes in some spectrograms



varied significantly throughout the morning, with the highest levels in the first hour after dawn and declining thereafter (Fig. 4a; $F_{4,67} = 7.3$, $P < 0.0001$). Atonal solo vocalisation rates did not vary with time of day ($F_{4,67} = 0.4$, $P = 0.81$). Duets where both birds sang tonal phrases (two-tonal duets) varied significantly with time of day, with the highest levels in the first hour after dawn (Fig. 4b; $F_{4,67} = 4.7$, $P = 0.002$). Duets where one or both birds contributed atonal vocalisations did not vary significantly with time of day ($F_{4,67} = 1.4$, $P = 0.25$). Chorus rate did not appear to vary with time of day (Fig. 4c; $F_{4,4} = 0.34$, $P = 0.84$), although we had only two groups with more than two individuals.

Song output also varied significantly with breeding stage for solo tonal vocalisations (Fig. 5; $F_{3,32} = 3.6$, $P = 0.02$); tonal solos were given more often during the nestling stage than during the nest building and incubation stages. There was no significant variation with breeding stage for two-tonal duets ($F_{3,36} = 1.5$, $P = 0.22$), duets where one or both birds contributed atonal vocalisations ($F_{3,28} = 0.6$, $P = 0.64$), or choruses ($F_{3,1} = 0.5$, $P = 0.75$), although we had only two groups with more than two individuals.

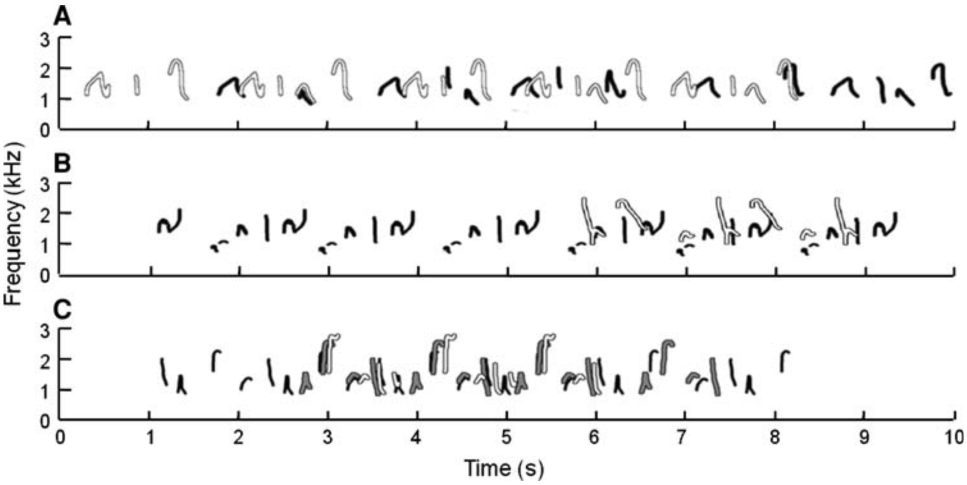


Fig. 2 Stylised sound spectrograms of Rufous-naped Wren songs. **a** Example of a duet with the male and female both singing the same tonal phrase type, **b** a duet with two birds singing different tonal phrase types, and **c** a chorus with three birds all singing the same tonal phrase type

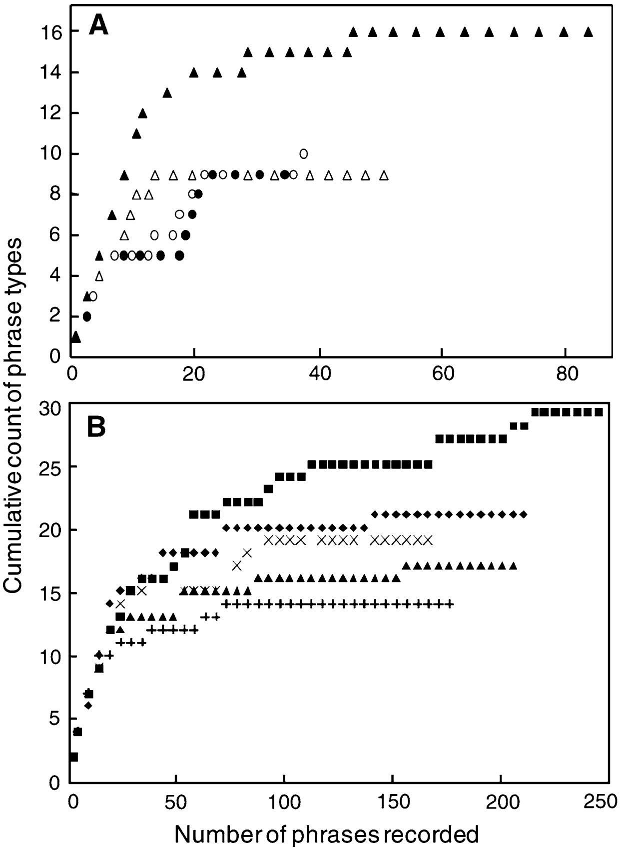


Fig. 3 **a** Repertoire curves for four Rufous-naped Wrens from two mated pairs. One pair is depicted by *triangles* and the other by *circles*; males are depicted as *solid symbols* and females as *open symbols*. **b** Repertoire curves of five territorial pairs of Rufous-naped Wrens. Complete repertoire sampling (indicated by a stable asymptote) was complete for four pairs and incomplete for one pair (the pair depicted by the *solid squares*)

Repertoires and phrase-sharing

Territorial groups of Rufous-naped Wrens showed variable repertoire sizes (Fig. 3b), with an average repertoire size of 20.8 ± 1.1 songs per group ($n = 16$ groups where the repertoire curve reached a stable asymptote). Repertoire sizes were significantly smaller (20.1 ± 1.0) for pairs than for groups of three (27.0 ± 0.5; ANOVA $F_{1,17} = 4.4$, $P = 0.05$). Groups shared 11.5 ± 0.28 phrases (58.0 ± 1.39% of their repertoire) with other groups in the study population. Birds were more likely to share phrase types with groups occupying territories closer than groups further away (Mantel test: $r^2 = -0.26$, $P = 0.005$). A quadratic linear regression of phrase-sharing and distance of territory separation revealed a highly significant correlation ($r^2 = 0.79$, $P < 0.0001$).

Of the 88 phrase types identified in this study, most phrase types (42) were unique to a single group and not shared with any other. At the other extreme, six phrases were shared across all 19 groups.

Discussion

Rufous-naped Wrens produce an extraordinary array of complex vocalisations including solos, duets and choruses by combining repeated phrases of tonal syllables and/or atonal vocalisations. Males and females produce similar tonal phrases, although male songs have lower frequency components than female songs. Rufous-naped Wrens produce tonal vocalisations at different rates depending on time of day and breeding stage. In contrast, vocalisation rates where one or both birds produce atonal sounds, either as solos or in a duet, did not vary with time of day. Chorus rates also did not vary with time of day or breeding stage, although the power of this analysis was low. Although groups share most of their tonal phrases with at least one other group, and several phrases are shared throughout the population, the majority of phrases are unique to single groups. We also found that phrase-sharing is higher between groups occupying territories closer together than

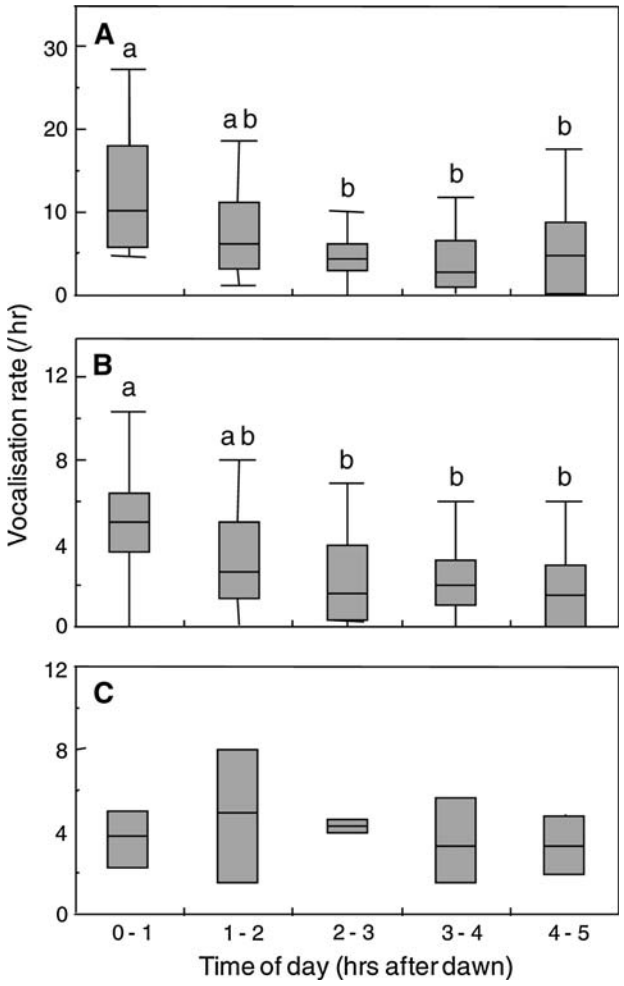


Fig. 4 Variation in song output of Rufous-naped Wrens in relation to time of day ($n = 19$ groups). Solo song rates were significantly higher in the first hour of the day (first light at ~0500 hours) than in the third, fourth and fifth hours (**a**). Duet output followed a similar pattern, with groups producing significantly more duets in the first hour of daylight than in the third, fourth and fifth hours (**b**). Chorus rates did not appear to vary in relation to time of day (**c**). Note the different scales on the vertical axes of the top graph and the bottom two graphs. *Box plots* show *horizontal lines* for 10th, 25th, 50th, 75th and 90th percentiles

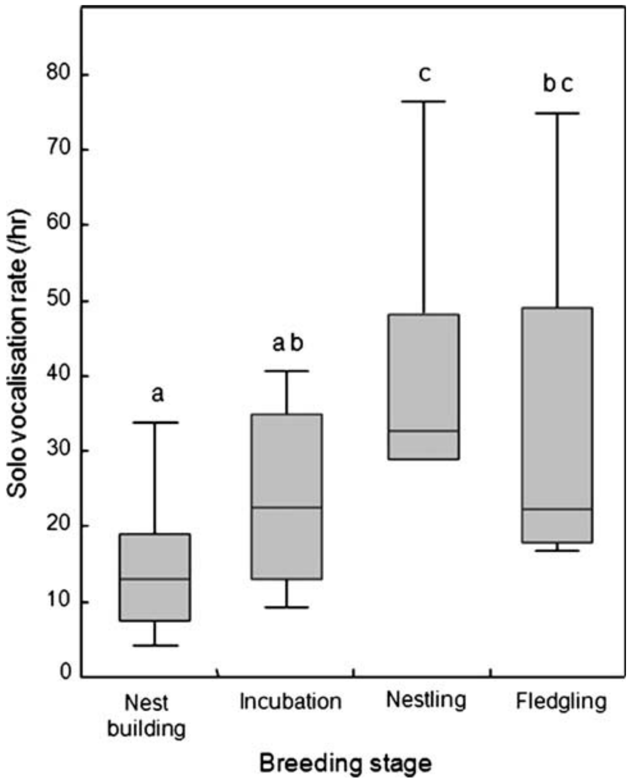


Fig. 5 Variation in solo song output of Rufous-naped Wrens in relation to breeding stage ($n = 19$ groups). Columns sharing *letters* are not significant different. *Box plots* show *horizontal lines* for 10th, 25th, 50th, 75th, and 90th percentiles

between more distant groups. These findings are the first formal description of the vocal behaviour of the Rufous-naped Wren.

Our quantitative descriptions of the vocalisations of Rufous-naped Wrens in this study agree with the early qualitative descriptions provided by Skutch (1940, 1960) and Selander (1964). However, the difference we observed in frequency characteristics between male and female phrases has not been observed in previous studies of this species, although a similar pattern of females producing songs with higher frequency components than males has been found in *Thryothorus* wrens (Mann et al. 2009). This difference may relate to the greater body size of males, which may result in the production of lower frequency songs (Podos and Nowicki 2004). For Rufous-naped Wrens, size dimorphism is so pronounced that we could visually detect differences in body size between the sexes when a pair was perched close together. Although we did not collect adequate data to verify this, Selander (1964) measured multiple specimens of the Costa Rican *capistratus* subspecies of the Rufous-naped Wren and found that males were larger than females across all body regions measured. This is consistent with our own ringing records (unpublished data).

Typical of most birds, diurnal variation in Rufous-naped Wren song output is consistent with the production of a dawn chorus, both in terms of tonal solos and two-tonal duets. The dawn chorus in many bird species is thought to play several roles which are thought to be best achieved at dawn (reviewed in Staicer et al. 1996): mate attraction (e.g. McNamara et al. 1987), guarding paternity (e.g. Welling et al. 1995), or territorial defence (e.g. Kacelnik and Krebs 1983). Because Rufous-naped Wrens are insectivorous and dependent on suitable light conditions for foraging, the semi-darkness of dawn is likely a suboptimal foraging time for wrens. It is therefore possible that dawn singing occurs as an alternative behaviour (Kacelnik and Krebs 1983).

Staicer et al. (1996) noted that diel variation in song production in tropical species has not been studied in detail. In the present study, both solo and duet song output peak at dawn, demonstrating that females as well as males exhibit a dawn chorus effect. We found that chorus rates do not show a similar trend, and appear to be produced at a consistently low rate throughout the morning. This suggests that choruses may serve distinct functions from solos and duets, although we make this interpretation with caution due to the low sample size of chorusing groups in the present study.

We also assessed variation in individual vocal production across different breeding stages. We found that solo vocalisation rates were highest during the nestling stage when adults were bringing food to the nest. This is unlike many other species, which show a peak in male vocal activity during the female fertile period (e.g. Cuthill and Macdonald 1990; Pinxten and Eens 1998; Topp and Mennill 2008). In this study, we included the female fertile period in the nest building stage, which exhibited the lowest solo vocalisation rate of all breeding stages. Increased vocal production during the nestling stage may be important in allowing group members to maintain contact whilst foraging, and as a way to determine the location of partners around the nest to coordinate parental effort.

Duet rates did not vary significantly across breeding stages. If duets function as a signal of the pairs' mated status to deter conspecifics who might be attracted to solo songs (Sonnenschein and Reyer 1983; Levin 1996), we would predict that pairs should produce more duets during the nest building stage when females are fertile. Alternatively, males may duet with females as a way of preventing paternity loss (Komdeur et al. 1999; Topp and Mennill 2008), in which case, again, we would predict that duet rates should peak in the nest building stage when females are fertile. Neither of the above predictions were met in this study, suggesting that duets are not used as a mate-guard or paternity-guard for Rufous-naped Wrens. Instead, our data suggest that duets represent cooperation between males and females in maintaining contact (Thorpe 1963), or in joint territory defence (Hall 2004; Mennill 2006). Under both of these hypotheses we would predict duet rates to be relatively stable across breeding stages, and this prediction is not refuted by our data. We found that chorus rates also did not differ across breeding stages. Hypotheses for the function of chorusing are similar to those of duetting (Hale 2006), one of the most compelling of which is an inter-group signal in the collaborative maintenance of territories (Reyer and Schmidl 1988; Brown and Farabaugh 1991; Wingfield and Lewis 1993; Seddon 2002; Baker 2004; Hale 2006). This hypothesis predicts that chorus rates will be higher during nesting and fledgling stages when resource demand is highest. This prediction is not met in this study, although this may be due to a low sample size for the number of chorusing groups. Additionally, chorusing may function as a cooperative intra-group signal in maintaining group cohesion (Brown et al. 1988), or serve a conflicting role in establishing and maintaining social hierarchies with the group (Reyer and Schmidl 1988). Predictions generated by these hypotheses are unclear based on song rates obtained from passive recordings, such as those made in this study. More intensive sampling of family groups in manipulated contexts may provide deeper insight into temporal variation in chorusing behaviour.

The majority of Rufous-naped Wren tonal phrases are shared across territorial groups, and especially between groups occupying nearby territories. Communication between neighbouring territorial groups has been shown in other studies to occur most effectively when song types are shared (Kroodsma 2004), as this gives birds the ability to produce graded responses to territorial threats (Krebs et al. 1981). For example, song matching has been shown to be an honest signal of aggression (Vehrencamp 2001), so sharing song types allows a bird to match a neighbour's song and escalate a conflict or not to match it and de-escalate a conflict (Krebs et al. 1981). The ability to reply to a neighbour's song in a variety of different ways reduces unnecessary and costly physical conflict, and confers advantages either through mate attraction or territorial defence (Beecher et al. 2000). Increased phrase-sharing between neighbouring groups in the present study population is expected under this model. Interestingly, we often heard groups matching phrase types when counter-singing occurred between neighbouring groups. That nearby groups share more phrase types than distant groups raises questions concerning the mechanism of song learning in this species. Does the pattern of increased sharing between nearby birds arise because Rufous-naped Wrens learn songs from their parents and then disperse over short distances, by dispersing birds acquiring songs over an extended period that encompasses the duration of dispersal, or by birds learning many phrase types and undergoing selective attrition after dispersal (Marler and Peters 1982)? We witnessed fledglings producing subsong within weeks of leaving the nest, which we could often identify as phrase types possessed by their parents, and fledglings regularly attempted to match phrase types and duet with other adults in the group (personal observations). The fact that we found a highly significant quadratic relationship between phrase-sharing and territory separation distance raises the possibility of a dual dispersal strategy. We suggest the possibility that Rufous-naped Wrens exhibit sex-biased dispersal, whereby one sex remains on the natal territory to queue for breeding opportunities whilst the other sex disperses to fill vacant positions in nearby groups. This pattern of dispersal has been shown in the congeneric Stripe-backed Wren (*C. nuchalis*) (Zack and Rabenold 1989), where males remain and females disperse. Although our study provides a description of Rufous-naped Wren vocalisations, further research may verify if dispersal patterns are conserved by following marked individuals of known sex after fledging. We also found that, although the majority of phrases in any group's repertoire were shared with other groups, most phrases in the population were unique to specific groups. This result is highly suggestive of the existence of group-specific vocal signatures, which has been shown to be important in recognition of group membership in other species (Brown et al. 1988; Price 1999; Hopp et al. 2001; Radford 2005). We suggest that large phrase repertoires in Rufous-naped Wrens permit groups to effectively communicate with neighbours and mediate territoriality, and to maintain social bonds with the existence of group-specific vocal signatures.

The general observations of group social behaviour of Rufous-naped Wrens in this study support the observations of Joyce (1993), who reports cooperative breeding in approximately 10% of nests. Although we did not definitively document extra-pair birds assisting in incubation or nestling provisioning, we did find groups of three birds that regularly took part in joint territorial defence in 10% of territories, and our observations suggested extra-pair birds provisioned nestlings in those territories. This type of cooperative breeding, characterised by group territoriality and singular breeding, is similar to other congeners (reviewed in Brown 1987; Barker 1999).

The neotropical genus *Campylorhynchus* ranges widely from the southern USA to southern Amazonia (Brewer 2001). The singing styles of the majority of species in this genus have been described only anecdotally, with the exception of the Stripe-backed Wren (Wiley and Wiley 1977; Price 1998, 1999, 2003; Zack and Rabenold 1989) and the Cactus Wren (*C. brunneicapillus*; Anderson and Anderson 1973), which have received more thorough treatment. Within this genus, there are 13 currently recognised species: 12 species are known to produce female song, 12 species produce duets and 12 species are thought to breed cooperatively. We found that female Rufous-naped Wrens sing, pairs produce duets and groups produce choruses. The method of duetting in the Rufous-naped Wren—by simultaneously producing repeated, synchronised vocal contributions—is similar to that of the majority of *Campylorhynchus* wrens (reviewed in Barker 1999). These include the best studied members of the genus, the closely related Bicoloured Wren (*C. griseus*; Ridgely and Tudor 1989) and the more distantly related Stripe-backed Wren (Wiley and Wiley 1977). We also found that pair repertoire size was high when compared to other *Campylorhynchus* species. It has been suggested that social and environmental circumstances leading to intense competition for resources favours the evolution of large repertoires (Kroodsma 2004). This study suggests that competition for both mates and territories may be higher in this species than in its congeners.

We found that Rufous-naped Wrens sing choruses consisting of simultaneously produced vocal parts. Although Skutch (1935, 1940, 1960), does not mention chorusing in this species, Selander (1964) briefly states that “groups of three or more birds sing choruses in unison”. This style of chorusing is similar to that of some other cooperatively breeding birds. Laughing Kookaburras (*Dacelo novaeguineae*; Reyer and Schmidl 1988; Baker 2004) produce a ‘laugh’ chorus and Green Woodhoopoes (*Phoeniculus purpureus*; Radford 2003, 2005; Radford and Du Plessis 2004) produce a ‘rally’ chorus consisting of structurally similar vocal parts produced by multiple group members simultaneously. In contrast, the Plain-tailed Wren (*Thryothorus euophrys*; Mann et al. 2006), the Black-breasted Wood-Quail (*Odontophorus leucolaemus*; Hale 2006), and possibly the White-browed Sparrow Weaver (*Plocepasser mahali*; Wingfield and Lewis 1993) produce precise, highly synchronised antiphonal choruses. Intermediate to the above two chorus styles are those produced by the Subdesert Mesite (*Monias benschi*), which vary in the amount of overlap between component vocal parts, from precise alternation to complete overlap (Seddon 2002). Varying degrees of synchronisation and complexity of vocal choruses may reflect the stability and tenure of social units, as the investment required to learn complex vocal performances must be offset by the benefits to cooperative breeding. A more detailed comparative study involving individually marked birds that investigates the type of cooperative breeding system, the level of effort made by non-reproducing individuals, and the complexity of chorusing behaviour, may elucidate the relationship between vocal investment and fitness benefits in cooperatively breeding birds.

Zusammenfassung

Einzel-, Duett- und Chorgesänge: Lautverhalten des
Rotnacken-Zaunkönigs (*Campylorhynchus rufinucha*),
eines kooperativ brütenden neotropischen Singvogels

Die Lautkommunikation von im Duett und im Chor singenden Vögeln ist ein wachsendes Forschungsgebiet in der Vogelökologie; dennoch weiß man nach wie vor eher wenig über die zeitliche Variation und die Variation auf Populationsebene in diesen komplexen Lautsignalen. In dieser Studie beschreiben wir die akustische Struktur und zeitliche Variation in Einzel-, Duett- und Chorgesängen beim Rotnacken-Zaunkönig, einem kooperativ brütenden neotropischen Singvogel. Wir haben Lautaufzeichnungen von 19 Gruppen gesammelt, um sowohl 24-stündige und jahreszeitliche Variation in der Lautproduktion als auch die populationsweite gemeinsame Benutzung von Lautsignalen abzuschätzen. Wir fanden, dass die Vögel eine komplexe Reihe von Lautäußerungen produzieren, einschließlich tonaler, frequenzmodulierter Silben, gruppiert in Phrasen, sowie stereotyper, atonaler Laute. Gesänge wurden einzeln produziert oder zu Duetten und Chören zusammengefasst. Einzel- und Duettgesänge zeigten einen Morgenchor-Effekt. Die Frequenz der Einzelgesänge, nicht jedoch die von Duett- oder Chorgesängen variierte zwischen den Brutphasen. Der Großteil der Phrasen wurde von den Gruppen gemeinsam benutzt, und zwar signifikant häufiger von Gruppen in benachbarten Territorien. Wir schlagen vor, dass Chorgesänge ein wichtiger Indikator für die Gruppenidentität sein und eine Rolle in der Aufrechterhaltung von Gruppenterritorien spielen könnten, nicht jedoch in Beziehung zum Brutzyklus. Das Ausmaß, in dem Phrasen populationsweit geteilt werden, lässt entweder auf Kurzstrecken-Abwandern oder verzögertes Gesangslernen schließen. Dieser Artikel liefert die erste detaillierte Beschreibung des Lautverhaltens dieser Art und verbessert unser Verständnis von Gruppengesang in einer komplexen sozialen Umwelt.

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