Ethology

Song Perch Height in Rufous-and-White Wrens: Does Behaviour Enhance Effective Communication in a Tropical Forest?

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Abstract

Animal signals are distorted as they transmit through the environment, but many species have evolved strategies to minimize distortion of vocal signals. Song structure can change over evolutionary time, or signallers can modify their behaviour, to reduce attenuation and degradation in a specific habitat. We investigated signalling behaviour in rufous-and-white wrens, *Thyothorus rufalbus*, a Neotropical songbird in which both sexes sing, with a specific focus on perch height. Based on previous findings, including a detailed sound transmission study, we predicted that rufous-and-white wrens would choose elevated song perches in order to maximize the distance their songs travel, and that males and females would show different perch height choices. We observed 30 birds in 18 territories in a tropical forest in Costa Rica to determine the perch heights of birds when singing, producing non-song vocalizations, collecting nesting material, foraging, and engaging in other behaviours. We found that both activity and sex influenced perch height. Birds sang from a variety of heights, but the highest perches were used as song posts by males. Males minimized singing from within 1 m of the ground, and they generally perched higher than females, which may reflect sex differences in communication strategies. Both sexes foraged on or near the ground. The finding that rufous-and-white wrens vary their perch height with specific activities suggests that they modify their singing behaviour to enhance long-distance communication.

Introduction

Like all forms of animal communication, acoustic signals are distorted from their original structure as they transmit through the natural environment from one individual to another (Wiley & Richards 1982; Bradbury & Vehrencamp 1998; Slabbekoorn 2004). Animals have evolved multiple strategies to ensure that their messages are heard by intended receivers (Arak & Eiriksson 1992; Mathevon et al. 2004). For example, the acoustic adaptation hypothesis proposes that animals' vocalizations change over time to become structured in a way that reduces attenuation (decrease in signal strength) and degradation (distortion of temporal and amplitude patterns) in their particular environment (Rothstein & Fleischer 1987; Brown & Handford 2000; reviewed in Boncoraglio & Saino 2007; Barker 2008). Evidence from broad multi-species surveys as well as various focal species studies have shown that habitat does appear to shape the structure of vocalizations in many instances (e.g. Shy 1983; Wiley 1991; Brown et al. 1995; Slabbekoorn & Smith 2002; Kopuchian et al. 2004), although there is conflicting evidence (e.g. Lemon et al. 1981; Williams & Slater 1993; Daniel & Blumstein 1998; Hylton & Godard 2001; Bosch & De la Riva 2004).

Animals may also use behavioural techniques to overcome obstacles to long-distance communication by vocalizing from a position that enhances signal propagation. Sound transmission experiments have shown that some species can increase the propagation distance of their acoustic signals either by vocalizing from some distance above the ground (Waser & Brown 1986; Arak & Eiriksson 1992; Mathevon et al. 1996), or by vocalizing from within an open midstory rather than a foliated canopy of a forest (e.g. Blumenrath & Dabelsteen 2004). Such behaviours may be particularly important in light of habitat disturbance. If an animal's vocalizations are structured for ideal transmission properties through its historical habitat but not through a subsequently altered one, the animal's behaviour may adjust more quickly to habitat changes than signal structure can, enabling animals to continue to communicate at long distances despite having vocalizations that are not ideally matched to their habitat. Despite the potential communication benefits that signallers may derive from choosing perch heights that facilitate sound transmission, only a few studies have systematically explored perch height choice in free-living animals (e.g. Hunter 1980; Krams 2001; Møller et al. 2006).

We investigated perch height choice in rufous-and-white wrens, *Thryothorus rufalbus,* a Neotropical passerine bird in which males and females both sing solo songs and combine their songs to form duets. Duets in this species have been demonstrated to play a role in acoustic contact, joint territory defence, and mate guarding (Mennill & Vehrencamp 2005; Mennill 2006; Topp & Mennill 2008; Mennill & Vehrencamp 2008). Rufous-and-white wrens are insectivores and are known to spend much time close to the forest floor, rarely moving above the midstory of the tropical forest. They feed primarily on the ground (Farabaugh 1982; Ahumada 2001) and they build their nests out of long strings of plant material and fungus which they collect from the ground or peel from tree trunks, thick branches, and vines. Performing songs from ground level can pose communication difficulties because, in general, animal sounds produced from very close to the ground tend to experience more attenuation than those produced at greater heights. This is the result of destructive interference of reflections off the ground as well as greater attenuation through scattering if there is substantial vegetation at ground level (Wiley & Richards 1978; Martens 1980; Embleton 1996). In a recent song transmission study of rufous-and-white wrens (Barker et al. 2009), we found that the songs of both sexes suffer substantial transmission disadvantages when produced from a height of 1 m above the ground when compared with higher perches of 5 or 7 m.

In the present study, we evaluate perch height choice by rufous-and-white wrens engaged in singing and non-song activities. Our goal was to examine whether rufous-and-white wrens systematically vary their perch heights to enhance the transmission distance of their songs. Previous findings have shown that rufous-and-white wren territories are very large (Mennill & Vehrencamp 2008) and that song plays an important role in territory defence (Mennill 2006); therefore, songs used in territorial defence must travel substantial distances to neighbours. Based on these results and those from our song transmission study (Barker et al. 2009), we predicted that rufous-and-white wrens would sing from elevated song posts. We also predicted that males and females would demonstrate different perch height choices, since previous research has shown that the sexes exhibit some divergent singing behaviours, suggesting that songs may serve different functions for males and females (Mennill & Vehrencamp 2005; Mennill 2006; Mennill & Vehrencamp 2008; Topp & Mennill 2008). Finally, we predicted that activities other than singing would also influence perch height, given that they may involve particular resources (e.g. food, nesting material) which are present at specific heights.

Methods

Rufous-and-white wrens are resident Neotropical passerines ranging from Mexico to northern South America. Our study took place in Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica (10°40′N, 85°30′W). Within this site, rufous-and-white wrens inhabit areas of mature humid forest as well as regenerating late successional forest. During the breeding season, from 5 May to 13 August 2007, we collected behavioural observations of male and female rufous-and-white wrens in 18 territories. Birds were given unique combinations of three coloured leg bands and one numbered metal band. All 18 males were individually marked, and 14 of 17 females were individually marked; the remaining females were easily distinguished on the basis of their location and individually-distinctive song repertoires (Mennill & Vehrencamp 2005).

We conducted behavioural observations between approximately 0500 and 0630 h (CST) each morning by following birds around their territory for an extended time period. We recorded all vocalizations produced by both males and females during these observation sessions using digital recorders (Marantz PMD-660) and directional microphones (Sennheiser ME-66 or MKH-70). During recording sessions, we estimated perch heights at any point when we knew a bird's location, and then dictated into the microphone the estimated height, the bird's identity and its activity (see below). Over the course of the field season, we collected perch height observations from 17 males and 13 females over 68 recording sessions, with an average recording session length (± SE) of 72.14 ± 1.57 min (range: 29.17–109.50 min). We collected an average (± SE) of 6.46 ± 0.63 observations per recording session. Heights were estimated to a precision of 1 m, and flagging tape height markers around the study site acted as references to aid with height estimation. Like many wrens, rufous-and-white wrens are extremely difficult to visually observe because of their habit of skulking through thick underbrush (Brewer 2001). Consequently, our observation periods included extended periods of not being able to see the focal bird(s), punctuated by brief encounters where we could observe their behaviour. If we visually observed any individual for an extended period of time, we collected only one height observation per perch, and waited for the bird to move to a new perch before we collected another height observation. To further limit the possibility of inter-dependent perch height observations, we omitted observations that were collected within one minute of any other observation, except in instances when the activity was different between subsequent perches, or the height difference between the two perches was greater than 1 m. Because females sing much less frequently than males and also seemed to be more secretive, we collected many more observations of males (398 observations of 17 males) than females (41 observations of 13 females), on average collecting 23.4 ± 3.5 (range: 4–45) observations per male and 3.15 ± 0.8 (range: 1–11) observations per female. The final data set consisted of 439 perch height observations, where the mean (± SE) time difference between subsequent observations was 5.43 ± 0.35 min (range: 0.03–86.29 min; in the case of the minimum, there was a change in height of 6 m between subsequent perches).

When transcribing the data collected during observation sessions, we divided the activities of the wrens into five categories: (1) singing; (2) producing non-song vocalizations (including species-typical harsh chattering calls and low pitched hooting calls); (3) collecting nesting material; (4) foraging; and (5) other behaviours that were observed more rarely (including building the nest, feeding young, preening, perching prior to or after a flight and engaging in semi-aggressive chases). We analysed data for all observations (n = 439) in SPSS (SPSS Inc., Chicago, IL, USA) using a mixed model factorial ANOVA with sex (two levels) and activity (five levels) as fixed factors and perch height as the dependent variable. Territory was included as a random factor to control for variability among individuals and in habitat structure between territories; the mature forest in some territories was sometimes taller than the regenerating forest in other territories. Tukey HSD was used for *post hoc* analyses. All values are reported as mean ± SE, median. All tests are two-tailed with a significance threshold of $\alpha = 0.05$.

Results

We collected a total of 439 perch height observations of 30 rufous-and-white wrens engaged in a variety of song and non-song activities at a variety of perch heights. Mixed model factorial ANOVA showed a significant effect of activity ($F_{4,125} = 4.75$, $p = 0.001$) on perch height (Fig. 1). *Post hoc* comparisons revealed that birds perch significantly higher when they sing (mean ± SE: 4.91 ± 0.19 m, median: 4.50 m) than while foraging (0.73 ± 0.46 m, 0.00 m, $p < 0.001$) or engaging in other activities (2.15 ± 0.42 m, 1.00 m, $p < 0.001$), but not while collecting nesting material (4.72 ± 0.79 m, 3.00 m; $p = 0.99$). There was also a non-significant trend suggesting that birds performed songs at higher perches than non-song vocalizations (3.54 ± 0.50 m, 3.13 m; $p = 0.058$). The perches that birds foraged at were significantly lower than those used during non-song vocalizations ($p = 0.01$) and nest-material collection ($p < 0.001$), but not those used during other activities ($p = 0.46$; Fig. 1). There was overlap in the heights of perches used during non-song vocalizations, nest-material collecting and other activities. The biggest difference was between the heights of singing birds and the heights of foraging birds (Fig. 1).

Rufous-and-white wrens appeared to minimize singing from perches below 1 m (Fig. 2). Foraging birds, in contrast, were almost exclusively observed at 1 m or below (Fig. 2). All other activities showed a range of heights, including heights below 1 m and up to 13 m (Fig. 2).

Mixed model factorial ANOVA showed a significant effect of sex on perch height, such that males perched higher than females, on average (median for males: 4.00 m; females: 1.00 m; $F_{1,13} = 5.71$, $p = 0.03$). The interaction between activity and sex was also

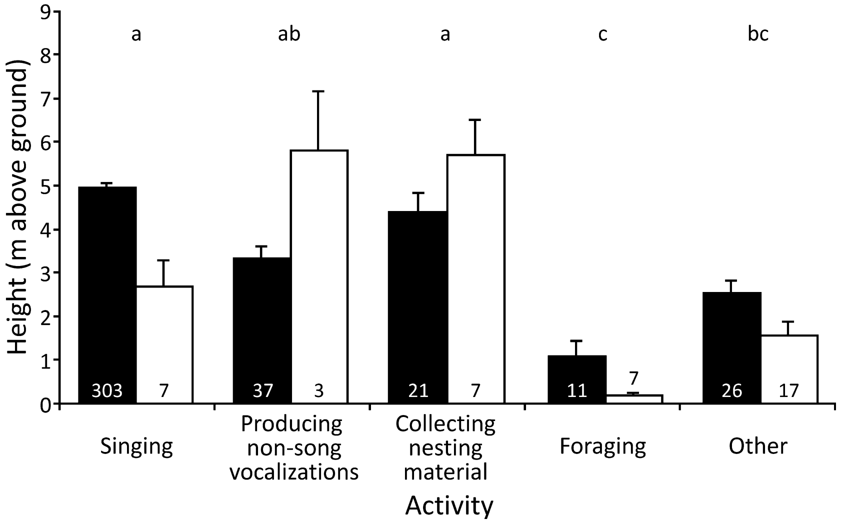

Fig. 1: Average perch heights for rufous-and-white wrens when engaging in different activities, demonstrating the significant main effect of activity and the interaction between activity and sex. Males are shown in black and females in white. Error bars represent standard error; the number of observations is indicated on each bar. Activities sharing the same letter are not significantly different.

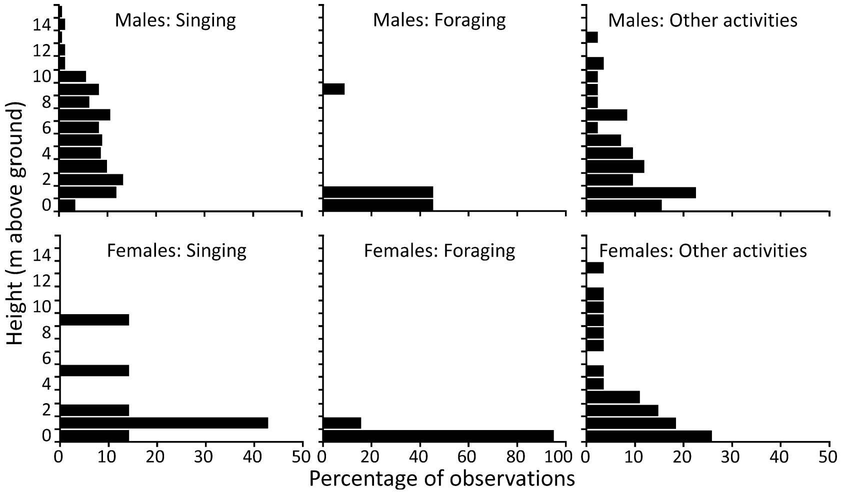

Fig. 2: Distribution of perch heights for all 439 observations of male and female rufous-and-white wrens during singing, foraging and all other activities (i.e. producing non-song vocalizations, collecting nesting material, and other less common activities).

significant ($F_{4,25} = 4.07$, $p = 0.01$), indicating that the perch height difference between males and females was not consistent across all activities (Fig. 1). The random factor, territory, did not have a significant influence on perch height overall ($p = 0.50$); however, the interaction between territory and sex was significant ($F_{9,87} = 3.63$, $p = 0.001$), indicating that the difference between males and females varied among territories.

Discussion

Rufous-and-white wrens sing from perches that range in height from ground level to 15 m, yet they appear to minimize singing from very close to the ground relative to how much time they spend near the ground engaged in other activities. The highest perches are used by males during singing. Our analyses corroborate previous findings that foraging in this species occurs on or near the ground (Ahumada 2001). All other measured activities occur at overlapping intermediate heights. Males seem to use higher perches than females overall, although the sex difference varied with activity and microhabitat conditions.

Many bird species use elevated song posts (e.g. Harrison 1977; Götmark & Post 1996), even when foraging is suboptimal at those heights (Greig-Smith 1983), so it stands to reason that birds must find some advantage in using elevated song posts. One possibility is that auditory and visual communication is enhanced by singing from particular perches (Hunter 1980; Beck & George 2000). Another is that perching higher may place birds in open or exposed sites, enabling them to better detect and then hide from predators, which may be particularly relevant if song attracts predators (Hunter 1980; Beck & George 2000; Krams 2001). Finally, it may be that birds use elevated song posts to enhance their ability to see and hear conspecifics (Holland et al. 1998; Mathevon et al. 2005; reviewed in Dabelsteen 2005).

Many song transmission experiments have demonstrated that excess attenuation of songs can be reduced by singing from elevated songs posts (e.g. Dabelsteen et al. 1993; Mathevon et al. 1996, 2005). Generally, singing from within 1 m of the ground causes increased excess attenuation (Marten et al. 1977), which can be avoided by choosing higher song posts. We found that although rufous-and-white wrens used a wide range of perch heights for singing, they sang very few songs from within 1 m of the ground compared to how much time they spent low to the ground engaged in other activities, which is consistent with our prediction that they would choose elevated song posts. Although some species have songs seemingly structured to match the environmental conditions of their preferred foraging and song post heights (Nemeth et al. 2001), the ground-level foraging height of rufous-and-white wrens may provide such a difficult acoustic environment that they must choose elevated song perches to enhance within-pair and extra-pair communication. One demonstrated function of duet song in rufous-and-white wrens is the maintenance of acoustic contact between pair members (Mennill & Vehrencamp 2008). As the average distance of separation between duetting partners is 19.2 m, and pairs have been measured performing duets from as far apart as 144.3 m (Mennill & Vehrencamp 2008), avoiding singing from heights below 1 m may ensure that their songs are heard by their breeding partners. Furthermore, playback studies have demonstrated that solo and duet songs function in territorial defence against conspecific rivals in this species (Mennill 2006). Since rufous-and-white wren territories are large, and the unoccupied space between territories is substantial (Mennill & Vehrencamp 2008), there may be strong pressure to reduce excess attenuation of their songs to better communicate with neighbours.

Proposed hypotheses for duetting behaviour in birds have revolved around cooperative behaviour between the sexes and also conflict between the sexes. Our results for rufous-and-white wrens suggest that males and females differ in the heights they perch at, and that this sex difference depends on activity. Males appear to use much higher perches for singing than females do (Fig. 1), but males and females forage and engage in other activities at similar heights. Males may benefit by singing from higher perches because this enhances opportunity for exchanging intrasexually-aggressive signals with rival males in adjacent territories. Females, in contrast, may sing from lower perch heights if this is satisfactory for maintaining acoustic contact with their breeding partner within the territory.

Vegetation structure can vary between habitats and microhabitats. Birds may not be choosing specific heights to perch at, but may instead be choosing particular layers in the forest. For example, transmission experiments have shown that songs experience substantial attenuation when they are broadcasted from within a foliage layer (Martens 1980; Wilczynski et al. 1989; Blumenrath & Dabelsteen 2004). Some birds may also choose exposed perches to enable visual components of their advertisement displays (e.g. Beck & George 2000). Conversely, some birds sing within more foliated areas, perhaps to conceal themselves from predators (e.g. Hunter 1980; Parker & Tillin 2006). The forest structure at our study site is quite variable, so if rufous-and-white wrens use song posts based on foliage density at a fine scale (either avoiding or preferring), we would expect a wide variety of perches used during singing, such as those shown in our study. Anecdotally, it often seemed that singing male rufous-and-white wrens chose perches in the highest branches of the large shrub layer or in the lower branches of the subcanopy. In both positions, birds were situated in a relatively open vegetation layer below the canopy, which may benefit song transmission (Bradbury & Vehrencamp 1998; Blumenrath & Dabelsteen 2004). One possible avenue for future research would be to evaluate perch height choice in relation to microhabitat variables to determine whether some variation in perch heights between individuals can be further explained by very fine scale vegetation features.

Song transmission is not the only consideration for choosing perches; other factors may include budgeting time between singing and other activities (collecting nest material, foraging, mate guarding, etc.), and the variation in song perch heights may reflect a tradeoff between the ideal locations for each of these activities. We found that most activities, other than those dependent on a resource that was available at particular heights (such as collecting nesting material), were performed at relatively low heights. Perhaps rufous-and-white wrens choose to perform most activities in the foliated understory because it offers concealment from predators. Predation risk may ultimately constrain the selective influence that communication has on birds by reducing song perches to lower heights than would be expected based solely on song propagation and sexual selection (e.g. Møller et al. 2006). Indeed, wrens (family Troglodytidae) are notorious for their secretive behaviour, and they have cryptic plumage colour (Brewer 2001), which may reflect a phylogenetic history heavily influenced by avoiding predation.

It has been suggested that elevated perches are even more effective as listening posts than song posts (e.g. Mathevon et al. 2005). The results of song transmission experiment (Barker et al. 2009) showed some evidence that rufous-and-white wrens achieve a slight receiver advantage of perching at 7 m when listening to male songs, or at 1 or 5 m when listening to female songs. Males, who appear to have a more active role in territorial defence (Mennill 2006; Mennill & Vehrencamp 2008), may choose high song posts so that they can listen for intruders and keep track of neighbours who may respond to their songs (Dabelsteen 2005). Males may also tend to perch higher than females to help prevent loss of paternity. One proposed function of rufous-and-white wren duets is mate guarding, where males show significantly higher duet responsiveness to female songs during the female fertile period, presumably as a way of advertising her mated status and minimizing partnership or paternity loss (Topp & Mennill 2008). Males may therefore use higher perches to ensure that they hear songs given by their females as well as any responses from nearby males.

It could be suggested that differential levels of foliation at various levels in the forest may have led to a bias in our ability to observe birds at different heights, particularly if birds were difficult to observe when singing from low perches or foraging at high perches. Although this species is secretive and challenging to observe, our experience over four months of data collection for this study taught us that we were capable of observing birds at various heights regardless of their activity. The distribution around the means for singing perch height (Fig. 2) indicates that we were capable of visualizing birds across a variety of perch heights when they sang. We found that birds were most difficult to observe while foraging because they were silent at this time, yet we observed them foraging primarily on the ground, which is among the more visually-occluded levels of the forest at our study site. If birds were singing from the ground, we would likely be able to observe them better than if they were foraging, since their songs would make them easier to localize. Like Hunter (1980), we interpret our results as revealing a true pattern of perch height usage.

In conclusion, rufous-and-white wrens sing from a variety of perch heights, but they occupy the highest perches when singing, they sing from significantly higher perches than their typical foraging height, and they appear to minimize singing from perches low to the ground. We conclude that rufous-and-white wrens modify their behaviour to enhance acoustic communication, in agreement with predictions made based on a detailed song transmission study (Barker et al. 2009). Males generally perch higher than females, and may use higher song perch heights because they have a more active role in territory defence, because male and female songs have different functions, or to prevent partnership or paternity loss.

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