

Bachelor and paired male rufous-and-white wrens use different singing strategies

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Abstract To attract a breeding partner, males may behave differently when they are bachelors compared to when they are paired. Comparisons between groups of paired males versus groups of unpaired males in temperate-breeding animals have revealed such differences in signalling behaviour. Few studies, however, have explored how individual males alter their signalling behaviour with changes in pairing status, and very few investigations have explored paired versus unpaired male behaviour in tropical animals. During a 5-year study in Costa Rica, we analysed changes in the singing behaviour of male rufous-and-white wrens (*Thryothorus rufalbus*) when they were paired and when they were bachelors. We compared three aspects of male vocal behaviour: gross differences in song output, variation in repertoire use and differences in song structure. Males as bachelors had significantly higher song output and switched song types less frequently. Contrary to our expectation, bachelors sang significantly fewer song types from their repertoire compared to when those same males had a breeding partner. Songs sung by bachelor males were higher in syllabic diversity and had broader-bandwidth terminal syllables than the songs those males sang only when paired. Within song types, the fine structure of songs remained consistent across pairing status. Our results demonstrate that males change their singing behaviour with

pairing status, delivering songs at a higher rate but with less variety when they are bachelors. Rufous-and-white wrens are renowned for their vocal duets, and we discuss the pattern of repertoire use in light of their duetting behaviour. These results enhance our understanding of how male behaviour varies with pairing status and the importance of vocal signalling behaviour in socially monogamous tropical animals.

Keywords Acoustic communication · Bachelor · Bird song · Vocal duetting · Mate attraction signals

Introduction

Males use a variety of elaborate signals and display behaviours to attract females. For socially monogamous animals, males that have not yet attracted a female at the start of the breeding period and males who lose their partner during the breeding period will have an especially strong motivation to attract a breeding partner. These bachelor males are likely to emphasise certain features about themselves to maximise mating opportunities. Males may reveal their quality through honest indicators such as conspicuous colouration and elaborate ornaments, which are costly to produce and therefore difficult to express falsely (Zahavi 1975). As a result, honest indicators of quality provide prospecting females with reliable signals to assess males (e.g. colouration in guppies, Evans et al. 2004; call frequency in frogs, Bosch et al. 2000; song output in chickadees, Otter et al. 1997).

Song plays an important role in mate attraction for birds (Catchpole and Slater 2008), and therefore bachelor male songbirds are expected to exhibit different singing behaviour than paired males. Many studies have examined

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differences in singing behaviour of paired and bachelor males in temperate birds. Song rates differ between groups of paired males and bachelor males, where bachelor males generally have high song rates. This is true across many species of temperate birds, including great tits (*Parus major*; Krebs et al. 1981), European starlings (*Sturnus vulgaris*; Cuthill and Hindmarsh 1985), nightingales (*Luscinia megarhynchos*; Roth et al. 2009), Kirtland's warblers (*Dendroica kirtlandii*; Hayes et al. 1986) and black-capped chickadees (*Poecile atricapilla*; Otter and Ratcliffe 1993). Elevated song rates for bachelors may act as an honest indicator of male quality or territory quality (Vehrencamp 2000; Gil and Gahr 2002).

Bachelor and paired males also show differences in repertoire use. Across many bird species, males appear to advertise the size of their repertoire in an attempt to attract a mate. For example, male European starlings showcase their repertoire in the presence of females (Eens et al. 1993), and male song sparrows (*Melospiza melodia*) with larger repertoires have significantly higher pairing success when controlling for territory size (Reid et al. 2004). Across many species, males increase their song switching rate when presented with a female receiver stimulus (Vehrencamp 2000; although some wood warblers show a different pattern, e.g. Staicer et al. 2006). In general, bachelor males appear to display larger repertoires to increase their attractiveness to females and thereby increase their chances of pairing.

Unpaired males may emphasise songs that contain specific features that are attractive to females. In many species, certain songs are apparently attractive to females because they contain characteristics such as rapid trills and notes with wide bandwidths, which are thought to be costly to produce (reviewed in Podos and Nowicki 2005; Ballentine et al. 2004). Motor constraints have been associated with song complexity (e.g. Podos 1997), supporting the idea that some song features can only be produced by high-quality individuals. These features may be especially attractive to females looking for a high-quality mate. Finally, males may deliberately alter the fine-structural properties of their songs, for example by increasing the frequency of certain notes, to make themselves more appealing to females (e.g. Lambrechts 1997).

These patterns have been explored in temperate songbirds, but very little information exists on how individuals of tropical species change their behaviour with pairing status (but see Levin 1996). This study focuses on the singing behaviour of bachelor versus paired male rufous-and-white wrens (*Thryothorus rufalbus*), a non-migratory socially monogamous neotropical songbird where both sexes sing and often coordinate their songs in vocal duets (Mennill and Vehrencamp 2005, 2008). Male song output is dramatically higher than female song output in rufous-and-white wrens, as

it is for many other duetting wrens (e.g. Mann et al. 2003; Cuthbert and Mennill 2007; Valderrama et al. 2008), and the sexes show divergent seasonal patterns in singing behaviour (Topp and Mennill 2008). Rufous-and-white wrens have song repertoires which they sing with eventual variety, repeating a song type several times before switching to a new type (Mennill and Vehrencamp 2005). As a tropical species, rufous-and-white wrens offer a special opportunity for understanding the function of song in mate attraction in the tropics. As a duetting species, rufous-and-white wrens provide a chance to understand the function of solo vocalisations in a duetting animal.

To understand how vocal behaviour changes with pairing status, we compared the songs and singing behaviour of male rufous-and-white wrens when they were bachelors versus when they were paired. We compared the same males across changes in pairing status through analyses of singing behaviour, repertoire use and fine structure of songs. We predicted that bachelor males would have higher song output, that bachelors would emphasise their repertoire size by switching song types more frequently and that bachelors would emphasise songs with fine-structural properties which may be attractive to prospecting females such as broadband terminal syllable notes and syllabic diversity. Our goal was to determine how unpaired males alter their singing behaviour and song structure for mate attraction in rufous-and-white wrens.

Materials and methods

Field methods

Our study took place in mature humid forests and late-succession regrowth forests of Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica (10° 40' N, 85° 30' W). In five successive field seasons ranging from March to August, 2003 to 2007, we captured rufous-and-white wrens on their territories using mist-nets and gave each individual a unique combination of coloured leg bands. We distinguished males from females by body size dimorphism and differences in vocalisations (see Mennill and Vehrencamp 2005).

We considered a male rufous-and-white wren to be paired if we observed him affiliating, copulating, duetting and/or nest building with the same female throughout an hour-long observation session or recording session. We considered a male to be a bachelor in three different situations: (1) when a male had not been observed with a female or heard duetting with a female during an observation session of at least 1 h at the start of the field season (the vast majority of birds in our study population are paired at the start of the field season and are easily

recognised as such during a 1-h observation session); (2) when a male was known to have been divorced by his female (i.e. the female was observed affiliating, copulating, duetting and/or nest building with another male in the population); (3) when a male's partner was known to have died or had gone missing from the study population. Many years of experience working with this species in the field make us confident that these observation sessions allowed us to accurately detect a male's bachelor or paired status.

We recorded 16 males, both when they were bachelors and when they were paired, using focal recordings and automated recordings. For focal recordings, we followed each male throughout his territory and recorded his vocalisations using a directional microphone (Sennheiser MHK-70 or ME-67) and a solid-state digital recorder (Marantz PMD-660 or PMD-670). Focal recording sessions for each male were conducted in the early morning, when song output is high (Mennill and Vehrencamp 2005) and lasted from 1.0 to 4.0 h, usually from the bird's first song of the morning and throughout the dawn chorus period. Some males were also recorded with automated recording devices consisting of an omni-directional microphone (Sennheiser ME-62) and a solid-state digital recorder (Marantz PMD-670; see Hill et al. 2006 for details). We positioned the automated recorders in the centre of the male's territory during two 24-h recording periods. We analysed only the first 4 h of the morning from these 24-h recordings to maintain consistency with the timing of our focal recordings. On average, we recorded males for 1.8 ± 1.4 h when they were bachelors and for 3.8 ± 1.7 h when they were paired (average \pm SE).

Analyses of singing behaviour and song structure

We conducted three types of analysis. First, we conducted behavioural analyses of variation in male song output between bachelor and paired males, to test whether singing behaviour varies with male pairing status. Second, we conducted sound-spectrographic analyses of repertoire use by bachelor versus paired males, to test whether bachelors sing song types that have particular structural features that are different from the song types they sing as paired males. Third, we conducted sound-spectrographic analyses of the fine structure of individual song types that were recorded from males both when they were bachelors and paired, to test whether song structure varies in subtle ways across changes in pairing status.

To compare singing behaviour of bachelor versus paired males, we investigated three parameters: (1) *song output*, calculated as the number of songs a male sang divided by the length of the recording (in minutes); (2) *song switching frequency*, calculated as the number of times a male changed song type during a single recording session

divided by the total number of songs sung by the male within that recording; and (3) *evident repertoire size*, calculated as the total number of different song types a male was recorded singing as a paired male or as a bachelor male divided by the total number of songs recorded from the male. We calculated song output and song switching frequency for each individual recording and then calculated an average across all recordings for each male when he was recorded as a bachelor and when he was recorded as a paired male ($N=16$ males). After controlling each variable by the length of the recording or the total number of songs sung by the focal male, we treat these three variables as independent. Four males were excluded from our analyses of song output because their recordings were not stored as continuous audio files (each song was stored as an individual file, omitting the silent intervals between songs, allowing us to calculate only song switching frequency and evident repertoire size for these four males).

Rufous-and-white wrens are renowned for their vocal duets (Mennill and Vehrencamp 2005, 2008), and prior experience suggests that paired males often switch song types in the middle of a song bout when their partner contributes a song to produce a duet. To test whether song-type switching and duetting are related, we compared the proportion of times that a paired male changed his song type in order to contribute a song to a duet to the proportion of songs that each paired male sang as a duet. We also compared the frequency of song-type switches for bachelor males to the frequency of song-type switches within the solo songs of paired males, ignoring the switches in song type that occurred within duets for paired males.

To compare patterns of repertoire use by bachelor versus paired males, we measured all of the song types recorded from each bachelor and compared them to song types recorded when each male was paired. We were particularly interested in exploring the features of songs that were recorded from paired males but not from bachelors (see "Results"). We investigated four parameters: (1) *song length* (beginning of the first introductory syllable to the end of the terminal syllable); (2) *syllabic diversity* (number of different types of syllables per song); (3) *frequency of maximum amplitude (FMA) of the trill component of the song*; and (4) *bandwidth of the terminal syllable* (the difference in frequency between the maximum and minimum frequency of the terminal syllable). Rufous-and-white wren songs are all structured similarly with three main sections: an introductory phrase of one to six notes, a middle section comprised of three to 35 repeated trill notes and a terminal phrase comprised of usually one emphatic syllable (Mennill and Vehrencamp 2005). At least one of these three sections in rufous-and-white wren songs differ in each song type within each bird's repertoire, making different song types easily distinguishable by sound and

when visually represented as spectrograms. These four variables were chosen because they describe the three prominent sections of rufous-and-white wren song with the fewest variables possible (Mennill and Vehrencamp 2005). Fourteen males who exhibited different repertoire sizes as bachelors versus paired males were used in this analysis (two males exhibited their full repertoires both as bachelors and paired males and were excluded from this analysis).

To compare the fine-structural properties of songs recorded from males both when they were bachelors and when they were paired, we selected three examples of one song type that was recorded from each male both when he was a bachelor and a paired male. Whenever possible, we chose example songs recorded on different days. Otherwise, we chose songs that were at least ten songs apart. We measured the same four structural variables of these songs as in our analysis of repertoire use: (1) *song length*; (2) *syllabic diversity*; (3) *FMA of the trill*; and (4) *bandwidth of the terminal syllable*. Fifteen males for which we had high-quality recordings of three examples for one song type across both bachelor and paired status recordings were used in this analysis.

For all sound-spectrographic analyses, we isolated songs of interest and eliminated background noise by filtering the raw recordings with a high-pass frequency of 500 Hz and a low-pass frequency of 3,500 Hz using Audition (Adobe, San Jose, CA, USA). We then normalised songs to -1 dB using Audition. For our comparison of the song types recorded from males when they were bachelors versus the song types recorded from males when they were paired, we measured songs using the time and frequency cursors in Syrinx-PC (J. Burt, Seattle, WA, USA). Spectrograms were generated with a fast Fourier transform length of 1,024 points and viewed as a Blackman window, allowing a frequency resolution of 5 Hz and a temporal resolution of 0.003 s. For our comparison of song types recorded both from bachelors and paired males, we used the automatic parameter measurements tool in AviSoft SAS Lab Pro (R. Sprecht, Berlin, Germany). We set a threshold of -16 dB and a hold time of 10 s as the criteria for AviSoft to determine where each note began and ended. The automated parameter measurements collected through AviSoft allowed us to calculate song length, trill FMA and bandwidth of the terminal syllable without human bias, which was particularly important when comparing subtle differences in fine structure within song types across changes in pairing status.

Three of the 16 males were recorded first as a bachelor and later as a paired male; the remaining 13 males were recorded first as a paired male and later as a bachelor. For males that were recorded with different females over the 5-year study, we used recordings only from the male's first pairing. In most instances, males

were only bachelors for a short period of time in only one field season, and both their bachelor and paired recordings were collected within the same breeding season. One male was a bachelor in two different seasons, and we pooled his bachelor recordings from both years.

Statistical analysis

We used paired Student *t* tests to compare males' songs and singing behaviour when they were bachelors versus when they were paired. This method provides analyses that are robust to inter-individual differences in singing behaviour. Data for singing behaviour analyses were log-transformed. All results are reported as means \pm SE. All tests are two-tailed with a significance threshold of 0.05. All statistical analyses were conducted in JMP (v 6.0, SAS Institute, Cary, North Carolina).

Results

The singing behaviour of male rufous-and-white wrens changed with pairing status. Males sang at significantly higher song rates when they were bachelors compared to when they were paired (paired *t* test: $t_{11}=5.4$, $P=0.0002$; Fig. 1a). Males switched song types significantly less as bachelors than as paired males ($t_{15}=2.7$, $P=0.02$; Fig. 1b). Contrary to our expectation, bachelors exhibited a significantly smaller evident repertoire size than when these same males were paired ($t_{15}=3.5$, $P=0.003$; Fig. 1c).

For two of 16 males, all song types within their repertoire were recorded both during the period when they were bachelors and paired males. For the remaining 14 males, we compared the fine structure of the song types that each male sang as a bachelor (5.6 ± 0.5 song types per male) to the song types in his repertoire that he did not sing as a bachelor (4.9 ± 0.7 song types per male). The length of songs sung by bachelors did not differ significantly from the songs that those males sang only as paired males (paired *t* test: $t_{13}=0.8$, $P=0.46$; Fig. 2a), and song types sung by bachelors had a similar trill frequency to the song types that those males sang only when paired ($t_{13}=0.5$, $P=0.64$; Fig. 2b). However, song types sung by bachelors had significantly higher syllabic diversity than the song types that those males sang only as paired males ($t_{13}=2.5$, $P=0.02$; Fig. 2c). Song types sung by bachelors had significantly broader-bandwidth terminal syllables than the song types that those males sang only as paired males ($t_{13}=2.4$, $P=0.03$; Fig. 2d; Fig. 3).

By comparing song types that we recorded from males both when they were bachelors and when they were paired, we found that fine structure of a particular song type did not

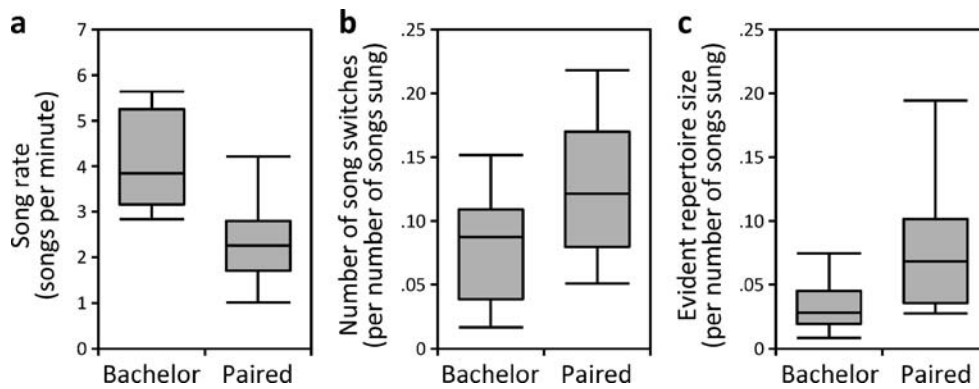


Fig. 1 Male rufous-and-white wrens exhibited different singing behaviours when they were bachelors compared to when they were paired. **a** Males sang at significantly higher rates as bachelors than when paired. **b** Males as bachelors had significantly fewer song switches (controlled for the number of songs sung) compared to when

they were paired. **c** Males as bachelors had significantly smaller evident repertoire sizes compared to when they were paired. *Box plots* show the range of data, with *horizontal lines* representing the 10th, 25th, 50th, 75th and 90th percentiles

vary with pairing status. Song length did not change with pairing status (bachelor 2.31 ± 0.05 s, paired 2.29 ± 0.05 s; paired t test: $t_{14}=0.4$, $P=0.68$, $N=15$ comparisons of one song type per male). The syllabic diversity of songs did not change with pairing status (bachelor 4.0 ± 0.02 , paired 4.0 ± 0.02 ; $t_{14}=0.6$, $P=0.58$). The frequency of the trill did not change with pairing status (bachelor 957 ± 4 Hz, paired 950 ± 4 Hz; $t_{14}=0.6$, $P=0.12$). The bandwidth of the terminal syllable did not change with pairing status (bachelor 768 ± 34 Hz; paired 740 ± 34 Hz; $t_{14}=0.8$, $P=0.42$).

Rufous-and-white wrens are duetting songbirds, and we assessed whether paired males' higher song switching frequency (above) was related to their duetting behaviour. For each male, we compared the proportion of song type switches that occurred during a duet to the proportion of all songs that were sung as a duet. On average, $14.9 \pm 1.5\%$ of song type switches occurred during a duet, which was significantly greater than the $9.0 \pm 1.5\%$ of all songs that

were sung as a duet (paired t test: $t_{15}=3.5$, $P=0.004$). We then compared the song switching frequency of bachelor males to the song switching frequency of paired males but ignored switches that occurred within the context of duets. We found that song switching frequency of bachelors ($8.2 \pm 4.0\%$ of songs were song type switches) was not significantly different from the song switching frequency within the solo songs of paired males ($12.2 \pm 2.0\%$ of solo songs were song type switches; $t_{15}=2.0$, $P=0.07$). These two analyses suggest that males change song types more often when they are paired compared to when they are bachelors primarily as a result of their duetting behaviour.

Discussion

Male rufous-and-white wrens altered their singing behaviour when they were bachelors compared to when

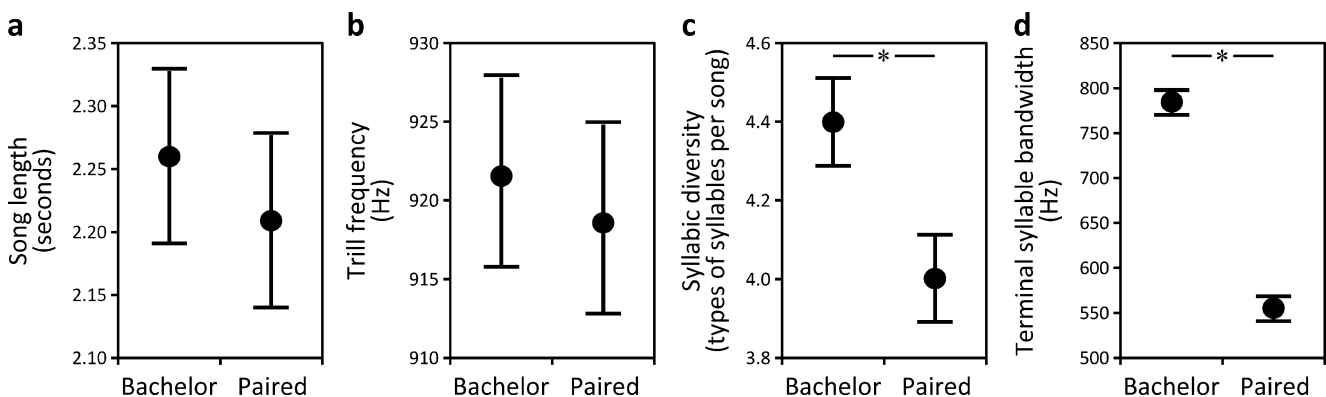


Fig. 2 Male rufous-and-white wrens sang songs of similar length (**a**) and with similar trill frequency (**b**) when they were bachelors compared to when they were paired. Bachelor males sang songs with

significantly higher syllabic diversity (**c**) and terminal syllable bandwidth (**d**) compared to when they were paired. *Dots* show mean values and *whiskers* show standard errors

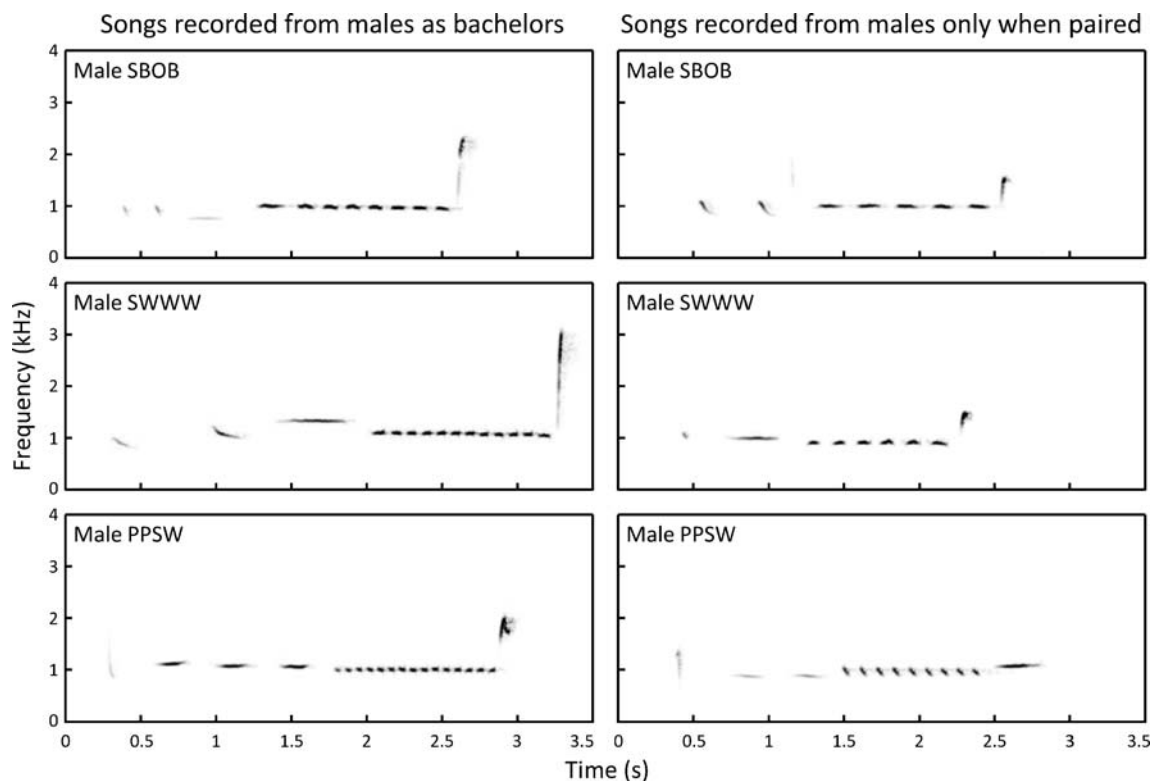


Fig. 3 Sound spectrograms of rufous-and-white wren songs recorded from three different males. Spectrograms show structural differences in song types emphasised by males when they were bachelors (*left*)

and when they were paired (*right*). Males as bachelors emphasised songs that were higher in syllabic diversity and that had wider terminal syllable bandwidths

they were paired, exhibiting significantly higher song rates, fewer switches in song type and smaller repertoire sizes as bachelors. An analysis of song types that we recorded from bachelors versus paired males revealed that bachelors preferentially sang songs with higher syllabic diversity and broader-bandwidth terminal syllables. A comparison of the structure of song types that were sung by males both when paired and unpaired showed no differences in fine-structural properties. These results demonstrate that male rufous-and-white wrens alter their singing behaviour with pairing status; bachelor males increase song output but sing fewer total song types, preferentially singing songs with higher syllabic complexity.

Singing behaviour

Bachelor male rufous-and-white wrens showed elevated song rates relative to when those same males were paired. This is consistent with previous research regarding song rate in a variety of bird species (e.g. Krebs et al. 1981; Otter and Ratcliffe 1993; Amrhein et al. 2004; Staicer et al. 2006) including the related bay wren *Thryothorus nigricapillus* (Levin 1996). Song rate has been shown to be an honest indicator of quality in many species (reviewed in Gil and

Gahr 2002). As such, rufous-and-white wren bachelors may actively indicate their quality to females through elevated song rate, thereby increasing their chance of attracting a breeding partner.

Rufous-and-white wren males switched song types less frequently when they were bachelors compared to when they were paired. This matches a pattern observed in other bird species, such as temperate American redstarts (*Setophaga ruticilla*) and tropical Adelaide's warblers (*Dendroica adelaidae*), where bachelor males sing more repeats of a given song type and therefore have a lower number of song-type switches than paired males (Staicer 1996; Staicer et al. 2006). That rufous-and-white wrens show a lower switching rate as bachelors than as paired males may be related to a number of factors. First, paired rufous-and-white wrens perform duets according to a duet code (*sensu* Logue 2006); males and females combine specific song types non-randomly so that certain combinations are far more common than expected by chance (Mennill and Vehrencamp 2005), a feature they share in common with other *Thryothorus* wrens (Mann et al. 2003; Logue 2006). As a result, paired male rufous-and-white wrens may change song types more frequently than bachelor males because they are motivated to reply with the song type that matches their partner's song type.

This behaviour would result in higher song switching rates for paired males, and our finding that song-type switching is associated with duets suggests that this is the case for rufous-and-white wrens. A second possibility is that song switching frequency is influenced by the dynamics of male–male countersinging interactions. In the closely related banded wren (*Thryothorus pleurostictus*), paired males use their repertoire to type match their opponent during male–male countersinging exchanges (Molles 2006). Rufous-and-white wrens, when paired, may engage in more male–male countersinging exchanges, in defence of both their territory and their partnership. The dynamics of these male–male exchanges may produce a higher switching rate among paired males. Our field observations suggest that the first explanation is more likely, since male–male countersinging exchanges are relatively uncommon in this species.

Bachelor rufous-and-white wrens displayed a significantly smaller evident repertoire size than when they were paired, which stands in contrast with our predictions based on the widely supported female preference for males with larger repertoires (e.g. Yasukawa et al. 1980; Searcy 1984; Eens et al. 1993; Hasselquist et al. 1996; Mountjoy and Lemon 1996). This observation, like the song switching patterns discussed above, may be related to the duetting behaviour of rufous-and-white wrens. Given that rufous-and-white wrens perform song types according to a duet code (Mennill and Vehrencamp 2005), males may have to use these additional songs in their repertoire specifically for duetting, to complete the duet code with their mate. Indeed, we found that paired males change song type to perform a duet more often than expected by chance. Therefore, paired males may exhibit a larger repertoire size because of the influence that duet codes have on song-type choice. Rather than repertoire size acting as a sexually selected male trait as it does in some temperate species (e.g. song sparrows; Reid et al. 2004), the evolution of repertoires in tropical birds such as the rufous-and-white wren may also be driven by duetting behaviour.

Repertoire use

We found that the smaller evident repertoire of bachelor rufous-and-white wrens tended to be comprised of song types that had greater syllabic diversity and broader-bandwidth terminal syllables. Songs with these particular characteristics may help to attract mates if they act as honest indicators of male quality. Complex songs with broad-bandwidth syllables are thought to be relatively difficult to produce and therefore may be more attractive to females than songs with narrow-bandwidth syllables (Podos and Nowicki 2005; but see

Kunc et al. 2007). Broad-bandwidth terminal syllables may have the additional function of increasing locatability of the singing bird, since broadband frequency-modulated syllables should be easier to locate than narrow-band pure-tone syllables (Klump and Shalter 1984; Catchpole and Slater 2008). One further possibility is that rufous-and-white wrens choose to sing song types with broader-bandwidth terminal syllables simply because those are the syllables that they can produce with the highest amplitude (Mennill and Vehrencamp 2005); sound transmission distance may be more important to bachelor males than “sexy” songs. In all situations, rufous-and-white wrens appear to choose song types that facilitate attracting a mate.

Song structure

We found that male rufous-and-white wrens made little alteration to the fine structure of their songs when they were bachelors versus paired. This is likely explained by the fact that rufous-and-white wrens are thought to be close-ended learners, where songs are presumed to crystallise early in life (Beecher and Brenowitz 2005). The time frame for the critical learning period and song crystallisation in the rufous-and-white wren is not known, but based on research on other wrens (e.g. Bewick’s wren *Thryomanes bewickii* and the long-billed marsh wren *Cistothorus palustris*; Kroodsma 1999) we expect that rufous-and-white wrens reach this period of song crystallisation before establishing territories and attempting to attract mates. If adult rufous-and-white wrens no longer have the ability to alter the fine structure of their songs, we would expect similarity in song structure regardless of pairing status, as we observed.

Overall conclusions

We used three analyses to examine differences in the vocal behaviour of rufous-and-white wrens in relation to pairing status by comparing singing behaviour and song structure in the same males when they were bachelors versus when they were paired. Our results clearly demonstrate that males change their vocal behaviour with pairing status, delivering more syllabically complex and broader-bandwidth songs at a higher rate but with less song-type variety, as bachelors. Several of these observations correspond with expectations based on previous studies of how temperate male birds attract breeding partners. Our surprising observations regarding smaller repertoire sizes and lower song switching frequencies by bachelor males probably relates to this species’ duetting behaviour; in contrast to the widely supported function of song repertoires in temperate birds

as a trait that is important in female mate attraction (Searcy and Yasukawa 1996), in duetting birds the function and evolution of repertoires may be driven by the complexities of song-type use in the context of duets. These results enhance our understanding of how male behaviour varies with pairing status in a duetting song bird and shed new light on the functions of vocal signalling behaviour in the context of mate attraction in socially monogamous tropical animals.

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Ethical standards The authors' methods for this study complied with current rules and regulations within Canada and Costa Rica.

Conflicts of interest The authors declare that they have no conflict of interest.

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