PROCEEDINGS
OF
THE ROYAL
SOCIETY B

Proc. R. Soc. B (2006) **273**, 1907–1912
doi:10.1098/rspb.2006.3535

Vocal performance influences male receiver response in the banded wren

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In a variety of songbirds the production of trilled song elements is constrained by a performance tradeoff between how fast a bird can repeat trill units (trill rate) and the range of frequencies each unit can span (frequency bandwidth). High-performance trills serve as an assessment signal for females, but little is known about the signal value of vocal performance for male receivers. We investigated the relationship between trill rate and frequency bandwidth in banded wren (*Thryothorus pleurostictus*) songs. Trilled song elements showed the same performance tradeoff found in other passerines and individuals differed in performance of some trill types. We tested the hypothesis that males of this species assess each other based on trill performance with a two-speaker experiment, in which territory owners were presented with alternating renditions of the same song type manipulated to differ in trill rate. Subjects were significantly more likely to approach the faster trill stimulus first. However, subjects that received trill types closer to the performance limit spent less time close to the fast speaker. Our results show that male banded wrens discriminate and respond differently to songs based on their vocal performance. Thus, performance of physically challenging songs may be important in intra- as well as inter-sexual assessment.

Keywords: bird song; sexual selection; trill rate; *Thryothorus pleurostictus*; performance limit; acoustic playback

1. INTRODUCTION

Sexual selection acts on song structure and singing behaviour in birds through the mechanisms of mate attraction and territory defence (Catchpole & Slater 1995). While choosy females often appear to favour features such as song output, song complexity, local song structure and vocal performance, many of the well-studied features known to be assessed by males in vocal contests involve song-type selection signals such as type matching and switching or temporal patterns of singing such as overlapping (Vehrencamp 2000; Collins 2004; Searcy & Nowicki 2005). However, some evidence suggests that structural features may also be used by males in the assessment of rivals. For example, low-frequency song elements, harsh note structure and frequency jumps are associated with larger body size or better condition and may indicate fighting ability (Appleby & Redpath 1997; Galeotti *et al.* 1997; Galeotti 1998; ten Cate *et al.* 2002). Repetitive note production, often in the form of a trill, is associated with aggressive contexts and dominance in several species (Lambrechts & Dhondt 1986; Ritchison 1988; Leitao & Riebel 2003). Studies of trill structure demonstrate a tradeoff between how fast a bird can repeat trill units (trill rate) and the range of frequencies each unit can span (frequency bandwidth). In most species studied, the maximal values of frequency bandwidth tend to decrease with increasing trill rates. This tradeoff between trill rate and bandwidth defines a performance constraint on song production (Podos 1997). High-performance variants are believed to be more difficult to produce because they require precise coordination of vocal tract movements and air flow (Hartley & Suthers 1990; Westneat *et al.* 1993; Podos 1996; Hoese *et al.* 2000). Therefore, the production of physically challenging songs could reflect male quality during male–male conflicts (Suthers & Goller 1997; Gil & Gahr 2002). Males who perform songs near this limit could be perceived as a higher threat by male territorial owners. While it is known that females prefer trilled songs closer to the production limit (Draganoiu *et al.* 2002; Ballentine *et al.* 2004), no study has shown experimentally that male passerines discriminate between such variants.

We studied fine-scale variation in trill structure and its signal value to male receivers in the banded wren (*Thryothorus pleurostictus*). Male song types contain unique combinations of introductory notes, middle notes or syllables, a terminal trill, and a final flourish note (see figure 3*b* and Trillo & Vehrencamp 2005 for spectrograms of complete songs). The terminal trill is often the longest, loudest and most repetitive phrase. Males possess song repertoires of 20–25 distinctive types (Molles & Vehrencamp 1999), and trill repertoires of 15–20 types. The range of performance values each male uses in his trill repertoire makes the banded wren a good model species for this study. In addition, certain song types with extremely rapid, broadband trills tend to be used during close boundary encounters and trill structure can vary between males (A. Illes 2004, personal observation). Males signal different levels of aggressive motivation in other ways, including song-type matching, switching, song overlapping and varying short-term song-type diversity (Molles & Vehrencamp 1999, 2001; Hall *et al.* 2006; Molles in press). In different contexts, males also selectively use

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Received 18 January 2006
Accepted 28 February 2006

song types differing in duration, bandwidth and the presence of harsh notes (such as 'rattles', see figure 2), as well as trill structure (Trillo & Vehrencamp 2005).

We first examined the relationship between trill rate and frequency bandwidth and documented within- and between-male variation in these parameters. Employing a two-speaker playback experiment, we then presented each subject with alternating renditions of the same song type that differed in trill rate, allowing subjects to choose between a relatively fast or slow trill. Different males received different trill types of varying frequency bandwidths, allowing for a between-trial analysis of the combined effects of trill rate and frequency bandwidth. We predicted that males would respond more strongly to stimuli closer to the performance limit.

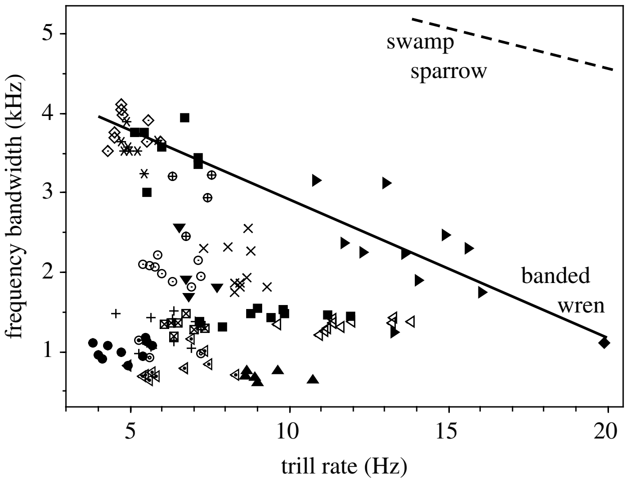

Figure 1. Graph of trill rate versus frequency bandwidth for 695 trills recorded from 13 individuals and including 16 trill types. Each symbol type represents a different trill type. The banded wren upper-bound limit is shown with a solid line and the swamp sparrow limit (Ballentine *et al.* 2004) with a dashed line.

2. MATERIAL AND METHODS

(a) *Study area, population and recording methods*

We conducted this study from 2003 to 2005 in Santa Rosa National Park in the Guanacaste Conservation Area of north-western Costa Rica. For details on habitat and study population see Molles & Vehrencamp (1999). All subjects were individually colour-banded. For acoustic analyses and experimental stimuli, we selected songs from recordings made throughout the 2003–2005 breeding seasons. Each male was recorded on three mornings for 1.5–2 h, starting with his dawn chorus and including about 1 h post-dawn chorus, with a Sennheiser ME67 directional microphone and Marantz PMD 690 digital solid-state recorder. Songs selected for analysis were from multiple singing bouts throughout the recording sessions, were sung a minimum of 5 min apart, and showed high signal-to-noise ratios.

(b) *Relationship between frequency bandwidth and trill rate*

To determine the relationship between trill rate and frequency bandwidth, we analysed 16 trill types from 13 males, for a total of 695 songs. We measured a mean of 53.5 exemplars of each trill type, and for each male, a mean of 5.5 exemplars per type. All acoustic analyses were conducted on spectrograms generated with XBAT 0.6.1 sound analysis software (H. Figueroa, www.xbat.org). Spectrogram settings were: FFT size = 1024, window size = 1, window function = Hanning and FFT overlap = 87.5%, giving a frequency resolution of 21.5 Hz and temporal resolution of 6 ms. To measure frequency bandwidth of each trill, we used the inter-percentile range measure from the energy distribution measurement plugin. This measurement method computes upper and lower frequencies encompassing a user-specified percentage of the total aggregate spectral energy of a trill note identified in a selection box (K. Cortopassi, see www.birds.cornell.edu/brp/research/algorithms). We specified a frequency range encompassing 99% of the note energy. We averaged the frequency bandwidth measure of three notes for each trill. Trill rate was measured as: (total number of trill notes − 1)/(trill duration − 1 note length). All rate and bandwidth values of the measured exemplars were averaged for each trill type for each bird.

From the resulting plot of frequency bandwidth versus trill rate (figure 1), we calculated an upper-bound regression following the method of Blackburn *et al.* (1992). For data with a triangular distribution pattern, this method bins trills by rate (here, 1 Hz bins), and the trill with the maximum frequency value is selected from each bin. The two lowest rate bins (3–5 Hz) were pooled to avoid the inclusion of submaximal events. A linear regression on this subset defines the performance limit for the tradeoff between trill rate and frequency bandwidth. The performance score for each experimental stimulus was calculated by determining the minimal orthogonal distance to this upper-bound regression line (Podos 1997), so that vocal performance scores increased in value the closer they were to the limit (figure 2).

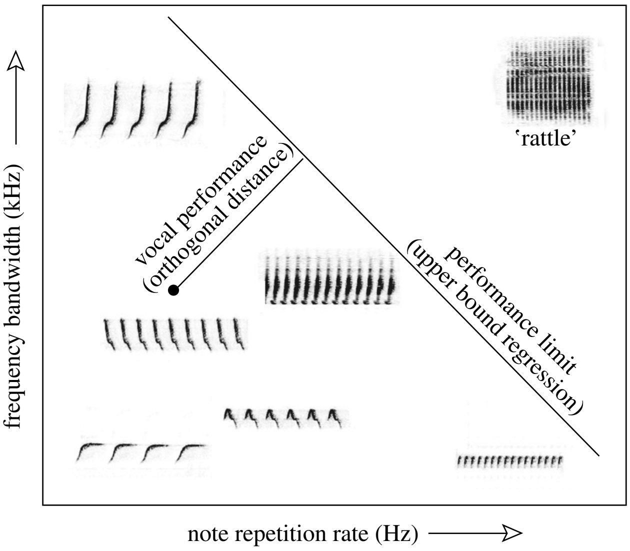

Figure 2. The relationship between a performance limit and a variety of banded wren trill types. Vocal performance is represented by the minimal orthogonal distance from the regression line. Rattles (upper right corner) are harsh, atonal, introductory syllable types known to be used in aggressive contexts.

To provide an indication of the consistency of trill performance within males, we selected two commonly occurring song types and measured trill rate, frequency bandwidth and vocal deviation for 10 song samples per male from 10 males. We computed repeatability estimates from model 2 ANOVA analyses (Lessells & Boag 1987).

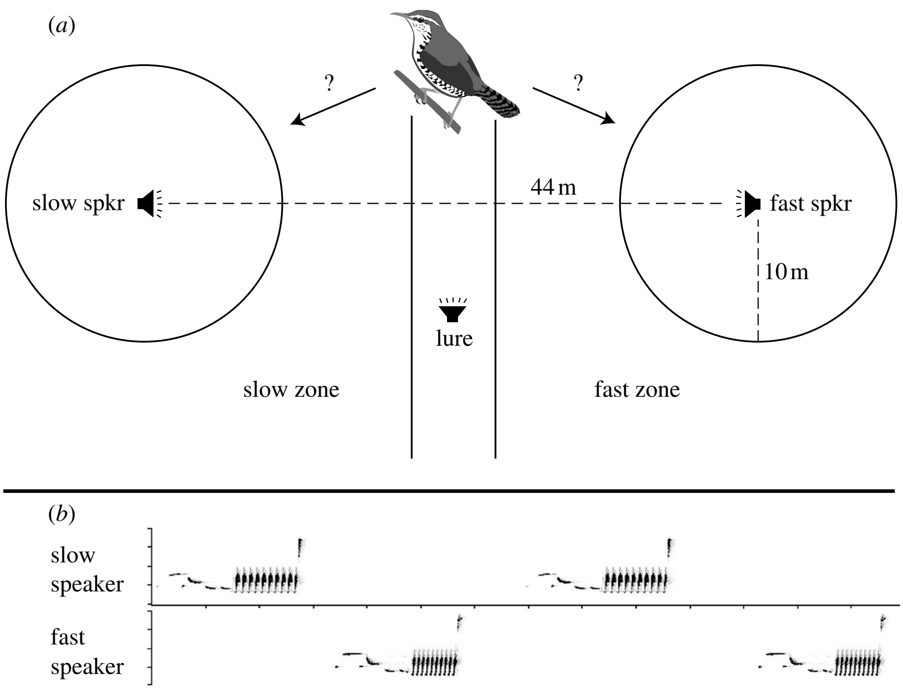

Figure 3. Playback set-up. (*a*) Schematic map of speaker placement and zones. Solid lines represent the central corridor and 10 m radii around experimental speakers. Dashed lines show distances. Experimental playback began once a subject entered the central corridor. (*b*) Spectrogram of a portion of a stimulus used for playback illustrating fast and slow trill versions of one song type. Time marked in 0.5 s increments, frequency in 2 kHz increments.

(c) *Response to experimental manipulation of trill performance*

We conducted playback experiments from 20 May to 9 Aug 2004, presenting 31 subjects with a choice between fast-trill and slow-trill experimental stimuli. Stimuli were created from high-quality recordings of songs from 25 males, including 19 song types and 12 trill types. Recordings from males known to be in their first breeding season were avoided. We used the cursor-delimited filter in the program SYRINX (John Burt, www.syrinxpc.com) to filter out noise. To build each stimulus pair, we selected the same song type from two different males. We manipulated each song to make a fast or slow version by copying one trill note and pasting it at constant intervals and selected notes that were similar in duration and frequency range for replicating. This manipulation eliminated between-note variation in rate, frequency range and amplitude, which might be additional performance indicators. Each song type pair had the same number of trill notes but different durations. At least five trills from different birds were measured to obtain natural slow and fast rates for each song type and all stimuli constructed fit within this range. To build the final two-channel files, we used Adobe AUDITION 1.0 to copy and paste fast and slow songs into separate channels and to amplify songs to the same peak amplitude.

To reduce the possibility that the subject would interpret the first stimulus type played as a leader and the second as a follower (see Naguib *et al.* 1999) we increased intersong intervals by a constant increment after each song. Two timing patterns were used, one with five alternating renditions of each treatment, with a total of 10 songs separated by intervals starting at and increasing by 1 s each and the second with seven alternating renditions of each treatment, with a total of 14 songs separated by intervals starting at and increasing by 0.5 s. Experimental stimuli averaged 86.2 s in duration (range = 69–114.3 s). The leading stimulus type (fast or slow) was randomised between trials.

Playback set-up consisted of two experimental speakers placed equidistant from a third speaker, which served as a lure (figure 3*a*). We surveyed each subject's territory to determine boundaries and nest placement, placing speakers well within the subject's territory boundaries (greater than 20 m) and equidistantly from known nests. The lure and the midpoint between the two experimental speakers formed the basis of a 6 m wide, 38 m long central corridor, which we flagged with coloured tape and considered equidistant from the experimental speakers. The playback computer was placed 12 m behind the lure speaker, within the central corridor. Depending on the topography and vegetation in each bird's territory, the experimental speaker pair was 40–44 m apart and 21.5–23.5 m from the lure. We placed speakers 1.5–2.0 m high and flagged a 10 m radius around each experimental speaker. The experimental area was divided into five zones: the central corridor was the central zone, the area on the same side of the corridor as the fast stimulus was the fast zone, the corresponding area on the opposite side was the slow zone and the 10 m radius circles were the 10 m fast and 10 m slow zones. The three speakers (Anchor Audio Mini-Vox PB-25) were connected to a Compaq Evo N800c laptop computer, and song files were played from within the program SYRINX. Experimental speakers were calibrated to natural banded wren song amplitudes (90 dB at 1 m, measured with a RadioShack Realistic 33–2050 sound pressure level metre).

During the pre-playback phase of the trial, the subject was interactively lured into the central zone with a standard set of banded wren call stimuli. Due to the interactive nature of the lure phase and variation in latencies of males to enter the corridor, each subject heard a different number, rate and arrangement of lure sounds. If the subject did not enter the central corridor within 15 min, we occasionally lured with song (non-neighbour song of a different type to the experimental stimulus). If the subject did not come to the centre corridor within 20 to 25 min, we aborted the trial and returned no sooner than 5 days later. The experimental phase of the trial began once a subject was sighted within the central corridor, whereupon we played the experimental stimulus. Each subject heard non-neighbour stimuli, with fast trill versions of a given song type from one speaker, and slow trill versions of that same song type from the other speaker. In three trials, the subject appeared in the corridor before a lure had been played and we proceeded directly to the experimental phase without playing a lure. During a 3 min post-playback phase we continued to monitor the bird's behaviour. Successful trials were executed on 31 males. Four trials were omitted from analyses of time spent close to the speakers due to interference from neighbours mid-way through the trial.

After the experimental stimuli began to play, we recorded the direction of the subject's first approach, defined as a flight of 1 m or more towards either the fast or slow speaker. Any movement of 1 m or more away from the speakers and within the corridor was scored as a retreat, and the next movement towards a speaker was scored as the first approach. We also recorded time spent in fast and slow zones, time spent in each 10 m radius and time spent in the central zone.

3. RESULTS

(a) *Relationship between frequency bandwidth and trill rate*

Frequency bandwidth shows more variation at lower than higher trill rates and a triangular distribution (figure 1), as expected when variation is limited by a tradeoff between these variables (Podos 1997). The resulting upper-bound regression has a significant negative slope (linear regression, $R^2=69.4$, $F_{1,12}=27.2$, $p=0.001$, $y=4.64-0.170x$). We used ANCOVA to compare our upper-bound regression to the equivalent regression for swamp sparrows reported by Ballentine *et al.* (2004). The slopes did not differ (trill rate × taxon interaction term effect, $F_{1,20}=1.56$, $p=0.227$), but elevation was significantly higher for the sparrow (taxon main effect, $F_{1,20}=181.7$, $p<0.0001$; figure 1).

An exhaustive analysis of within- and between-individual variation in trill characteristics was beyond the scope of this study because the large number of song and trill types in this species makes collecting adequate sample sizes difficult. However, for the two song types we tested, Model 2 ANOVA analyses of between- versus within-male variation were highly significant ($F_{9,88}=44.8$ and $F_{8,79}=61.6$, both $p<0.0001$). Repeatability of trill performance scores between multiple song renditions within males was 81.9% and 86.2% for the two types measured, respectively. For additional trill types, an indication of the between-male variation can be gleaned from the scatter of same-symbol points on the graph in figure 1.

(b) *Response to experimental manipulation of trill performance*

All subjects approached one or both of the experimental song stimuli and vocalized in response to playback. Nearly half of the birds (14 out of 31) made their first approach during the first song or prior to the second song. Of the remaining 17 birds that heard both stimuli before responding, 13 made their first move towards the fast trill song and 4 first approached the slow trill song (two-tailed binomial test, $p=0.049$; power, 58.5). Birds were not more likely to approach the leading speaker first (7 of 17, $p=0.63$).

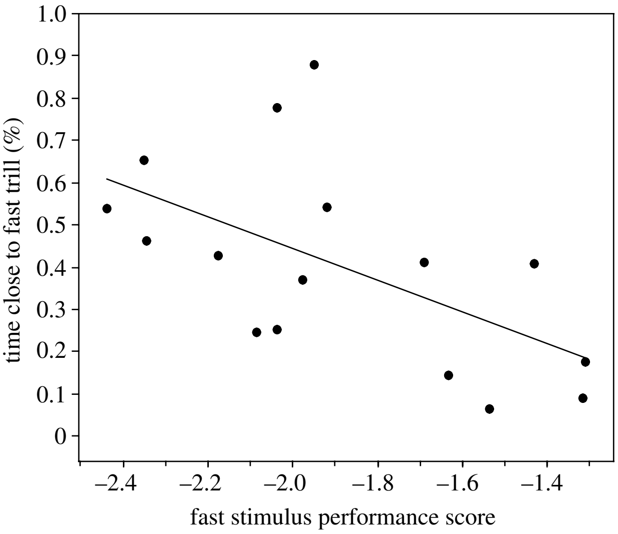

Figure 4. Relationship between vocal performance of fast stimulus and time spent within 10 m of the fast speaker.

Twenty-five of the 31 subjects approached within 10 m of a speaker. More than twice as many birds approached within 10 m of the fast stimulus first as approached within 10 m of the slow stimulus first (binomial test, fast=18, slow=7, $p=0.043$, power=60.5). Most of these males made an initial approach of a short flight, then stopped to sing, call aggressively or quietly search for the intruder(s), before approaching the speaker more closely. However, 4 of the 25 birds that closely approached a speaker flew directly to a 10 m radius on their first approach and may not have heard more than one song before approaching. The difference remains significant when these birds are eliminated from the analysis (fast=16, slow=5, $p=0.027$, power=68.9). For males approaching within 10 m of either stimulus, the proportion of time spent close to the fast versus slow speaker did not differ from random expectation (one-sample *t*-test, observed mean proportion=0.625, expected proportion=0.5, $n=21$, $p=0.182$). Five birds approached both speakers. Likewise, time spent in the fast versus slow zone was also not significantly different from random (observed mean proportion=0.548, $n=27$, $p=0.583$).

Subjects received song type stimuli that varied over a wide range of deviations from the upper-bound performance limit. We therefore examined time close responses among trials as a function of the performance score of the song stimuli played to each subject. The 16 males that entered the 10 m fast circle at some point during the trial spent less time there the higher the performance score of their stimulus trill (linear regression, $R^2=32.9$, $F_{1,14}=6.85$, $p=0.020$, $r=-0.574$; figure 4). For subjects approaching the slow speaker, this relationship was not significant (linear regression, $R^2=16.8$, $F_{1,8}=1.61$, $p=0.240$, $r=0.410$).

4. DISCUSSION

Our playback results clearly demonstrate that male banded wrens attend to the fine trill structure of simulated rival male songs. Although male birds attend to larger-scale differences in song structure (ten Cate *et al.* 2002;

Leitao & Riebel 2003), and fine-scale song structure may vary with context (Appleby & Redpath 1997; Galeotti *et al.* 1997; Galeotti 1998), discrimination between structural variants of agonistic signals at this scale has not been previously described for male passerines. Furthermore, banded wren (Troglodytidae) trills show a tradeoff between trill rate and frequency bandwidth similar to that found in emberizid passerines and the canary (Fringillidae) (Podos 1997; Draganoiu *et al.* 2002; Ballentine *et al.* 2004). The bounded nature of the trill rate—bandwidth relationship provides an unambiguous interpretation of responses to playback that is consistent with findings in other songbird species. Lastly, demonstration of the relationship in a family distantly related to those previously studied suggests that the tradeoff may be widespread within Passeriformes.

There are several possible reasons why the banded wren's upper-bound regression line is lower in elevation than the swamp sparrow line. Swamp sparrows and many other emberizids form their trills with short alternating low- and high-frequency pulses or clicks and the power spectrum averaged across the whole trill often exhibits a bimodal shape (Podos 1997). The high and low notes are probably produced from different sides of the syrinx. The overall frequency bandwidth can therefore be very broad while the note repetition rate is simultaneously very high. Banded wrens, on the other hand, form their trills as a continuous frequency-modulated note (figure 2), probably with a smooth transition from one side of the syrinx to the other, as in northern cardinals *Cardinalis cardinalis* (Suthers & Goller 1997). The power spectra of banded wren trills are usually unimodal. Such trill notes may be more difficult to produce at both a fast rate and with a very large bandwidth. Moreover, banded wren trills can be very loud, 90–95 dB at 1 m (Trillo & Vehrencamp 2005), whereas similarly sized emberizids produce songs 5–10 dB lower in amplitude (Brackenbury 1979). Thus, wren trill production could operate under stronger constraints with respect to the note rate—bandwidth tradeoff. Interestingly, banded wrens do produce a phrase type (the 'rattle', see figure 2) composed of repeated units at maximal rates and bandwidths greater than that of trills and the use of song types with rattles is correlated with aggressive contexts (Trillo & Vehrencamp 2005). However, the very high-performance value, lower amplitude and noisy atonality of rattles suggest that they are probably produced with pulsatile expiration (no minibreaths), as in the very rapid trills of cardinals and canaries (Suthers & Goller 1997). Therefore, rattles may be subject to different physiological constraints than are trills.

When faced with a choice, male banded wrens discriminated between high- and low-performance signals by approaching the fast trill first. Consistent with the interpretation of aggressive responses in other two-speaker experiments (Naguib *et al.* 1999; Leitao & Riebel 2003; Mennill & Ratcliffe 2004), this suggests that fast-trilled songs are more threatening than slow-trilled songs. On the other hand, between-trial analysis of trill performance as a graded signal showed that males subsequently spent less time close to the fast stimulus if it was a higher-performance type. This repulsive effect was not evident among males that closely approached the slow trill stimulus. Together these results highlight a recognized dilemma in the interpretation of responses of territorial male receivers to playback of threatening acoustic stimuli—should more threatening signals repel male receivers or incite approach and attack (Falls 1992; Searcy & Nowicki 2000; Collins 2004)? Like most playback experiments, ours measures and interprets the tendency of a *territory owner* to *approach* a simulated intruder. A more direct method of measuring a signal's territorial defence function would be to test the tendency of an *intruder* to *retreat* from, or be repelled by, a stimulus. Owing to the methodological difficulties of conducting the required speaker-replacement experiments (Searcy & Nowicki 2000), we could not do this, nor is it often done. However, in our study, the subsequent decrease in aggressive response by the receiver suggests that the highest performance signals posed a threat so extreme that they effectively repelled rivals, even territory owners. These results provide further insight into the adaptive function of male–male signals during on-territory playback experiments.

Both female and male songbirds respond to variation in trill performance (Draganoiu *et al.* 2002; Ballentine *et al.* 2004; and this study), and it seems likely that both inter- and intra-sexual selection act on passerine trill structure to create high-performance signals with dual functions. Male banded wrens differed in their performance of a given trill type, although we do not yet know whether such differences are consistent across all song types and reflect individual singing ability. Our study describes the signal value of high-performance trills for males and an adaptive function in aggressive encounters. The mechanism that maintains signal honesty remains to be determined. Additional study of performance costs could aid the search for correlates of male quality and place trill structure into a cost-based signal classification scheme as an index or handicap signal (Vehrencamp 2000).

We thank Kate Neville and Elizabeth Ochoa for assistance with field trials and ACG staff for facilitating our long-term project at Santa Rosa. Feedback from Jesse Ellis and two anonymous reviewers greatly improved the manuscript. Barbara Ballentine and Jeff Podos kindly provided their upper-bound regression data and Harold Figueroa and Kathy Cortopassi provided valuable assistance with sound analysis. This project was funded by NIH grant R01MH060461.

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