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Animal behaviour

Swamp sparrows modulate vocal performance in an aggressive context

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Vocal performance refers to the proficiency with which a bird sings songs that are challenging to produce, and can be measured in simple trilled songs by their deviation from an upper bound regression of frequency bandwidth on trill rate. Here, we show that male swamp sparrows (*Melospiza georgiana*) increase the vocal performance of individual song types in aggressive contexts by increasing both the trill rate and frequency bandwidth. These results are the first to demonstrate flexible modulation by songbirds of this aspect of vocal performance and are consistent with this signal feature having a role in aggressive communication.

Keywords: bird song; aggressive signalling; vocal performance

1. INTRODUCTION

In aggressive signalling, receivers should be interested in two attributes of opponents: aggressiveness and fighting ability. Aggressiveness may be encoded in 'strategic signals', which all signallers are able to produce (Hurd & Enquist 2005); a likely example is the low amplitude 'soft song' produced by some songbirds (Searcy *et al.* 2006). Fighting ability may be conveyed by 'index signals', signals whose performance is constrained by physical ability (Hurd & Enquist 2005). Likely examples include dominant frequency of calls in frogs and toads (Davies & Halliday 1978; Wagner 1989), lowest peak frequency of songs in oropendolas (Price *et al.* 2006) and formant dispersion of roars in red deer (*Cervus elaphus*) (Reby & McComb 2003; Reby *et al.* 2005).

For songbirds, vocal performance refers to the ability to produce songs that are challenging to sing owing to constraints on vocal production mechanisms. A particularly well-understood example involves the ability of birds to produce repeated, or 'trilled', syllables both rapidly and with a broad frequency bandwidth (Podos & Nowicki 2004). The mechanics of vocal production are expected to produce a trade-off between the trill rate and bandwidth, such that the two measures cannot be maximized simultaneously (Westneat *et al.* 1993). Podos (1997) demonstrated that, as predicted, the simple trilled songs of sparrows (Emberizidae) exhibit a triangular distribution between the frequency bandwidth and trill rate, with maximum observed bandwidth negatively related to the trill rate. Given such a distribution, vocal performance can be estimated by the deviation from the upper bound regression of bandwidth on the trill rate, with smaller deviations indicating higher performance (Podos 1997). The songs of swamp sparrows (*Melospiza georgiana*) exhibit this negative upper bound relationship, and female swamp sparrows prefer songs with low deviations from the upper bound (Ballentine *et al.* 2004).

Because females prefer songs of high vocal performance, it seems reasonable that males might also use this parameter to assess aggressive opponents. This hypothesis has been tested in banded wrens (*Pheugopedius pleurostictus*) (Illes *et al.* 2006) and red-winged blackbirds (*Agelaius phoeniceus*) (Cramer & Price 2007) using territorial playback. In both species, males respond differentially to songs depending on their deviation from upper bound regressions of bandwidth on trill rate. The two species differ, however, in whether they respond more strongly to low deviation songs (Illes *et al.* 2006) or to high deviation songs (Cramer & Price 2007), making it difficult to conclude which songs represent higher quality males.

This study tests the hypothesis that vocal performance functions in male–male communication using a different approach: by examining whether male swamp sparrows modify their vocal performance in aggressive contexts. We examined two mechanisms by which performance could be manipulated. First, in aggressive situations males might choose to sing the highest vocal performance song types in their repertoires. Second, males might modulate the vocal performance of individual song types when producing them in aggressive contexts, by increasing the trill rate and/or frequency bandwidth.

2. MATERIAL AND METHODS

Playback experiments were conducted in a population of swamp sparrows in Crawford County, PA, USA between 17 May and 22 June 2007.

To test the prediction that males preferentially sing high performance song types in aggressive signalling, we compared the predominant song types sung during aggressive and control trials. During aggressive trials, we simulated an intrusion on a subject's territory using playback of conspecific song from just within his boundaries; during control trials, we played songs of white-crowned sparrows (*Zonotrichia leucophrys*), which do not breed in this area. Subjects received control and aggressive treatments on consecutive days (except for two individuals whose trials were separated by 3 and 6 days). Treatments were assigned in alternating random order. Playbacks consisted of 5 min of song at a rate of four songs/minute. Playback songs were recorded from male swamp sparrows captured in 2005–2006 in the study population and from free-living white-crowned sparrows on San Juan Island, WA in 2004. Twenty song exemplars of each stimulus type were used, with each exemplar played to two males. Stimuli were played from a directional speaker on the edge of the subject's territory facing in. The speaker was a Nagra DSM loudspeaker in an open box lined with sound attenuating foam. Playback stimuli were 82–85 dB 1 m in front of the speaker, and were 24–26 dB lower 1 m behind the speaker.

If the focal male did not sing during the first 5 min, playback was repeated up to three times (maximum of 20 min). During aggressive trials, subjects received a mean of 7.5 min of playback (range 5–15) and during control trials a mean of 7.75 min (range 5–20). If no song was recorded from the focal male in 20 min, the trial was abandoned. Songs of focal males were recorded using a Marantz PMD 670 recorder, a RadioShack 33-3001 microphone and a Sony 33 parabolic reflector.

Songs were analysed using Signal v. 4.0 software (Engineering Design, Belmont, MA, USA) following the methods of Ballentine *et al.* (2004) (256 point transform length, 5.8 ms time resolution, 172.3 Hz frequency resolution). We approached the choice of song

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type in two ways. For the song type sung most often in a trial (the 'predominant song'), we measured the trill rate and the frequency bandwidth for the first 10 exemplars of sufficient quality for analysis. The trill rate was measured as syllables s^{-1}, averaged across the entire song. The frequency bandwidth was measured as the difference between the maximum and minimum frequencies at −36 dB relative to the peak amplitude frequency. In cases where fewer than 10 exemplars were available, we measured as many as possible (mean=5.7; range=1–10). The vocal performance was calculated as the orthogonal distance from the upper-bound regression line of frequency bandwidth on the trill rate, calculated for the Emberizidae by Podos (1997). The vocal performance was averaged across exemplars for statistical analysis. Secondly, we measured the average vocal performance for every song type in a male's repertoire, using all song types recorded during playbacks and during additional recording of males singing undisturbed. Songs were ranked within the repertoire according to their vocal performance, and a Wilcoxon signed-ranks test was used to determine whether the rank of songs used in the aggressive context differed from the mean rank of the remaining songs in the repertoire.

Modulation of the vocal performance during aggressive trials might change vocal performance rank of a song. To control for this possibility, we did a second analysis of choice of song type, concentrating on males for which we had recordings from a neutral context of the predominant song type given in the aggressive context. To increase the sample of such males, we used additional recordings made while males were singing undisturbed without any simulated or natural encounters. We then compared the vocal performance of the predominant aggressive song type when given in neutral contexts to the performance of other song types given in neutral contexts.

To test for modulation of vocal performance, we concentrated on males that gave the same song type in the aggressive context and a neutral context. We again measured either the first 10 exemplars or as many as were recorded (mean=7.8; range=2–10). The vocal performance was measured as above, and averaged for each trial across the 10 (or fewer) exemplars. A paired *t*-test was used to compare the vocal performance between contexts.

3. RESULTS

(a) *Song choice*

Of the 40 males tested, 31 used only one song type during the aggressive trial, seven males used two and two males used three. In all cases, one song type represented over 50 per cent of the songs sung and was designated the predominant song type.

We found no difference in the vocal performance of the predominant song types used in aggressive and in control trials ($t=-0.28$, $p=0.78$). When we analysed the trill rate and frequency bandwidth independently, we again found no significant difference between the predominant aggressive and control songs (trill rate: $t=-0.09$, $p=0.93$; frequency bandwidth: $t=0.47$, $p=0.64$). Comparison of the rank of songs sung in the aggressive context (1.90±0.88) to the average rank of remaining songs in the repertoire (2.09±0.50) also showed no difference ($z=1.09$, $p=0.28$).

For 23 males, we recorded the predominant song type used in the aggressive trial in a neutral context as well. The performance of these song types in neutral contexts did not differ from the average performance of the rest of the repertoire ($t=0.016$, $p=0.99$), nor did the performance rank of these song types differ from the average rank of the rest of the repertoire ($z=1.44$, $p=0.15$).

Given a mean repertoire of 3.1 songs in our study population (Ballentine *et al.* 2004), by chance the predominant song would be the same in the aggressive and the control trials 1/3.1 or 32 per cent of the time. In our sample, 8 out of 40 males (25%) used the same song type as their predominant song in both trials. The difference from random was not significant ($\chi^2=2.65$, $p=0.10$).

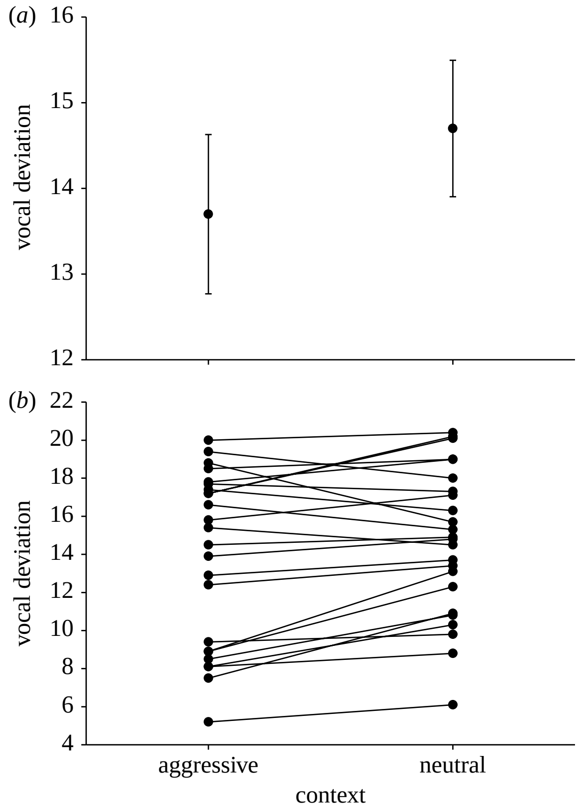

Figure 1. Vocal performance for cases in which the same song type was recorded in both the aggressive trials and neutral contexts. (*a*) Means (±s.e.) of deviation from the upper bound regression of bandwidth on the trill rate. (*b*) Vocal deviations for individual males recorded in both contexts. Note that low deviation equals high performance.

(b) *Modulation of vocal performance*

In the case of song types shared between the aggressive and neutral contexts, males increased both the trill rate (mean±s.d.: aggressive=7.10±2.68 syllables s^{-1}, neutral=6.94±2.61; $t=4.67$, $p<0.001$) and the frequency bandwidth (aggressive=4960.9±444.4 Hz, neutral=4870.4±359.6; $t=2.08$, $p=0.05$) during the aggressive trial. This resulted in significantly higher vocal performance (smaller deviation) during the aggressive trial (mean±s.d.: aggressive=13.75±4.55, neutral=14.66±3.90; $t=-2.51$, $p=0.02$, figure 1).

4. DISCUSSION

The results confirm our second prediction: males modulate the performance of a given song type in aggressive interactions in the direction that should increase their perceived quality, consistent with the hypothesis that vocal performance functions in male–male interactions. To our knowledge, this is the first demonstration that songbirds modulate deviation from the trill rate/frequency bandwidth upper bound in a functional context.

We have interpreted vocal performance as an index signal. An index is defined as 'a signal whose intensity is causally related to the quality being signalled and

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which cannot be faked' (Maynard Smith & Harper 2003, p. 15); thus, modulation of vocal performance might seem to counter the classification of this trait as an index signal. Other well-established index signals, however, are modulated in a parallel fashion (Searcy & Nowicki 2005). When interacting with other males, some frogs lower the dominant frequencies of their calls (Wagner 1989; Bee & Perrill 1996), Montezuma oropendolas (*Psarocolius montezuma*) lower the lowest peak frequencies of their songs (Price *et al.* 2006) and red deer minimize the formant dispersion of their roars (Reby & McComb 2003). These and other examples suggest a general rule that index signals are physically constrained only within limits, with signallers modulating such signals in an adaptive fashion within those limits.

We found no tendency of males to prefer using high performance song types in aggressive contexts. Cramer & Price (2007) found a similar result in red-winged blackbirds. Given that males modulate the performance of individual song types, we do not think this means that males are not trying to maximize their vocal performance during aggressive signalling. Instead, this result may indicate that vocal deviation fails to capture all aspects of vocal performance, or that there are other reasons why birds choose to sing particular song types.

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