



## Song type matching and vocal performance in territorial signalling by male swamp sparrows

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In songbird species with repertoires of multiple songs, individuals in territorial interactions can engage in song type matching, in which one bird responds to another using the same song type. Song type matching is thought to be associated with aggressive intent, although empirical support for this hypothesis is mixed. Here we test the alternative hypothesis that males selectively use song type matching, depending on singing ability, to optimize their relative performance in a communication network. We recorded the responses of male swamp sparrows, *Melospiza georgiana*, to playback trials in which they heard stimulus songs of higher or lower vocal performance relative to their own version of those songs. We predicted that, if males use song type matching to influence the perceptions of conspecifics outside the interacting dyad, males would (1) match stimulus songs that they themselves could perform better and (2) respond with a different song type to stimulus songs that they could not perform as well. We found that males song-type matched more often than expected by chance across trials, but contrary to our expectations, they were at least as likely to match to playback of higher-performance songs as to playback of lower-performance songs. As in previous studies, we also found that males sang with higher vocal performance in response to playback than when singing spontaneously, and that they did not preferentially respond with their highest-performance song type as a countersinging strategy. Our results support the idea that in swamp sparrows, song type matching functions primarily within the dyad rather than to broadcast superior performance ability to other conspecifics in the communication network.

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Songbirds use song as a signal in territorial interactions. Even when these interactions directly involve only two birds, the songs of each bird may be heard not only by the opponent but also by other conspecifics in the area. Central to the concept of eavesdropping within communication networks is the idea that eavesdroppers can gain more information from hearing an interaction between two males than from hearing each male separately (McGregor & Dabelsteen, 1996). If eavesdropping ultimately affects the fitness of the signallers, then an individual may make signalling decisions that account for both the opponent and a wider audience (Logue & Forstmeier, 2008). One of these signalling decisions, in species with repertoires of multiple song types, is which song to sing next. Does a bird merely select songs from its repertoire at random, or does it choose particular songs, and if the latter, what drives this choice? Here we investigate the interaction of two

phenomena that might affect the choice of songs in aggressive vocal interactions: vocal performance and song type matching.

One factor that can influence a male's choice of song is the song type sung by the intruder itself. When two birds share one or more types, song type matching is a possible outcome. First proposed to direct a signal to a particular rival (Brémond, 1968, cited in Armstrong, 1973), song type matching was then described as a signal of threat to new rivals. Male great tits, *Parus major*, were observed to decrease matching after habituation to playback (Krebs, Ashcroft, & Orsdol, 1981) and match more often to unfamiliar males than to neighbours (Falls, Krebs, & McGregor, 1982). These observations have been repeated in other species as well (e.g. song sparrows, *Melospiza melodia*: Beecher, Stoddard, Campbell, & Horning, 1996; western meadowlarks, *Sturnella neglecta*: Falls, 1985). Further studies linking song type matching with conflict escalation between neighbours (Burt, Campbell, & Beecher, 2001) and with indirect measures of aggression (Vehrencamp, 2001) also suggested that matching may function as a signal of threat.

Song type matching does not always predict physical attack, however. Simulations of territorial intrusions using song playback

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and a taxidermy mount found that song type matching does not predict whether a male will attack the mount in song sparrows (Searcy, Anderson, & Nowicki, 2006) or in swamp sparrows, *Melospiza georgiana* (Ballentine, Searcy, & Nowicki, 2008). Furthermore, while song type matching was found to predict escalated signalling and subsequent attack in a western population of song sparrows (Akçay, Tom, Campbell, & Beecher, 2013), this result was not replicated in an eastern population (Searcy, DuBois, Rivera-Cáceres, & Nowicki, 2013). These results indicate that we still do not know the extent to which song type matching functions as a signal of aggression or escalation in these species.

Another potential function of song type matching, not mutually exclusive with aggressive signalling, is to facilitate direct comparison of the two singers based on their songs (Logue & Forstmeier, 2008). When two interacting birds song-type match, the acoustic features of those songs can be compared directly. Individual differences in song quality should be particularly easy to detect during the countersinging bouts that commonly occur in territorial disputes, in which the two singers alternate in rapid succession. Such comparison might be useful to the singers themselves, helping them decide how to proceed in the interaction, and also to potential rivals and mates evaluating each singer's competitive ability and mate quality (Bateson & Healy, 2005; McGregor, 1993).

To compare singing ability, listeners need a reliable metric for comparison. One measure of vocal performance that could function as this metric concern the rate and frequency bandwidth of trilled syllables. This type of vocal performance was first studied in swamp sparrows, whose songs consist of a single repeated syllable (Podos, 1997; Fig. 1). Male swamp sparrows face constraints on beak movement that result in a trade-off between the maximum rate at which they can sing these trilled syllables (trill rate) and their frequency bandwidth (Podos & Nowicki, 2004; Podos, 1997). An upper bound regression of frequency bandwidth versus trill rate, based on all of the songs in a population, represents a theoretical performance maximum. Actual performance, which varies across song types and across males, can be assessed relative to this maximum: high-performance songs, and high-performance renditions of a given song type, deviate relatively little from the upper bound, and low-performance songs or renditions deviate further. Female swamp sparrows give more copulation solicitation displays to higher-performance renditions (those with less vocal deviation) of a given song type (Ballentine, Hyman, & Nowicki, 2004), and males generally respond more aggressively to playback of high-performance renditions than to low-performance ones (DuBois, Nowicki, & Searcy, 2011; Moseley, Lahti, & Podos, 2013). Males can modulate their vocal performance to some extent (DuBois, Nowicki, & Searcy, 2009), but for a given song type, within-male variation in performance is generally lower than between-male variation (DuBois et al., 2011). The relative vocal performance of two swamp sparrow males singing the same song type in a territorial interaction might therefore be informative to the interacting males and to conspecifics in the area.

The roles of song type matching and relative vocal deviation in territorial signalling thus far have been studied separately. In this study, we examine how the two measures interact. Specifically, we investigate whether the likelihood of song type matching in swamp sparrows is affected by relative vocal performance, using vocal deviation as the performance measure. In a playback experiment with paired trials, we recorded males' responses to stimuli of higher or lower vocal performance relative to their own renditions of the same type. We then tested whether differences in vocal performance between focal males and their perceived rivals predicted the frequency of song type matching. We predicted that males would song-type match more often when they could produce a higher-performance version of that type than the perceived

opponent (i.e. in response to low-performance playbacks), because matching in this situation enables the focal male to demonstrate vocal superiority. We also predicted that males would not match when confronted with relatively high-performance song of a given type, because matching in this case would reveal the subjects' own lower performance. In this case, males might be expected to reply with a different song so that listeners cannot as easily compare song quality across the two singers. These predictions are in line with the model of Logue and Forstmeier (2008) simulating the conditions that confer network-dependent advantages to song type matching.

Our experimental design additionally enabled us to assess whether males respond to playback using their highest-performance song type when not song-type matching. DuBois et al. (2009) found that male swamp sparrows do not consistently respond to playback with their highest-performance song type, but song type matching was not considered in that study. We examined whether singing one's highest-performance song type represents an alternative strategy from song type matching and, if so, whether its use depends on the performance level of the playback song. Males might be expected to use such an alternative strategy in high-performance playback trials, in which they could not respond with a higher-performance rendition of the playback song type. Finally, male swamp sparrows can modulate their vocal performance and sing with higher performance when confronted by a perceived intruder (DuBois et al., 2009). We asked whether males modulate their responses to low- and high-performance playback to similar or different degrees.

## METHODS

### *Ethics and Animal Welfare*

Research protocols for this study were approved by the Institutional Animal Care and Use Committee of Duke University (A113-05-04) and the Pennsylvania Game Commission (30-2008). All recording and playback procedures were performed on wild, free-living birds. To minimize invasiveness, we limited the duration of recording to that required for full repertoire sampling and tested each male with only one song type (two trials per male). We did not revisit the territories after playback trials were completed.

### *Field Recordings and Playback Stimuli*

The complete song repertoires of 31 territorial free-living male swamp sparrows were recorded from 9 May to 15 June 2008 in Conneaut Marsh, Pennsylvania, U.S.A. (41°35'26"N, 80°15'54"W). Males were recorded between 0530 and 1200 hours Eastern Standard Time (EST) using a Marantz PMD660 digital recorder, a Sony parabolic reflector PBR-330 and a Shure SM57 Dynamic microphone. Most males were already present and singing when we began recording, but when necessary, we played at most two songs outside the territory to determine whether the male was present. We did not record males if they were countersinging with another male. Most males were not colour-banded but were readily identified by their song posts, territorial boundaries and vocal repertoires. Each male's repertoire was recorded within 2 days.

Swamp sparrow songs consist of one multinote syllable repeated in a continuous trill (Fig. 1). Song types are thus identified by the unique sequence of two to five note types that comprise its repeated syllable (Marler & Pickert, 1984). The ranges of vocal performance values differ across song types as well as across males (Ballentine et al., 2004). To calculate the vocal performance of each song type for each male, we first viewed recordings as waveforms in Audacity v.1.2.6 (<http://audacity.sourceforge.net>) and selected six

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