



A test for repertoire matching in eastern song sparrows

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Repertoire matching occurs when one songbird replies to another with a song type that the two birds share. Repertoire matching has previously been demonstrated to occur at well above chance levels in a western population of song sparrows, where it is hypothesized to serve as a low level threat in a hierarchy of aggressive signals. Here we test for repertoire matching in an eastern population of song sparrows. Previous work indicates that this eastern population differs from the western one in having lower levels of song sharing between neighboring males and in showing no association between song sharing and territory tenure. Here we confirm that males in this eastern population on average share few whole songs with their neighbors. The eastern males are familiar with their neighbors' repertoires, as evidenced by a stronger singing response to stranger song than to neighbor song. Males in the eastern population did not repertoire match: when played an unshared song type from a specific neighbor, they did not reply with a song type shared with that neighbor more often than expected by chance or more often than in response to playback of a control song (an unshared stranger song). The results thus demonstrate a qualitative difference in vocal signaling strategies between two populations of the same species.

Song type matching is a behavior in which one songbird replies to another with the song type that the other has just sung. Song type matching contrasts with repertoire matching, in which a male replies to another with a shared song type (Beecher et al. 1996) without type matching the other's most recent song (Beecher et al. 2000a). Both forms of matching have been hypothesized to be part of a hierarchy of aggressive signals in song sparrows *Melospiza melodia*, with song type matching representing a higher level of threat than repertoire matching (Beecher and Campbell 2005, Searcy and Beecher 2009). To perform either category of matching, individuals must possess multiple song types and share some song types with others. Given these conditions, it is possible for both forms of matching to occur by chance alone. Song type matching has been shown, however, to occur more frequently than expected by chance in many songbird species (Hinde 1958, Lemon 1968, Krebs et al. 1981, Schroeder and Wiley 1983, Falls 1985, Stoddard et al. 1992, Rogers 2004, Burt and Vehrencamp 2005, Gammon et al. 2008, Price and Yuan 2011). To our knowledge, repertoire matching at above chance levels has been demonstrated only in song sparrows and only in a single population, located in Seattle, Washington, at the western edge of the species' range (Beecher et al. 1996, 2000a). Here we test for repertoire matching in a second population of song sparrows, this one located in Pennsylvania, in the eastern part of the species' range.

Song sparrows in the Seattle and Pennsylvania populations have many similarities in singing behavior (Searcy et al. 2014a), as would be expected of populations of the same species. In both populations, males have song

repertoires of moderate size, usually in the range of 6 to 12 song types (Peters et al. 2000). In both populations, males match playback of wholly shared songs at frequencies substantially above chance levels (Stoddard et al. 1992, Anderson et al. 2005). Males in both populations also match playback of partially-shared songs, for example songs sharing only their introductory phrases (Burt et al. 2002, Anderson et al. 2005).

In other respects, singing behavior differs between the two populations. One difference is that song sharing is substantially more frequent in Seattle than in Pennsylvania. Dyads of immediately adjacent neighbors share a mean of 24% of their repertoires in Seattle (Hill et al. 1999) compared to only 3% of their repertoires in Pennsylvania (Hughes et al. 1998). These estimates, however, are based on somewhat different criteria for what constitutes whole song sharing; therefore one goal of the present study is to estimate sharing per neighbor in Pennsylvania using the same criteria for whole song sharing used in Seattle (Hill et al. 1999) and in other recent song sparrow studies (Foote and Barber 2007, Searcy et al. 2014b).

A second difference between the populations is that song type matching seems to be a more informative signal in Seattle than in Pennsylvania. Type matching has been hypothesized to be an aggressive signal across songbirds (Krebs et al. 1981, Searcy and Beecher 2009). Some of the best supporting evidence comes from a two-part playback experiment in the Seattle population of song sparrows, in which Akçay et al. (2013) showed that males that type match a playback at their boundary are more likely to give a highly aggressive

display (wing-wave) in response to a subsequent playback in the center of their territory and are also more likely to attack an associated taxidermic mount, compared to males that do not match the boundary playback. By contrast, in the Pennsylvania population, type matching a boundary playback does not predict escalation of aggressive display in response to playback at the center of the territory (Searcy et al. 2013), and matching a center playback does not predict attack on a taxidermic mount (Searcy et al. 2006).

A third difference between the populations is that the level of song type sharing between a male and his neighbors is positively associated with years of territory tenure in Seattle (Beecher et al. 2000b) and in another western population (Wilson et al. 2000), but no such association is found in Pennsylvania (Hughes et al. 2007). Because territory tenure is expected to be positively associated with lifetime reproductive success (Smith 1988), these results imply that song type sharing is positively associated with fitness in western but not eastern populations.

The differences between the Seattle and Pennsylvania populations in levels of song type sharing and in the importance of song type sharing to fitness suggest that matching behaviors are in general less important in Pennsylvania, which also fits with the lesser importance of type matching as a signal in Pennsylvania compared to Seattle (Searcy et al. 2014a). The hypothesis that song matching and sharing are relatively unimportant in Pennsylvania predicts that song sparrows in Pennsylvania will not perform repertoire matching, despite their doing so in Seattle. Here we test this prediction employing the same experimental design used by Beecher et al. (1996) in their demonstration of repertoire matching.

Repertoire matching requires that territory owners recognize their neighbors by song. Song recognition in territorial songbirds has been studied at two levels (Falls 1982): the ability to discriminate the class of neighbors from the class of strangers (neighbor-stranger discrimination) (Weeden and Falls 1959, Falls and D'Agincourt 1981), and the ability to discriminate individual neighbors from all others (individual recognition) (Falls and Brooks 1975, Godard 1991). Both levels of song recognition have been demonstrated in Seattle song sparrows (Stoddard et al. 1990, 1991). The playback design used here to test for repertoire matching allows a test for neighbor-stranger discrimination but not for individual recognition.

To summarize, the main goal of the present study is to test for repertoire matching in an eastern population of song sparrows. Two subsidiary goals are to measure song sharing between pairs of adjacent neighbors using standard criteria for sharing (to see how often neighbors have the song types needed to repertoire match) and to test for neighbor-stranger song discrimination (to see whether Pennsylvania song sparrows have the knowledge of each other's repertoires needed to repertoire match).

Material and methods

Study area and subjects

The study was carried out during May and June of 2013 and 2014 at three sites within 6 km of Hartstown, Crawford

County, Pennsylvania, USA (41°30.07'N, 80°22.65'W). Two of the three sites were among those used by Hughes et al. (1998) in their study of song sharing; the third site was about 9 km distant from the other two. Song sparrows at these sites held territories in old fields, especially along hedgerows bordering the fields but also in the centers of the fields if there were sufficient bushes and small trees. Of the 32 males whose repertoires were recorded for the study, 30 were banded with unique combinations of colored leg bands.

Song sharing

Song sparrows were recorded using a digital recorder (Marantz PMD 660 or 670) and an omnidirectional microphone (Shure SM58) in a parabolic reflector (Sony PBR-330). Previous work suggests that the entire repertoire of most song sparrows can be captured with 200 songs, but that occasionally a new song type is found between 200 and 300 songs (Searcy et al. 1985). We obtained more than 300 songs for 30 of 32 males that we recorded (range 303–359); for the remaining two birds, we recorded 253 and 274 songs. Because of the large number of type switches (22 and 41 respectively) recorded for these last two birds, we believe we recorded entire repertoires for them as well as for the other birds in the sample.

Spectrograms of repertoire recordings were inspected using Syrinx (<www.syrinxpc.com>, John Burt, Univ. of Washington). Songs were visually classified into song types, with classification agreed upon by two researchers (WAS, ALD). Some males produced songs that had the same introductory phrases but were otherwise dissimilar. Such songs were classified as separate song types if they were sung in separate bouts and were classified as two versions of the same song type if the bird sang them intermixed within bouts.

For each dyad of adjacent neighbors, we compared repertoires of the two males to assess levels of sharing. To assess whole-song sharing, we used the criteria proposed by Hill et al. (1999) in their study of two western populations of song sparrows, which have been adopted in subsequent studies of eastern populations (Foote and Barber 2007, Searcy et al. 2014b). By these criteria, two songs are considered wholly-shared if 2/3 or more of their component phrases match. Trills are considered to match if the component notes are similar in shape, timing and frequency. Note complexes are considered to match if they share half or more of their notes. In borderline cases, sharing of introductory phrases is considered especially important, because these are less variable between renditions and are more important to song sparrows in classifying song types than are later parts of the song (Horning et al. 1993).

We also assessed partial sharing within each dyad of males based on the number of songs with shared introductory phrases (Fig. 1). Sharing of parts of songs such as introductory phrases and internal trills is considerably more common in the Pennsylvania population than is whole song sharing (Hughes et al. 1998). We concentrated on shared introductory phrases in particular because there is evidence that the beginnings of songs are especially important to song sparrows in classifying song types (Horning et al. 1993) and because it has been shown for both the Pennsylvania

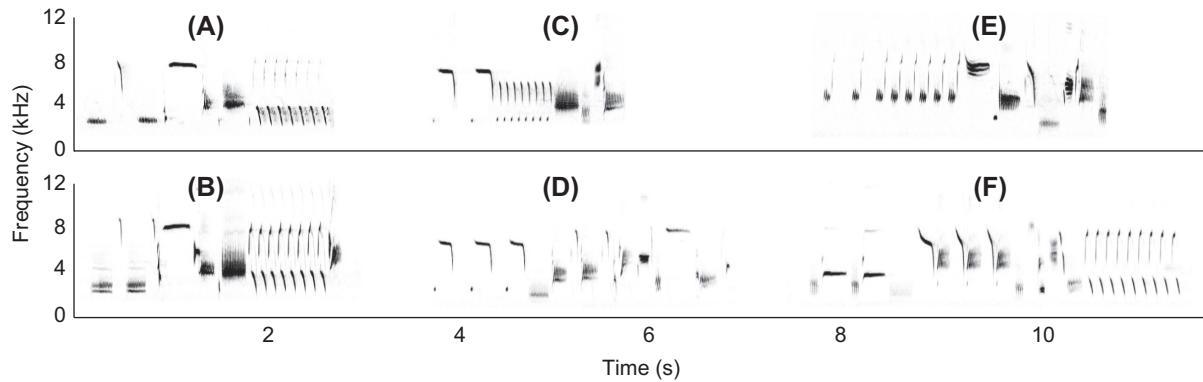


Figure 1. Pairs of songs illustrating categories of song sharing between male song sparrows. (A and B) Two songs from neighboring males classified as shared whole songs. (C and D) Two songs from neighboring males classified as partially shared due to shared introductions. (E and F) two songs from neighboring males classified as unshared.

population (Anderson et al. 2005) and the Seattle population (Burt et al. 2002) that males match songs that share only their introductory phrases.

For both wholly-shared and partially-shared songs, we used as the metric of sharing $2N_s/(R_1 + R_2)$, where N_s is the number of song types shared between two males and R_1 and R_2 are their respective repertoire sizes (Harris and Lemon 1972, McGregor and Krebs 1982).

Playback experiment

The playback design was based on that used by Beecher et al. (1996) in the original demonstration of repertoire matching, except that we used two instead of three treatments. The three treatments used by Beecher et al. (1996) were a neighbor song of a song type shared by the subject, a neighbor song of a song type not shared by the subject, and a stranger song of a song type not shared by the subject. Seattle song sparrows repertoire matched the shared neighbor song in 15 of 17 cases (88%) and the unshared neighbor song in 10 of 12 cases (83%), both significantly more often than expected by chance. In most cases, subjects responded to a shared neighbor song with a song type other than the one used in the playback, i.e. they repertoire matched but did not type match. Many of our Pennsylvania subjects, however, shared only one whole song or partial song with the neighbor used for playback, and so would not be able to reply to playback of a shared song type with a shared type without type matching. Consequently, we did not use the shared neighbor song treatment and instead used only the unshared neighbor song and unshared stranger song treatments.

In the unshared neighbor song treatment, a subject was tested with an unshared song from a neighbor that he shared at least one song with (so that repertoire matching was possible). Because this treatment focused on dyads that shared at least one song, the random expectation of repertoire matching was higher than implied by the overall frequency of sharing in the population. The unshared stranger song treatment served as a control, to see how frequently songs that happen to be shared with a neighbor would be sung in response to playback when those songs could not have special relevance. Stimuli used in the stranger song treatment experiments in 2013 were recorded in 2011 and 2012 from birds living at

a site 10 km away from test subjects. Stimuli used in the stranger song treatment experiments in 2014 were recorded in 2013 at a site 9 km away from test subjects. All playback stimuli were high-pass filtered at 1800 Hz using Syrinx (< www.syrinxpc.com >, John Burt, Univ. of Washington), and normalized to -1.0 dB (relative to the peak amplitude of the signal) using Audacity (< <http://audacityteam.org/> >). Songs were repeated at 10 s intervals for 3 min, for a total of 18 songs presented.

We carried out playback trials with 24 of the 32 recorded males. Some males could not be used because they shared no songs with any neighbor. Order of the two treatments was counterbalanced by randomizing order for one male and reversing order for the next. Playback stimuli were broadcast at the edge of a subject's territory, just within the territory of a neighbor with whom the subject shared a song or song introduction, and whose songs were used as the neighbor stimulus. Songs were broadcast at 84–88 dB SPL (B&K Precision 32A sound level meter, A weighting) from an iPod Touch to an iMainGo X portable speaker (Portable Sound Laboratories, Van Nuys, CA, USA). The iMainGo X was placed in a small box, lined with polyurethane composite foam (Acoustical Surfaces, Chaska MN, USA) and open on one side. Sound was broadcast from the open side of this box, which reduced the amplitude of playback behind the speaker and box by approximately 20 dB, thus minimizing the possibility of attracting the attention of the adjacent neighbor at the boundary. During trials, one of the researchers (WAS) would lure the neighbor away to discourage the neighbor from singing or interacting with the subject male during the trial.

Songs sung by the subject during the three-minute playback and three-minute post-playback period were recorded using a Marantz PMD 660 digital recorder, Shure microphone, and Sony Parabolic Reflector-330. An observer verbally identified when the subject sang. If a subject did not sing within the six-minute trial period, the trial was dropped from the study. We waited at least 48 h before attempting another trial with a subject who had failed to sing previously. Subjects were tested at most three times with one treatment. One subject of 24 failed to sing in response to three trials with neighbor song; consequently we present results from 23 neighbor song playbacks and from 24 stranger song playbacks.

Spectrograms were created of all songs recorded during the six-minute response periods using Syrinx and compared to spectrograms made previously of the subject's repertoire to determine whether the subject sang a song type shared with the focal neighbor or an unshared song. Beecher et al. (1996) counted as the response the first song type the subject sang if he sang only one song type, and the second type he sang if he switched song types during the 6 min response period. We present results first using this same response criterion (first song type if only one is given/second song type if two are given). We also present results using the first song given for all subjects. Of the 24 subjects, 17 shared at least one whole song with the neighbor used in the playback experiment, whereas the other 7 shared only one or more song introductions with the focal neighbor. Consequently, we perform two separate sets of analyses, one for all 24 subjects that allows use of either a partially-shared or a wholly-shared song type to count as repertoire matching, and the other for the 17 subjects that shared a whole song with their neighbor that only allows use of a wholly-shared song type to count as repertoire matching.

To examine neighbor-stranger discrimination, we contrast the total number of songs given by subjects during the six-minute response periods for the unshared neighbor song treatment and the unshared stranger song treatment. As the playback speaker was located off the subjects' territories, we cannot use approach as a response measure.

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.199k8>> (DuBois et al. 2015).

Results

Song sharing

The usual way of representing sharing levels is to calculate a per male level of sharing, by averaging sharing levels for each male across his neighbors. Calculated in this way, the average proportion of whole-song sharing per neighbor was 0.082 (range 0–0.63) for the 32 males in our sample. Males shared a mean of 0.7 whole songs (range 0–6) per adjacent neighbor. The mean proportion of introductory phrases shared per adjacent neighbor was 0.18 (range 0–0.74), with males sharing a mean of 1.5 song introductions per neighbor (range 0–7).

A second way of representing song sharing, which is perhaps more illuminating with respect to the likelihood that neighbors will be able to interact through matching, is by examining sharing per dyad of adjacent neighbors. Of the 43 neighbor-dyads in our sample, 31 (72%) shared no whole song types, 6 (14%) shared one song type, and 6 (14%) shared two or more song types. With respect to partial song matching, 18 dyads (42%) had no shared introductory phrases, 6 (14%) had one shared introduction, and 19 (44%) had two or more shared introductions.

Repertoire matching

Including both whole song matches and introductory phrase matches, and using as the response the second song type

sung in those cases in which two types were given, subjects produced a repertoire matching song in response to playback of their neighbor's song in 5 of 23 trials (22%). The 5 matches were fewer than expected (7.65) from random responses based on the proportions of shared songs, but the deviation from the expected number of matches and non-matches was not significant ($X^2 = 1.375$, $p = 0.241$). Subjects responded to playback of a stranger song with a neighbor-matching song on 6 of 24 trials; the percentage matching (25%) on these control trials was slightly higher than for neighbor song playback, but again the difference was not significant ($X^2 = 0.07$, $p = 0.79$). If we instead use the first song type given as the response for all trials, the results are qualitatively unchanged: subjects gave fewer repertoire matches (4/23) than expected based either on the proportion of songs shared or on the control trials, but not significantly fewer.

If we restrict the analysis to whole song matches, the sample size decreases because some pairs of subjects did not share whole songs and therefore drop out of the analysis. Using as the response the second song type sung for those subjects that sang two song types, subjects sang a repertoire matching song type on 1 of 16 trials (6.3%). The 1 match was fewer than the expected (3.6), but the deviation from the expected number of matches and non-matches was not significant ($X^2 = 2.423$, $p = 0.120$). Subjects responded to stranger playback with a repertoire matching song type on 2 of 17 trials; thus percentage matching (12%) was slightly higher for control trials than for experimental ones, but again the difference in response was not significant ($X^2 = 0.29$, $p = 0.58$). Using as the response the first song type given on all trials again makes little difference to the results: subjects repertoire-matched on 2 of 16 trials for neighbor songs, a slightly higher proportion than for playback of stranger songs (1 of 17), but not significantly different from either the stranger response or the random expectation.

Neighbor-stranger discrimination

Of the 23 males who were tested successfully with both a neighbor song and a stranger song, 17 gave more songs in response to the stranger song and 5 gave more in response to neighbor song, with 1 tie. Mean number of songs was significantly higher for stranger song playback than for neighbor song playback (paired $t = 3.77$, $p = 0.0011$; Fig. 2).

Discussion

We found no evidence of repertoire matching in our eastern population of song sparrows. In most comparisons, including both those that counted partial matching and those counting only whole song matching, frequencies of repertoire matching in response to neighbor song were lower than expected by chance and lower than found in control playbacks. In no case did the frequency of repertoire matching to neighbor song differ significantly either from random expectation or from response to control playback. The sample sizes for our neighbor playbacks ($n = 23$ for partial matching, $n = 17$ for whole song matching) were larger than for the parallel analyses that demonstrated repertoire matching in the Seattle population ($n = 12$ for Beecher et al. 1996, $n = 11$ for

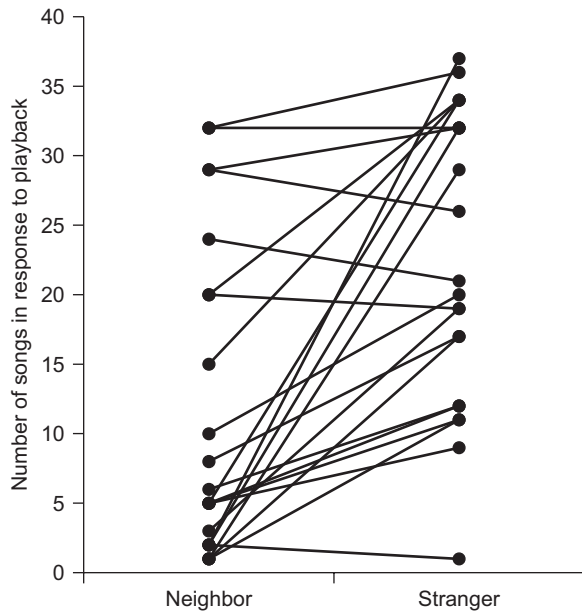


Figure 2. Numbers of songs given by individual male song sparrows in response to playback of neighbor and stranger song. Order of the two playback treatments was counterbalanced. Response was significantly higher for stranger song than for neighbor song.

Beecher et al. 2000a). Furthermore, the statistical power for detecting greater than random matching with a given sample size should be higher in our study than in the Seattle studies, because the lower level of song sharing in our population produces lower expected values against which to compare observed values. Nevertheless, we did not find greater than expected repertoire matching. In sum, the negative results of our study provide convincing evidence of the absence of repertoire matching in our study population.

Evidence from the Seattle population suggests that repertoire matching is used there as a low level signal of aggressive escalation, more threatening than an unshared song but less threatening than a type match (Beecher et al. 2000a, Beecher and Campbell 2005). Repertoire matching thus can be used to manage territorial interactions, escalating or de-escalating an interaction according to circumstances (Beecher and Campbell 2005, Searcy and Beecher 2009). Repertoire matching is arguably a more versatile signal than type matching, because a male can type match a neighbor only if the neighbor sings a shared song type, whereas he can repertoire match no matter what the neighbor sings (Beecher et al. 1996). If repertoire matching is both a useful and versatile signal, why then do Pennsylvania song sparrows forego it?

One possibility is that Pennsylvania song sparrows do not have the knowledge of each other's repertoires needed to repertoire match. In order to repertoire match, a male must know what song types are in a neighbor's repertoire, remember which song types he shares with the neighbor, and make a choice of song type contingent on that memory. Our results showing strong neighbor/stranger discrimination in our playback trials suggest that the males in our population do at least know what songs are sung by their neighbors, whether or not they are capable of the subsequent cognitive steps. Three earlier studies of eastern song sparrow popu-

lations (Harris and Lemon 1976, Kroodsma 1976, Searcy et al. 1981) found neighbor/stranger discrimination that was weak compared to the level found in the Seattle population (Stoddard et al. 1990). Stoddard et al. (1991) suggested that the difference in results was due to a difference in methodology: in the eastern studies the playback speaker was placed on the subject's side of the boundary with the focal neighbor, whereas in the western study the speaker was placed on the neighbor's side of the boundary. In the present study we found strong neighbor/stranger discrimination in an eastern population using speaker placement on the neighbor's side of the boundary, supporting the interpretation of Stoddard et al. (1991). This and other results from this population (Searcy and Nowicki 2006) suggest that Pennsylvania song sparrows do have the knowledge of each other's repertoires needed to repertoire match.

Another possibility is that song sharing levels are simply too low in Pennsylvania to support widespread use of repertoire matching. Our playback trials employed only dyads of focal males and neighbors that shared whole songs or introductory phrases, so that repertoire matching would be possible. Such dyads are in the minority in our population, at least with respect to whole song sharing. We found a higher level of whole-song sharing in our Pennsylvania population (8%) than found in a previous study of the same population (3%) (Hughes et al. 1998); the difference in these estimates can probably be ascribed mainly to our changing the criteria for what constitutes whole-song sharing to align with those used by Hill et al. (1999) for Seattle and by other recent studies of song sparrow populations (Foote and Barber 2007, Searcy et al. 2014b). Although higher than the previous estimate, our estimate of whole song sharing in Pennsylvania is still substantially lower than found for Seattle (24%) and for western populations in general (Cassidy 1993, Hill et al. 1999, Wilson et al. 2000). The problem low sharing poses for matching interactions is brought home by our dyad analysis, where we see that close to three quarters of neighbor/neighbor dyads share no whole songs, and thus are incapable of either type matching or repertoire matching using whole songs. Sharing of introductory phrases, however, is substantially higher, with about 60% of dyads sharing at least one introductory phrase, and thus capable of type matching or repertoire matching using partially shared songs. Song sharing levels in Pennsylvania thus reduce the possibilities for repertoire matching but do not totally preclude such behavior.

The two populations, Seattle and Pennsylvania, both show patterns of sharing and matching that are internally consistent (Searcy et al. 2014a). In Seattle, song sharing is high enough to enable widespread repertoire matching and type matching, both kinds of matching are used and are meaningful signals, and song sharing is positively associated with fitness. In Pennsylvania, song sharing is low, type matching is used but does not seem very meaningful, repertoire matching is not done at all, and song sharing is not associated with fitness. Although these syndromes seem internally consistent, it remains unclear why the syndromes differ between geographic areas, and why each syndrome is associated with the area in which it is found.

In conclusion, song sparrows show a qualitative difference in vocal signaling behaviors between a western and an eastern population, repertoire matching at very high levels

in the western population (Beecher et al. 1996, 2000a), and showing a total absence of this behavior in the eastern population (this study). This result points to the importance of studying intra-specific variation in signaling behavior.

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