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FINAL REPORT

A COMPARATIVE ANALYSIS OF SONG AND RESPONSES TO SONG PLAYBACK

IN THE AVIAN GENUS *PIPILO*

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Abstract

An experiment was undertaken to characterize the responses of Green-tailed Towhees (*Pipilo chlorura*) and Rufous-sided Towhees (*P. erythrophthalmus*) to each others' songs and to the songs of five other towhee species, plus one hybrid form. A total of 12 Green-Tailed Towhees and 10 Rufous-sided Towhees from Boulder and Gilpin counties were studied at three field sites: the Doudy Draw Trail, the National Center for Atmospheric Research (NCAR), and on private land at the mouth of Coal Creek Canyon. In May, each bird was mist-netted and banded to facilitate individual identification. During the subsequent playback phase in June and July, each individual received one three-part playback trial on each of 7 consecutive or near-consecutive days. A 9-min playback trial consisted of a 3-min "pre-play" period, during which the bird was observed in the absence of song playback, a 3-min "play" period, in which tape recorded song was played to the subject from a central point in his territory, and a 3-min "post-play" period when the bird was again observed in the absence of song playback. Order of presentation of song exemplars from different towhee species were randomized across birds. The main dependent measure was the change in the number of songs produced by the subject bird during song playback, relative to the pre-play period. Results showed that Green-tailed Towhees responded by significantly increasing their rate of singing, but only in response to Green-tailed Towhee songs. Rufous-sided Towhees significantly increased their rate of singing in response to Rufous-sided Towhee songs and in response to songs of Rufous-Sided X Collared Towhee hybrids. Rufous-sided Towhees did not respond significantly to Collared Towhee songs, even though the two species are known to occasionally hybridize in Mexico. Results are discussed from the perspective of towhee phylogeny.

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Objectives and Hypotheses

Towhees are finch-like birds that inhabit shrub-steppe habitats primarily in the southwestern United States. A major theme of past research on towhees has been that of speciation and species classification. Sibley (1950) showed that two species, originally considered by the American Ornithologist's Union (AOU) to be distinct and stable species -- the Rufous-sided Towhee (*Pipilo erythrophthalmus*) and the Collared Towhee (*P. ocai*) -- interbreed and form viable offspring in certain parts of Mexico. In other parts of Mexico, however, these two species are sympatric but do not hybridize. Mayr (1963) has called Sibley's findings, "perhaps the most thoroughly analyzed case of the breakdown of isolation between two species of birds," and it is often raised as a key problem for the Biological Species Concept's reproductive isolation criterion for species definition (Otte & Endler, 1989).

Sibley speculates that these two species evolved from the same parental population. Apparently, they had become geographically isolated as the result of niche differentiation, but human activities led to deforestation, and resulting secondary growth brought the two species back together before genetic isolation was complete. Sibley (1955) also speculated that towhees evolved in Mexico and migrated northward, with the Green-tailed Towhee (*P. chlorura*) being a close relative of both the Collared and Rufous-sided Towhee. In his opinion, the other four species in the genus -- Abert's Towhee (*P. aberti*), Canyon Towhee (*P. fuscus*), California Towhee (*P. crissalis*), and White-throated Towhee (*P. albicollis*) -- typically referred to as the "Brown Towhee Complex," represent a distinct lineage with the *Pipilo* genus. Sibley argues that, in fact, these birds may be more closely related to the *Melospiza* ground finches than to the Rufous-sided, Green-tailed, and Collared Towhee.

Zink (1988) used DNA analysis to study the phylogeny of the "Brown Towhee Complex." While the AOU had classified the California and Canyon varieties as members of a single species, the Brown Towhee, DNA analysis showed that Abert's Towhee is more closely related to the California Towhee than is the Canyon Towhee. Not only are the Canyon and California Towhees not conspecific, they are not even each others' closest relatives. Zink concluded that the California and Abert's towhees comprise one pair of sister species, and the Canyon and White-throated Towhees a second pair.

Furthermore, DNA analysis revealed that the Green-tailed Towhee is only distantly related to any of the birds in the "Brown Towhee Complex." Zink (personal communication) claims that the Rufous-sided and Collared Towhees are also sisters, though not genetically very close, and that the Green-tailed Towhee represents a separate but related line. In contrast, Sibley (personal communication) groups the Green-tailed and Collared Towhee together as sisters, with the Rufous-sided Towhee being separate. Sibley states that two cases of hybridization between Rufous-sided and Green-tailed Towhees have been documented in the last 5 years. Both theorists agree that grouping the "Brown Towhee Complex" and the "Rufous Towhee Complex" (Rufous-sided, Collared, and Green-tailed) together in one genus may be a mistake.

The current experiment represents one step in a larger project of studying all possible combination of cross-species responding in the avian genus *Pipilo*. Response to song playback and acoustic similarity of songs represent two pieces of evidence that are relevant in deciding bird phylogeny. Two towhee species inhabit northern Colorado, the Rufous-sided Towhee and the Green-tailed Towhee. These two species are sympatric in most of Colorado, including Boulder County, but rarely, if ever interbreed (not at all, as far as I know). Although great caution must be exercised in attempting to infer phylogeny from song playback studies, it is known that song production and song responsiveness in song birds is at least partially under genetic control (Marler, 1970). To the extent that song similarity across species correlates with phylogenetic relatedness, several predictions can be

made. First, there should be more cross-species responding within the Rufous or Brown Towhee Complexes than between the Rufous and Brown Towhee Complex. Second, Rufous-sided Towhees should respond to Rufous-sided X Collared Towhee hybrid songs, and possibly, though not necessarily to the Collared Towhee song (because of sub-species differences between *P. e. montanus* -- the Colorado population -- and *P. e. macronyx* -- the Mexican population). Third, depending on whether Sibley or Zink are correct about the genealogy of the Rufous Towhee Complex, one might expect the Green-tailed Towhee to respond more to one of the other of its closest cousins.

Methodology

A total of 17 Green-tailed and six Rufous-sided Towhees were banded near the Doudy Draw trail between 10 May 1995 and 22 May 1995. Each bird was outfitted with an aluminum leg band from the Federal Bird Banding Laboratory and with a colored leg band for field identification. In addition, one male Rufous-sided Towhee was netted who already had an aluminum band (#8051-05773); this bird was given a colored leg band too. A total of 7 of these Green-tailed and 5 of these Rufous-sided Towhees were included in the playback experiment along with four Green-tailed and one Rufous-sided Towhees from the NCAR Mesa, and one Green-tailed and four Rufous-sided Towhees from private property at the mouth of Coal Creek Canyon.

Stimuli

Songs from each of the seven towhee species plus Collared X Rufous-sided Towhees were obtained from a variety of sources, including tape recordings I made in Boulder County last year, the Borror Laboratory of Bioacoustics at the Ohio State University, the Library of Natural Sounds at Cornell Laboratory of Ornithology, the Bioacoustics Archive at the Florida Museum of Natural History, and Roger Tory Peterson's Field Guide to Western Bird Songs. An attempt was made to find enough song exemplars so that each bird was tested with a different exemplar of song from each of the 8 playback categories. The total number of songs of each species employed was Green-

tailed Towhee: 12; Rufous-sided Towhee: 10; Abert's Towhee: 7; California Towhee: 3; Canyon Towhee: 8; Collared Towhee: 10; White-Throated Towhee: 2; Collared X Rufous-sided Hybrid: 10.

Each tape recorded playback trial was 9 minutes long. The first three minutes were silent, and were used to assess baseline responding. The second three minutes contained the song playback presentations. Regardless of song duration, one song exemplar was played over and over again starting once every 7 second. Therefore, during the three-minute playback period, a song was repeated 26 times. The final three minutes were again silent.

Procedure

Each bird received one playback trial per day, with order of presentation of different species songs randomized across birds. An effort was made to test a bird on each of 8 consecutive days, but this was not always possible due to weather, time constraints, or inability to find the bird. Rarely did more than 48 hrs separate two trials, however.

The tape player was positioned in a central location in a bird's territory, typically between ground level and roughly two meters above the ground. Binoculars were used to visually follow birds during playback trials. The main dependent measures were (a) the number of songs emitted by the subject bird during each of the three phases of the playback trial, (b) the latency to approach within 5 meters of the loudspeaker, and (c) the number of times the subject bird flew over the loudspeaker. These latter two measures proved to be rather unreliable, because many birds failed to approach or fly-by the loudspeaker. Therefore, song production was selected as the dependent measure to-be-reported.

Results

Figure 1 shows the mean change in song production between the "pre-play" and "play" periods of the playback trials for Green-tailed Towhees. An asterisk above a data point indicates a significant increase in the number of songs produced. As can be seen, Green-tailed Towhees increased their rate of singing only in response to Green-tailed

Towhee song, $t(11) = 3.09$, $p < .05$. Although all four Green-tailed Towhees at the NCAR site responded to the Collared X Rufous-sided Hybrid song, overall there was no significant effect, $t(11) = 1.54$, $p > .10$

Figure 2 shows the results for Rufous-sided Towhees. Significant increases in rate of singing occurred in response to Rufous-sided Towhee song, $t(9) = 4.46$, $p < .01$, and Collared X Rufous-sided Hybrid song, $t(9) = 2.88$, $p < .05$, only.

Figures 3 and 4 show pilot results obtained with Abert's and Canyon Towhees in southeastern Arizona (not part of Boulder County Open Space research, but included to give the reader an idea about where the larger project is headed). Each graph shows partial results from two birds. Abert's Towhees (both individuals) increased their rate of singing in response to Abert's and California Towhee song, but not Canyon Towhee song. Canyon Towhees increased their rate of singing to all songs from the Brown Towhee Complex, especially White-throated and Canyon Towhee songs. They did not respond at all to Green-tailed Towhee song.

Conclusions

These song playback results show that cross-species responding in Green-tailed and Rufous-sided Towhees is minimal: it did not occur at all with Green-tails and occurred in Rufous-sided Towhees only to the song of Collared X Rufous-sided hybrids. It should be noted that Rufous-sided Towhees did respond to Rufous-sided Towhee song recorded in Mexico ($M = +11$, averaged across 3 songs, all three birds responded). Likewise, Green-tailed Towhees responded to Green-tailed Towhee song recorded outside of Colorado ($M = +10$, averaged across 4 songs, 3 of 4 birds responded). Therefore, there was no evidence that any regional dialects inhibited within-species responding.

The pilot data from Arizona suggest that cross-species responding might be greater among the "Brown Towhee Complex" than it is in the "Rufous Towhee Complex," although a more thorough study is called for (and will be carried out this summer). These results are consistent with the idea that species in the "Brown Towhee Complex" may be

more closely related to each other than are the species in the "Rufous Towhee Complex." Furthermore, the absence of cross-responding between "Brown" and "Rufous" Towhees so far is consistent with Sibley's speculation that a large genetic gap separates the two "sub-genuses."

While the value of these data are largely conceptual and related to issues in evolutionary theory and systematics, we now have a fairly large number of towhees that have been banded on Boulder County Open Space land. This gives us an opportunity to follow individuals longitudinally, and to examine life spans, territory sizes and nest successes. It will be possible to exam the effects of human use on all three of these variables, since some individuals have territories and build nests on relatively busy sections of the Doudy Draw Trail, while others select more less busy sites.

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Fig. 1

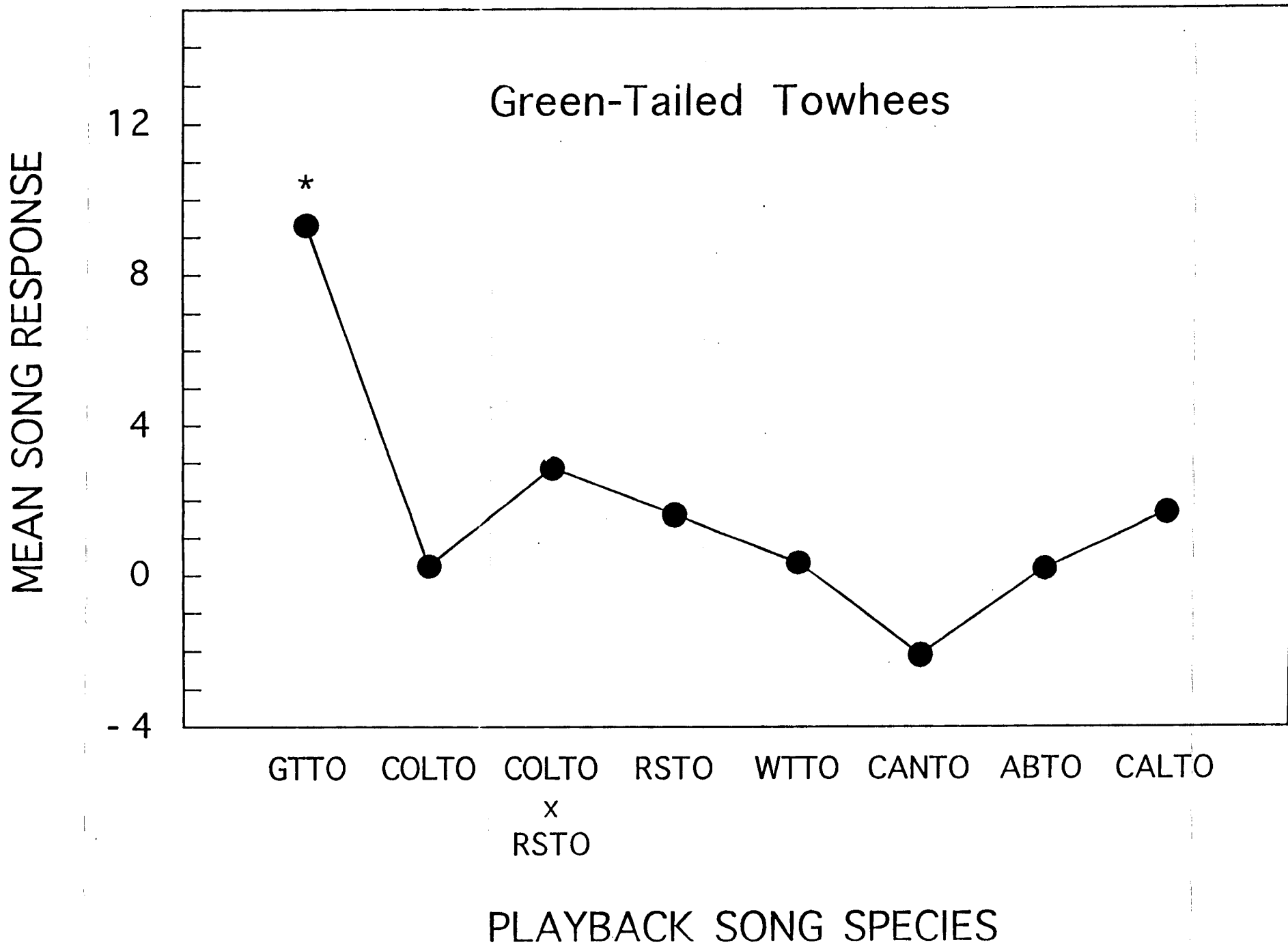
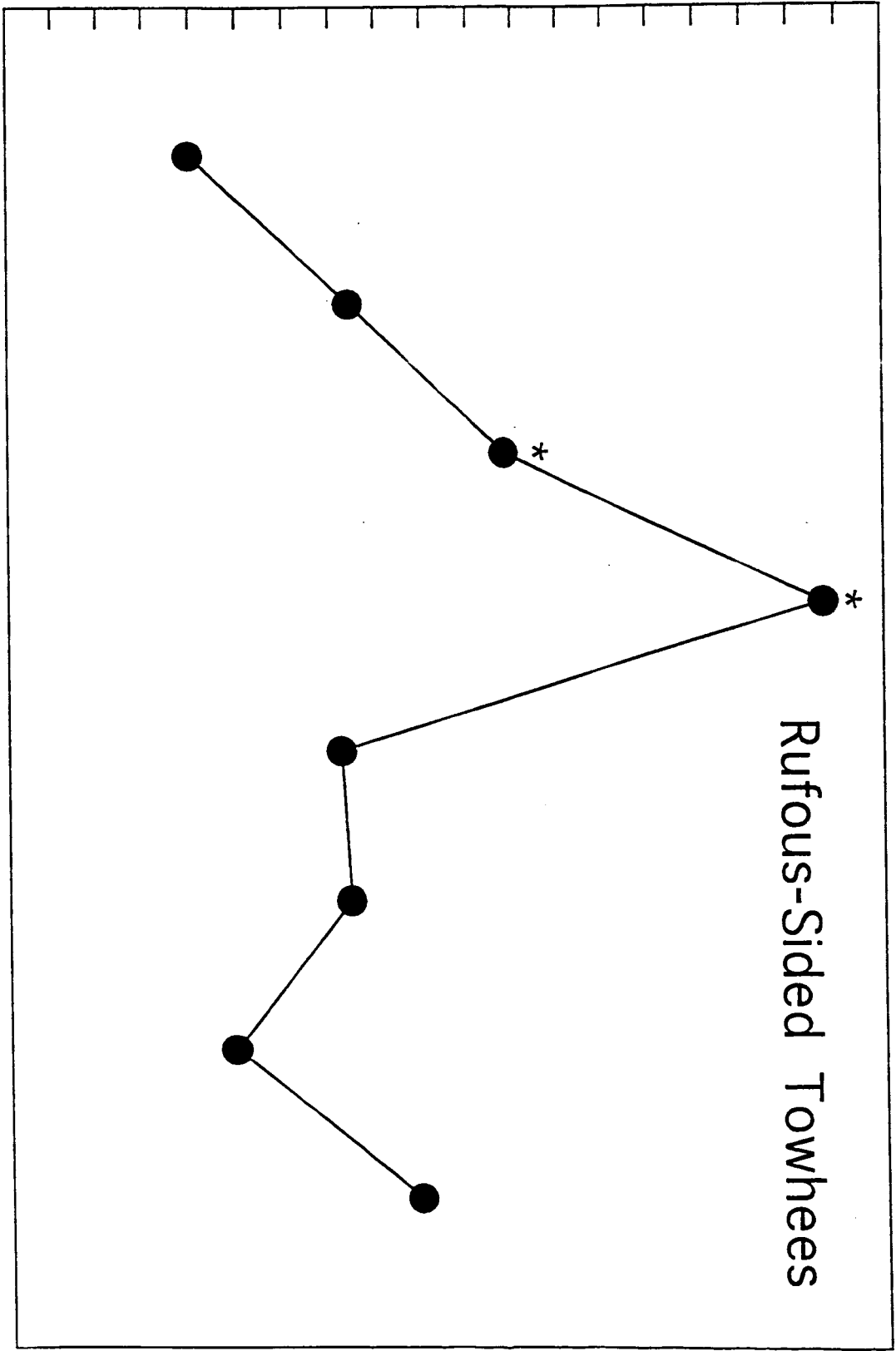


Fig. 2

MEAN SONG RESPONSE

12
8
4
0
-4



Rufous-Sided Towhees

GTTO COLTO COLTO RSTO WTTTO CANTO ABTO CALTO
X
RSTO

PLAYBACK SONG SPECIES

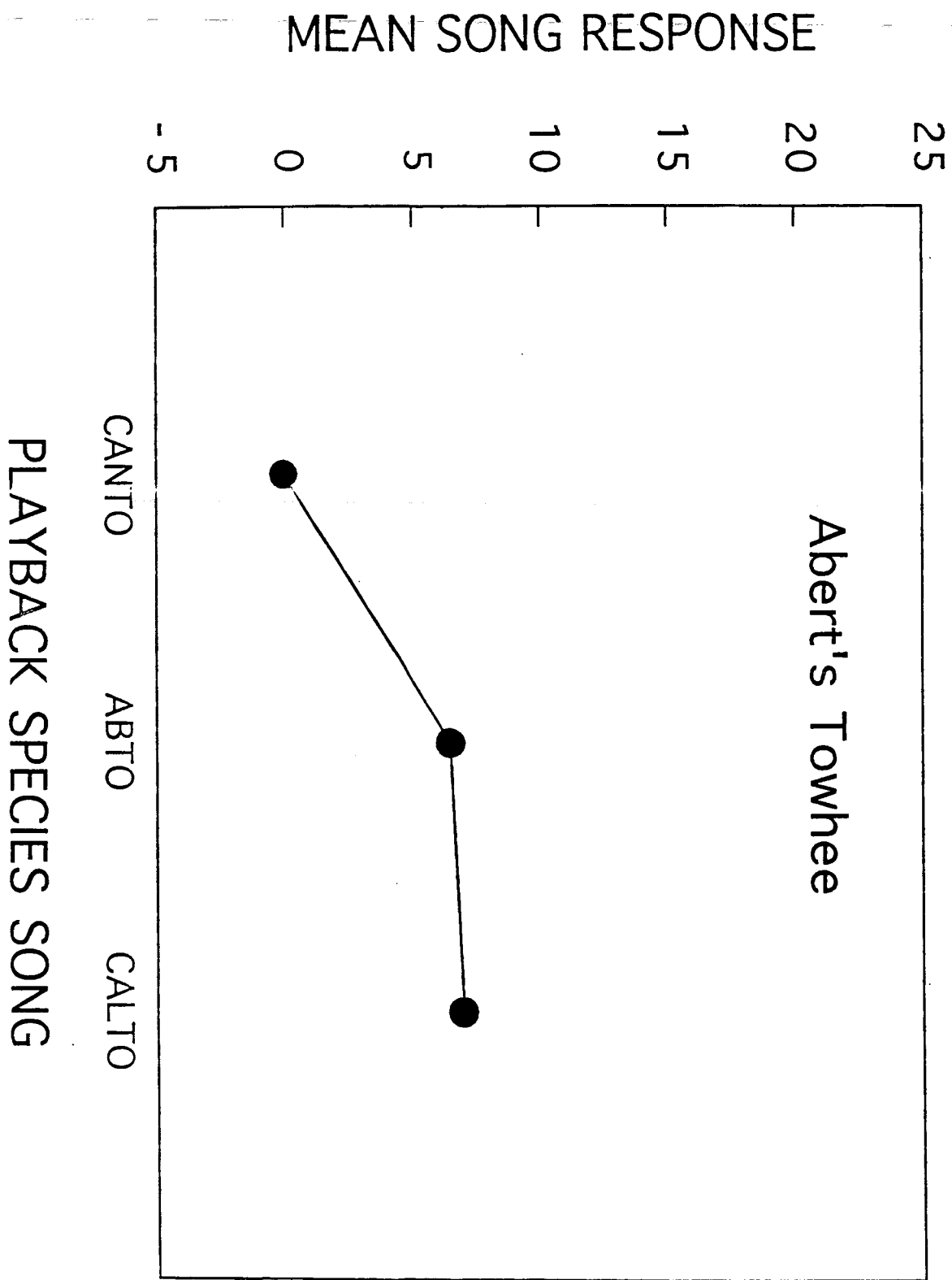


Fig. 4

