

RESPONSE BY MALE FOX SPARROWS TO BROADCAST OF PARTICULAR CONSPECIFIC SONGS

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Those oscines possessing more than 1 theme, or type of primary song, generally sing a prolonged bout consisting of 1 type of song before switching to another song-type. Fox Sparrows (*Passerella iliaca*), breeding in northern Utah, do not organize their songs, or singing, in such a manner. Typically, these Fox Sparrows possess 3 highly complex song-types (Martin 1976, 1977). Each song-type consists of an introductory portion composed of syllables of a type and sequence usually characteristic of each individual, and a terminal sequence of syllable-types that is stereotyped among birds. Thus, each song uttered could easily encode for messages, such as species (Mulligan 1966, Falls 1969) and individual identity (Brooks and Falls 1975a), population affiliation (Milligan and Verner 1971) and the sex, location, motivation and marital status of the singer (Marler 1956). An individual Fox Sparrow sings each of its song-types only once, until its entire repertoire is exhausted and then begins the sequence again. Sequence of song presentation is usually peculiar to each individual and seems to remain constant through time (Martin 1976).

I have proposed that this organization system, although unlike that of most oscines, functions to reduce the monotony or habituation of songs, or singing, to the singer and/or the receiver. Hypotheses similar to this have been offered to explain the organization of singing in birds that do not exhibit the Fox Sparrow "system" (Falls and Krebs 1975; Hartshorne 1956, 1958, 1973; Hinde 1958; Kroodsma 1977; Mulligan 1966; Isaac and Marler 1963; Dixon 1969; Lemon and Chatfield 1971, 1973). Presentation of song-types in bouts, with ultimate matching of song-types among countersinging individuals, has been suspected also of allowing countersinging rivals to hurl and retaliate with threats more forceful than those immediately being sung (Dixon 1969, Bertram 1970) and, potentially, matching of song themes among neighboring territorial males may facilitate neighbor-neighbor recognition (T. Keeney, pers. comm., abstracted in C.O.S. meeting 1977). An hypothesis quite similar to this has been offered and supported by Lein (1972, 1978). Working with Black-throated Green (*Dendroica virens*) and Chestnut-sided (*D. pensylvanica*) warblers, he has demonstrated that the various song-types sung by some species of warbler can be used to encode for, and transmit, different messages concerning the location of the singer on its territory and its level of aggressiveness. The song-types appear to "form a graded series of signals, in-

creasing the efficiency of male-male communication” more precisely than the use of a single song-type (Lein 1978:1266). Singing in the Yellow-throated Vireo (*Vireo flavifrons*) also may prove to be a complexly ordered graded series of signals (Smith et al. 1978).

It should follow that, if songs are of various valence to the singer and/or receiver, one would expect that particular songs would be sung more frequently than others and that matching of song-themes among countersinging contestants might occur. Further, such a system should result in varying levels of response to broadcast of particular types of conspecific song. Previous study has shown that Fox Sparrows tend not to sing preferentially any particular type of song from within their repertoire more than any other, and that matching of songs between countersinging rivals is virtually precluded by the manner in which Fox Sparrows organize their singing sessions (Martin 1976). However, inasmuch as all males do not share similar song-types, and playback experiments had not been performed previously, discussion as to the valence capabilities (or importance) of the various song-types has been inferential. Thus, in this study, I attempt to determine whether the various songs of Fox Sparrows function similarly in male-male territorial encounters and whether the level of agonistic response to the broadcast of particular types of conspecific song indicates that the valence among various song-types differs.

METHODS

Subjects.—All Fox Sparrows used in playback experiments were located in Logan Canyon, Cache Co., Utah. Arrival on the breeding ground and establishment of territories occurred from late March through mid-May. By early June all birds were paired and well into nest construction, egg-laying, or incubation. Testing was begun on 31 May and ended on 28 June in 1976. Only those data collected from birds which were paired territory-holders throughout the test period were considered. Birds were not captured and individually banded because of the potential trauma they might have associated with the use of conspecific playback to lure them into mist nets. However, birds were easily identified by the composition of their song repertoires (Martin 1976, 1977).

Song repertoire in Fox Sparrows.—Detailed description of song structuring in Fox Sparrows breeding in Logan Canyon is presented in Martin (1976, 1977). Males in the population possess a mean of 3.2 songs (SD = 0.8, N = 133). And, although birds may choose from some 49 complex syllable-types that I have defined to construct their songs, most songs consist of but 8 syllable-types (\bar{x} = 8.15, SD = \pm 1.2, N of songs analyzed = 416). Typically, the syllable-types and their sequence in the first half of a particular song varies among individuals, whereas the terminal portion tends to be similar in structure within the population (Fig. 1). This uniformity in the endings of songs allows virtually all songs to be grouped into 1 of 5 major song-types: A, B, C, D and E. A complete listing of the syllable-types, comprising the major song-types so far delimited from Fox Sparrows in northern Utah and southern Idaho, is given in Martin (1977 Appendix).

Equipment.—Song-types used as conspecific playback (Fig. 2) were recorded in 1975 using a Uher 517 microphone mounted in a 61 cm parabolic reflector with a Uher 4000 IC type

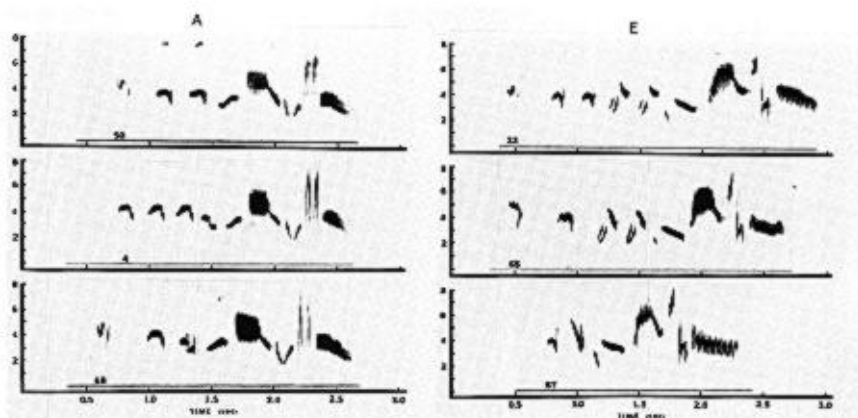


FIG. 1. Sound spectrograms of song-types A and E, each rendition from a different individual.

recorder at 19 cm/sec. These recordings were from individuals in a population breeding in Blacksmith Fork Canyon, 13.6 km south of Logan Canyon. Songs were later re-recorded onto Cousino tape-loops at 19 cm/sec while overall amplitude was maintained at a constant level. A Uher 4000 L tape recorder was used to broadcast song during field tests.

Playback procedure.—Each test session consisted of a 3-min silent observation period (pre-playback) followed immediately by a 3-min broadcast period (playback) and a final 3-min silent observation period (post-playback). A voice description of all overt behavior during each segment of test sessions was tape-recorded and transcribed at a later date. All tests were performed between 08:00 and 14:00 EST; no bird was tested more than once per day.

Only 1 song-type (A, B, C, D or E) was presented during each test day. Each song-type that was tested was presented to all birds on the same or following day. Sequence of presentation of song-types was A, B, C, D, E, A, B, C, D, E. Thus, each bird was tested twice with each song-type. This procedure hopefully lessened the potential affects of intra- and inter-individual variation resulting from weather conditions, phase of breeding cycle, etc. A visual model of a male Fox Sparrow was not present during playback testing.

Response measures.—Song in Fox Sparrows functions as one of a number of species-typical territorial displays. Displays accompanying disputes in which rivals are within a few meters of each other, or an intruder, and are on a resident's territory, tend to be dominated by "chirp" calls, short flights and posturing. After repelling an intruder the victor assumes an exposed perch and sings.

Criteria that were used to quantify the strength of an individual's response to playback of conspecific song were: (1) number of songs sung, (2) latency to utterance of the first song after playback had begun, (3) latency of approach to the speaker after broadcast of the first conspecific song, (4) number of "chirp" calls uttered, and (5) number of flights performed. Due to the rapidity with which Fox Sparrows may change postures while moving through the dense cover on their territories, postural displays and closeness of approach to the speaker were not easily quantified and were not included in the analysis.

Statistical significance was determined by *t*-tests since sample sizes were rather large and data sets were normally distributed. Nonnormality is generally "not too serious" and must be severe to have a marked effect on significance levels (Sokal and Rohlf 1969:377).

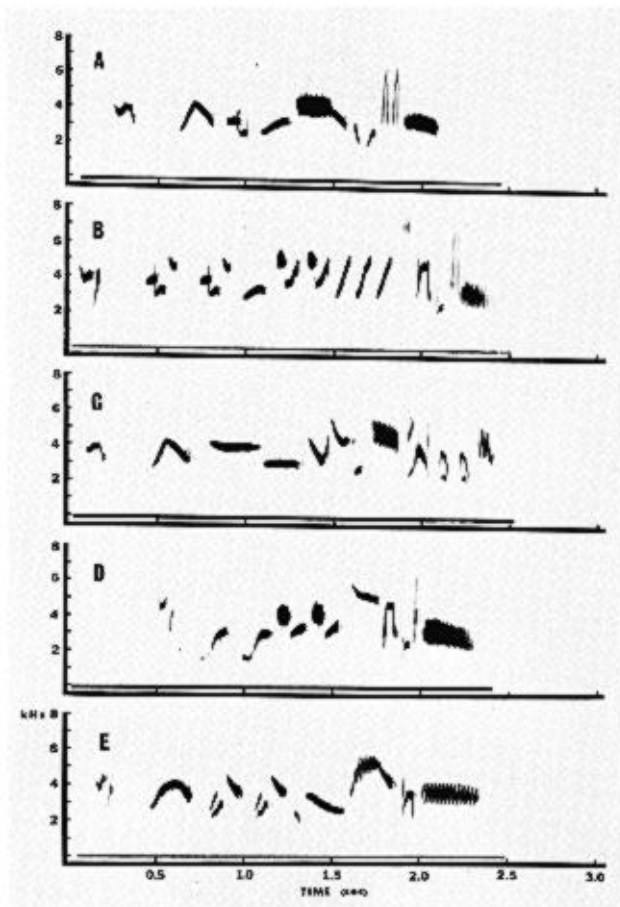


FIG. 2. Sound spectrograms of the song-types used for playback.

RESULTS

Response levels among test sessions.—Table 1 summarizes comparison of the levels of response among test sessions I and II. Throughout the study the level of response remained remarkably constant. Number of chirps and songs, latency of approach and latency of first song were essentially constant. Of the 8 instances of significant variation in the level of response, 6 were attributable to variation in the number of flights performed during the playback (4) and post-playback (2) periods. All instances of significant variation resulted from a decreased level of responsiveness in session II as compared with levels in session I.

TABLE 1
COMPARISON OF THE MEAN NUMBER OF RESPONSES TO PLAYBACK OF CONSPECIFIC SONG-TYPES BETWEEN TEST SESSIONS I AND II

| Response category | Ses- sion | Song broadcast | | | | | | | | | | | | | | |
|---------------------------|--------------|----------------|----------|----|-----------|----------|-------|-----------|----------|------|-----------|----------|------|-----------|----------|--------------|
| | | A | | | B | | | C | | | D | | | E | | |
| | | \bar{x} | \pm SD | N | \bar{x} | \pm SD | N | \bar{x} | \pm SD | N | \bar{x} | \pm SD | N | \bar{x} | \pm SD | N |
| Latency of approach(s) | I | 14.8 | 9.4 | 8 | 13.6 | 16.9 | 9 | 9.5 | 7.9 | 10 | 24.3 | 17.0 | 9 | 20.6 | 19.1 | ^b |
| | II | 15.2 | 10.9 | 12 | 11.0 | 5.5 | 9 | 11.9 | 7.3 | 8 | 7.6 | 5.0 | 10 | 11.9 | 10.0 | |
| Latency of first song(s) | I | 16.1 | 11.5 | 7 | 18.0 | 17.8 | 9 | 19.4 | 10.1 | 9 | 26.7 | 26.7 | 10 | 19.2 | 17.1 | |
| | II | 25.5 | 25.2 | 12 | 27.6 | 24.0 | 10 | 16.2 | 11.7 | 8 | 11.4*** | 10.7 | 10 | 13.9 | 12.5 | II |
| Songs per period | | | | | | | | | | | | | | | | |
| Pre-playback | I | 4.3 | 6.0 | 12 | 6.0 | 8.3 | 9 | 2.2 | 4.4 | 4 | 4.2 | 8.3 | 3.7 | 5.7 | 5.7 | |
| | II | 1.9 | 6.0 | 10 | 1.2 | 3.5 | 4 | 4.4 | 7.2 | 4 | 4.6 | 7.6 | 3.5 | 5.1 | 5.1 | |
| Playback | I | 15.5 | 4.1 | 11 | 15.4 | 3.4 | 9 | 18.3 | 3.4 | 15.8 | 4.8 | 13.8 | 5.0 | 5.0 | 5.0 | |
| | II | 16.8 | 3.3 | 10 | 14.5 | 2.4 | 14.9 | 4.2 | 17.8 | 1.9 | 16.8 | 2.8 | 2.8 | 2.8 | 2.8 | |
| Post-playback | I | 25.8 | 4.1 | 10 | 22.9 | 6.6 | 9 | 22.7 | 2.5 | 20.9 | 4.9 | 19.6 | 2.5 | 2.5 | 2.5 | |
| | II | 26.3 | 4.8 | 10 | 23.5 | 3.5 | 23.0 | 5.7 | 19.9 | 5.3 | 21.8 | 2.1 | 2.1 | 2.1 | 2.1 | |
| Flights per period | | | | | | | | | | | | | | | | |
| Pre-playback | I | 0.4 | 0.7 | 11 | 0.0 | — | 9 | 0.1 | 0.3 | 1 | 0.1 | 0.3 | 0.2 | 0.7 | 0.7 | |
| | II | 0.0 | — | 10 | 0.4 | 1.0 | 0.0 | 0.0 | — | — | 0.1 | 0.3 | 0.1 | 0.3 | 0.3 | |
| Playback | I | 17.7 | 3.0 | 11 | 12.3 | 4.2 | 9 | 14.8 | 4.2 | 11.3 | 3.2 | 11.6 | 2.9 | 2.9 | 2.9 | |
| | II | 7.8*** | 4.2 | 10 | 7.8* | 4.3 | 9.5** | 3.3 | 7.3* | 3.2 | 9.0 | 4.2 | 4.2 | 4.2 | 4.2 | |
| Post-playback | I | 3.6 | 2.4 | 11 | 2.4 | 2.5 | 9 | 2.0 | 1.5 | 2.3 | 1.4 | 1.8 | 1.9 | 1.9 | 1.9 | |
| | II | 0.5*** | 0.7 | 10 | 1.2 | 1.5 | 1.0 | 1.6 | 0.5** | 0.7 | 1.6 | 1.6 | 1.1 | 1.1 | 1.1 | |
| Chirps per period | | | | | | | | | | | | | | | | |
| Pre-playback | I | 0.8 | 2.5 | 10 | 0.0 | — | 9 | 0.0 | — | — | 0.0 | — | 0.0 | — | — | |
| | II | 0.0 | — | 10 | 0.0 | — | 0.0 | 0.0 | — | — | 0.0 | — | 0.0 | — | — | |
| Playback | I | 21.2 | 15.7 | 11 | 23.4 | 41.1 | 9 | 20.4 | 13.9 | 33.0 | 16.1 | 17.4 | 21.5 | 21.5 | 21.5 | |
| | II | 9.8 | 11.1 | 10 | 18.6 | 26.0 | 20.9 | 21.9 | 12.0 | 17.0 | 9.6 | 12.3 | 12.3 | 12.3 | 12.3 | |
| Post-playback | I | 0.9 | 1.6 | 10 | 0.4 | 1.0 | 9 | 0.8 | 2.3 | 1.4 | 2.0 | 2.0 | 3.8 | 3.8 | 3.8 | |
| | II | 0.0 | — | 10 | 0.0 | — | 0.2 | 0.4 | 0.0* | — | 0.8 | 1.5 | 1.5 | 1.5 | 1.5 | |

^a Response levels between session I and II significantly different at, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.
^b If blank, sample size is equal to the N value first encountered to the left.

Response to particular song-types.—The response of Fox Sparrows to playback of song-types A, B, C, D and E was similar. Analyses of variance tests among the song-types tested for latency of approach, latency of first song and number of songs, number of flights and number of chirps for each of the 3 test periods (pre-playback, playback and post-playback) revealed that the only significant variation ($P < 0.05$) was in the number of songs during post-playback in response to song-type A. Birds did not differ in their response to playback of any of the 5 major song-types.

Broadcast of conspecific song elicited a significant increase in the mean number of songs, flights and chirps from the Fox Sparrows compared with levels during pre-playback (Table 2). The mean number of songs sung during post-playback increased significantly over that of the playback level, whereas the mean number of flights and chirps presented by the birds decreased significantly (Table 2). Correlation tests demonstrated a persistent, albeit weak, inverse relationship between the mean number of songs and the mean number of flights and chirps during both the playback and post-playback periods.

Response by birds with and without the playback song-type.—A comparison among those birds which sang and those which lacked a rendition of the major song-type being broadcast during testing indicated that there was no significant difference in the levels of response for any criteria (Table 3). No comparison was possible using song-type C because all test subjects possessed at least one rendition of that song-type.

DISCUSSION

These results clearly show that male Fox Sparrows react similarly to the major song-types that may be sung by their neighboring conspecifics. Approach, flights, chirp calls and, undoubtedly, other behaviors emerge as the most dominant agonistic displays used in close-quarter confrontations with conspecifics. Song appears to be used primarily as a more distant territorial proclamation. Not surprisingly, then, the amount of song elicited during the playback period, which simulates a proximally located intruder, is less than that given during post-playback, which presents no proximal threat. This is not to say that song is not an effective close-quarters agonistic display. Rather, chirp calls are probably more effective for varying the rate and/or strength of the signal and birds simply cannot sing and chirp simultaneously. Also, visual displays may offer more input than auditory during that phase of male-male interaction.

The use of song in the Fox Sparrow as a distant threat among conspecifics differs somewhat from the use of song by other species in the closely related complex of *Passerella-Melospiza-Zonotrichia* sparrows. Playback of conspecific song to *Zonotrichia* sparrows elicits more song per unit

TABLE 2
MEAN NUMBER OF RESPONSES OF PLAYBACK TO CONSPECIFIC SONG-TYPES

| Song broadcast | Latency to first approach(s) | Latency to first song(s) | Response category | | | | | | | | | | | |
|----------------|------------------------------|--------------------------|-------------------------------|-----|----------------------|---------------------|--------------------|---------------------|--------------------|-----|---------------------|--------------------|--------|--|
| | | | Songs per period ^a | | | | Flights per period | | | | Chirps per period | | | |
| | | | pre-p | p | post-p | | pre-p | p | post-p | | pre-p | p | post-p | |
| A | \bar{x} | 15.0 | 22.0 | 3.3 | 16.1 ^{***b} | 26.2 | 0.2 | 13.0 ^{***} | 2.1 ^{***} | 0.3 | 15.8 ^{***} | 0.5 ^{***} | | |
| | SD | 10.0 | 21.3 | 6.1 | 3.7 | 4.3 | 0.5 | 6.2 | 2.3 | 1.7 | 14.6 | 1.2 | | |
| | N | 20 | 19 | 21 | ^c | | | | | | | | | |
| B | \bar{x} | 12.2 | 23.5 | 3.5 | 14.9 ^{***} | 23.2 ^{***} | 0.7 | 9.9 ^{***} | 1.8 ^{***} | 0 | 20.8 ^{***} | 0.2 ^{**} | | |
| | SD | 12.0 | 21.6 | 6.5 | 2.8 | 5.0 | 0.2 | 4.7 | 2.1 | 0 | 33.1 | 0.7 | | |
| | N | 17 | 19 | 19 | | | | | | | | | | |
| C | \bar{x} | 10.5 | 17.8 | 3.4 | 16.5 ^{***} | 22.8 ^{***} | 0.2 | 12.0 ^{***} | 1.5 ^{***} | 0 | 20.7 ^{***} | 0.6 ^{***} | | |
| | SD | 7.5 | 10.7 | 6.0 | 4.1 | 4.3 | 0.05 | 4.5 | 1.6 | 0 | 18.0 | 1.6 | | |
| | N | 18 | 19 | 19 | | | | | | | | | | |
| D | \bar{x} | 15.5 | 18.2 | 4.4 | 19.6 ^{***} | 20.4 [*] | 0.3 | 9.2 ^{***} | 1.4 ^{***} | 0 | 22.0 ^{***} | 0.7 [*] | | |
| | SD | 14.7 | 21.2 | 7.7 | 3.6 | 5.0 | 0.1 | 3.8 | 1.4 | 0 | 35.9 | 1.5 | | |
| | N | 19 | 19 | 19 | | | | | | | | | | |
| E | \bar{x} | 15.8 | 16.3 | 3.6 | 15.3 ^{***} | 21.3 ^{***} | 0.2 | 10.2 ^{***} | 1.7 ^{***} | 0 | 13.3 ^{***} | | | |
| | SD | 15.1 | 14.6 | 5.2 | 4.3 | 2.9 | 0.5 | 3.8 | 1.5 | 0 | 17.2 | 0.9 ^{**} | | |
| | N | 20 | 19 | 19 | | | | | | | | 2.1 | | |

^a Pre-playback period (pre-p), playback period (p), post-playback period (post-p).

^b Asterisks indicate a significant difference between that response level and that which is directly to its left (pre-p and p; p and post-p) (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

^c If blank, sample size equals the first one located to the left in that row.

time during the actual playback period than during the post-playback period (White-crowned Sparrow [*Z. leucophrys*], Verner and Milligan 1971; White-throated Sparrow [*Z. albicollis*], Brooks and Falls 1975b). Contradictory results for *Z. albicollis*, however, are available (Lemon and Harris 1974; Brooks and Falls 1975 a,b; Falls and Brooks 1976). The Song Sparrow (*Melospiza melodia*) responds to conspecific playback in a manner more similar to that in Fox Sparrows, with the greatest number of songs per unit time occurring during post-playback (Kroodsmma 1976a, Harris and Lemon 1976). In contrast to *M. melodia*, however, conspecific playback experiments with Lincoln's Sparrow (*M. lincolnii*) in June and July indicate that this species rarely uses song as an agonistic display during the playback session (Martin, pers. obs.).

The question persists as to why Fox Sparrows and most other oscines possess such elaborate songs and song repertoires. (However, see Lein 1972, 1978, concerning warblers [*Dendroica* spp.]). It appears that, regardless of whether birds possess complex songs (e.g., Indigo Bunting [*Passerina cyanea*] Shiovitz 1975) or rather simple songs (e.g., *Z. albicollis*, Brooks and Falls 1975b), only a small portion of the structuring of song is required for, or used in, species recognition by conspecifics (see also review in Emlen 1972). Singing behavior in Fox Sparrows seems to be highly redundant in conveying species identity. During 1973 1 male possessed only broken song and a much reduced syllable-type repertoire. This bird managed to establish itself in what I considered a "quality" Fox Sparrow territory, mate and fledge 3 young. The present study shows that the type of songs broadcast to males appears to have little effect upon their response, regardless of whether or not they possess a similar song-type. Species specificity apparently is encoded at the level of syllable-types, rather than at the level of entire songs. This fact is not totally unexpected. If other species of birds and humans can differentiate species by hearing only partial or broken songs (thus, for the most, using syllables), why should we not presume, or expect, Fox Sparrows to possess similar abilities?

Detailed study of habituation in Fox Sparrows to song repertoires of various sizes and composition of song-types, although as yet incomplete, indicates that male Fox Sparrows do not habituate faster to repertoires with fewer types of songs when songs are presented at the species-typical rate of singing (Martin, pers. obs.). The only noticeable, but statistically nonsignificant, waning of response to test procedures during the present study was in the number of flights and chirps performed during the playback period (Table 2). However, it is relevant that the behavior of singing itself did not appear to have been markedly affected during the testing.

Thus, with the above information and the knowledge of the equality of

TABLE 3
COMPARISON OF THE MEAN NUMBER OF RESPONSES TO PARTICULAR CONSPECIFIC SONG-TYPES AMONG BIRDS WHICH DID AND DID NOT
POSSESS SUCH A SONG-TYPE IN THEIR REPERTOIRE

| Criteria of response | Condition of response | Song broadcast | | | | | | | | | | | |
|--------------------------|-----------------------|------------------|----|-------|------------------|----|-------|------------------|----|-------|------------------|----|-------|
| | | A | | | B | | | D | | | E | | |
| | | $\bar{x} \pm SD$ | df | t | $\bar{x} \pm SD$ | df | t | $\bar{x} \pm SD$ | df | t | $\bar{x} \pm SD$ | df | t |
| Latency of approach(s) | with | 16.4 ± 10.2 | 18 | 0.670 | 13.6 ± 13.9 | 14 | 0.883 | 17.8 ± 15.7 | 15 | 0.548 | 14.3 ± 13.7 | 18 | 0.488 |
| | lacking | 13.1 ± 10.9 | | | 7.3 ± 3.9 | | | 12.5 ± 11.7 | | | 10.9 ± 11.0 | | |
| Latency of first song(s) | with | 22.4 ± 21.9 | 16 | 0.127 | 26.9 ± 23.3 | 14 | 1.499 | 19.2 ± 22.4 | 16 | 0.046 | 15.7 ± 18.0 | 18 | 0.824 |
| | lacking | 20.9 ± 24.6 | | | 8.9 ± 5.7 | | | 18.6 ± 19.4 | | | 23.8 ± 20.4 | | |
| Songs per | | | | | | | | | | | | | |
| Playback | with | 15.3 ± 3.8 | 19 | 1.823 | 14.8 ± 3.1 | 17 | 0.461 | 17.2 ± 1.3 | 17 | 0.214 | 17.0 ± 2.9 | 17 | 0.870 |
| | lacking | 18.3 ± 2.2 | | | 15.7 ± 0.6 | | | 16.8 ± 4.1 | | | 14.9 ± 4.4 | | |
| Post-playback | with | 26.2 ± 4.3 | 19 | 0.035 | 23.5 ± 5.4 | 17 | 0.565 | 18.0 ± 4.7 | 17 | 1.255 | 21.2 ± 2.9 | 17 | 0.403 |
| | lacking | 26.1 ± 4.5 | | | 21.7 ± 1.5 | | | 21.2 ± 4.9 | | | 20.7 ± 2.5 | | |
| Flights per | | | | | | | | | | | | | |
| Playback | with | 12.6 ± 6.8 | 19 | 0.366 | 10.3 ± 4.8 | 16 | 1.067 | 9.4 ± 2.4 | 17 | 0.508 | 8.6 ± 3.6 | 18 | 1.121 |
| | lacking | 13.7 ± 5.0 | | | 7.3 ± 4.9 | | | 8.2 ± 3.9 | | | 10.7 ± 3.7 | | |
| Post-playback | with | 1.8 ± 2.1 | 17 | 0.023 | 1.7 ± 1.9 | 17 | 0.485 | 1.8 ± 1.6 | 17 | 0.781 | 2.2 ± 1.9 | 17 | 0.749 |
| | lacking | 1.8 ± 1.8 | | | 2.3 ± 3.2 | | | 1.2 ± 1.4 | | | 1.6 ± 1.4 | | |
| Chirps per | | | | | | | | | | | | | |
| Playback | with | 11.8 ± 12.9 | 17 | 1.044 | 24.1 ± 35.3 | 17 | 0.960 | 11.0 ± 20.7 | 17 | 0.792 | 3.6 ± 6.4 | 18 | 1.563 |
| | lacking | 18.8 ± 16.2 | | | 4.0 ± 3.6 | | | 26.0 ± 39.9 | | | 16.7 ± 18.0 | | |
| Post-playback | with | 0.6 ± 1.5 | 19 | 0.858 | 0.2 ± 0.8 | 17 | 0.316 | 0.0 ± — | 17 | 1.177 | 0.3 ± 0.6 | 15 | 0.685 |
| | lacking | 0.1 ± 0.4 | | | 0.3 ± 0.6 | | | 0.9 ± 1.7 | | | 1.3 ± 2.3 | | |

response to the various playback tests, the major song-types of Fox Sparrows appear to be of equal valence to the intended male receivers. This contention, however, does not totally negate the possibility that song complexity is important in lessening the singer's habituation to the behavior of singing or, possibly, the female's ability to habituate to male song. This study only measures the response of the male receiver.

Song-types linked together in rather rigid sequences, as they are in Fox Sparrows, may be perceived as but a single behavioral event by the signaler and receiver—singing. However, with regard to the signaler and the female receiver, there may be a critical minimum that must be met, the length and complexity of which is about 2 songs in Fox Sparrows (Martin 1977), below which the extent and rapidity of habituation is much higher and is selected against. Thus, in Fox Sparrows there may be an important difference between habituation to the agonistic function or message of the display by rival males and the act of performing the display or the female's response to song. Although remote, song may even serve the "Beau Geste" function as proposed by Krebs (1976a,b; 1977), in which case habituation may have played but a minor role in the shaping of Fox Sparrow singing behavior. It seems reasonable to consider that natural selection may have molded song in the Fox Sparrow more in line with its epigamic functions rather than with its agonistic functions. Although such an hypothesis seems remote in a monogamous species which attracts only 1 female per breeding season (Krebs 1976b, 1977; Kroodsma 1977) song may be of importance in stimulation of the female and synchronization of the pair's breeding effort (Kroodsma 1976b). Further study designed to measure the times of spring arrival, pairing, nesting and also clutch-size, fledging success and territory quality should help clarify this possibility.

SUMMARY

Agonistic response to tape-recorded playback of particular conspecific song-types was measured in male *Passerella iliaca* breeding in Logan Canyon, Cache Co., Utah, during 1976. Only 1 song-type (either A, B, C, D or E) was presented during each test day; each bird was tested twice with each song-type. Parameters measured during pre-playback, playback and post-playback to indicate level of agonistic response were: number of songs sung, latency to first song and latency of approach after the first song of playback, number of "chirp" calls uttered and number of flights performed.

Response levels of all agonistic behaviors remained remarkably constant throughout the testing. However, a significant decrease in response between the first series of tests and the second series was noted in the mean number of flights performed during some of the playback and post-playback sessions. Except for a significant difference in the mean number of songs uttered during post-playback in response to song-type A, analysis of variance indicated no significant variation among song-types for any of the response criteria. However, mean number of songs, flights and chirps during playback increased significantly over pre-playback levels. Mean number of songs sung during post-playback also increased significantly over

that during playback, whereas mean numbers of flights and chirps decreased. Birds which were never heard to sing a particular song-type responded to its broadcast as strongly as those which did sing it.

These results are interpreted as indicating that male *P. iliaca* react similarly to all of the major song-types that may be sung by their neighboring conspecific. Song appears to serve mostly as a distant territorial proclamation, whereas flights, approaches and chirp calls are more important as close-quarter displays. Use of song by *P. iliaca* appears more similar to that observed in *Melospiza melodia* than that in *Zonotrichia* species. Possible reasons for the complex structure of song in *P. iliaca* and the use of more than 1 major song-type by individuals are discussed.

ACKNOWLEDGMENTS

This study was partially financed by a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and funds from the Division of Natural Sciences and Department of Biology at Pacific Lutheran University. Criticism of an earlier draft by J. A. Jackson and W. Thompson measurably improved the manuscript. Logistic support, space and equipment were kindly made available by the Department of Biology at Utah State University. My colleagues there are also thanked for engaging me in many profitable discussions concerning avian behavioral ecology. I especially thank L. R. Martin for her understanding during all aspects of this study.

LITERATURE CITED

- BERTRAM, B. 1970. The vocal behaviour of the Indian Hill Myna *Gracula religiosa*. Anim. Behav. Monogr. 3:79-192.
- BROOKS, R. J. AND J. B. FALLS. 1975a. Individual recognition by song in White-throated Sparrows. I. Discrimination of songs of neighbors. Can. J. Zool. 53:879-888.
- AND ———. 1975b. Individual recognition by song in White-throated Sparrows. III. Song features used in individual recognition. Can. J. Zool. 53:1749-1761.
- DIXON, K. L. 1969. Patterns of singing in a population of the Plain Titmouse. Condor 71:94-101.
- EMLEN, S. T. 1972. An experimental analysis of the parameters of bird song eliciting species recognition. Behaviour 41:130-171.
- FALLS, J. B. 1969. Functions of territorial song in the White-throated Sparrow. Pp. 207-232 in Bird vocalizations (R. A. Hinde, ed.), Cambridge Univ. Press, London.
- AND R. J. BROOKS. 1976. Individual recognition by song in White-throated Sparrows. II. Effects of location. Can. J. Zool. 53:1412-1420.
- AND J. R. KREBS. 1976. Sequences of songs in repertoires of Western Meadowlarks (*Sturnella neglecta*). Can. J. Zool. 53:1165-1178.
- HARRIS, M. A. AND R. E. LEMON. 1976. Responses of male Song Sparrows *Melospiza melodia* to neighboring and non-neighboring individuals. Ibis 118:421-424.
- HARTSHORNE, C. 1956. The monotony threshold in singing birds. Auk 73:176-192.
- . 1958. Some biological principles applicable to song behavior. Wilson Bull. 70:41-56.
- . 1973. Born to sing. Indiana Univ. Press, Bloomington, Indiana.
- HINDE, R. A. 1958. Alternative motor patterns in Chaffinch song. Anim. Behav. 6:211-218.
- ISAAC, D. AND P. MARLER. 1963. Ordering of sequences and singing behaviour of Mistle Thrushes in relationship to timing. Anim. Behav. 11:179-188.
- KREBS, J. R. 1976a. Habituation and song repertoires in the Great Tit. Behav. Ecol. Sociobiol. 1:215-227.
- . 1976b. Bird song and territory defense. New Sci. 70:534-536.

- . 1977. The significance of song repertoires: the Beau Geste hypothesis. *Anim. Behav.* 25:475-478.
- KROODSMA, D. E. 1976a. The effect of large song repertoires on neighbor "recognition" in male Song Sparrows. *Condor* 78:97-99.
- . 1976b. Reproductive development in a female songbird: differential stimulation by quality of male song. *Science* 192:574-575.
- . 1977. Correlates of song organization among North American wrens. *Am. Nat.* 111:995-1008.
- LEIN, M. R. 1972. Territorial and courtship songs of birds. *Nature* 237:48-49.
- . 1978. Song variation in a population of Chestnut-sided Warblers (*Dendroica pensylvanica*): its nature and suggested significance. *Can. J. Zool.* 56:1266-1283.
- LEMON, R. E. AND C. CHATFIELD. 1971. Organization of song in Cardinals. *Anim. Behav.* 19:1-17.
- AND ———. 1973. Organization of song of the Rose-breasted Grosbeaks. *Anim. Behav.* 21:28-44.
- AND M. A. HARRIS. 1974. The question of dialects in the songs of White-throated Sparrow. *Can. J. Zool.* 52:83-98.
- MARLER, P. 1956. Behaviour of the Chaffinch, *Fringilla coelebs*. *Behav. Suppl.* 5. 184 p.
- MARTIN, D. J. 1976. Structure of songs and the organization of singing in Fox Sparrows breeding in northern Utah and southern Idaho. Ph.D. dissert., Utah State Univ., Logan, Utah.
- . 1977. Songs of the Fox Sparrow. I. Structure of song and its comparison with song in other Emberizidae. *Condor* 79:209-221.
- MILLIGAN, M. M. AND J. VERNER. 1971. Interpopulation discrimination in the White-crowned Sparrow. *Condor* 73:208-213.
- MULLIGAN, J. A. 1966. Singing behavior and its development in the Song Sparrow, *Melospiza melodia*. *Univ. Calif. Publ. Zool.* 81:1-76.
- SHIOVITZ, K. A. 1975. The process of species-specific song recognition by the Indigo Bunting, *Passerina cyanea*, and its relationship to the organization of avian acoustical behavior. *Behaviour* 55:8-179.
- SMITH, W. J., J. PAWLKIEWICZ AND S. T. SMITH. 1978. Kinds of activities correlated with singing patterns of the Yellow-throated Vireo. *Anim. Behav.* 26:862-884.
- SOKAL, R. R. AND F. J. ROHLF. 1969. *Biometry*. W. H. Freeman and Co., San Francisco, California.
- VERNER, J. AND M. M. MILLIGAN. 1971. Responses of male White-crowned Sparrows to playback of recorded songs. *Condor* 73:56-64.

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ACCEPTED 1 APR. 1979.