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SONG OF THE RUFOUS-SIDED TOWHEE (Pipilo erythrophthalmus)
ON LONG ISLAND, NEW YORK

by

DAVID N. EWERT

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1978

David Ewert

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

SONG OF THE RUFOUS-SIDED TOWHEE

by

David Ewert

Adviser: Dr. Wesley E. Lanyon

I studied geographical variation in song, response to broadcast song and the development of song in the Rufous-sided Towhee (Pipilo erythrophthalmus) on Long Island, New York. Song repertoires of towhees are stable from year to year and largely consist of individually unique song-types. Only about 5% of 411 different song-types were shared by two or more birds and only 30% of 166 individuals from three localities on Long Island shared a song-type with one or more birds. While many syllables of song were shared between individuals, the distribution of birds having shared syllables was frequently not restricted to contiguous individuals. Consequently, populations of towhees on Long Island do not appear to have dialects. Banding data suggest that few juvenile birds return to their home site to breed. I believe that many young birds fail to locate their natal site after migrating north from their wintering grounds. Thus, migration, as a corollary of increased dispersal, may inhibit the formation of dialects in towhees. Data from other studies of song of resident and migratory populations of towhees from other parts of the United States and of White-crowned Sparrows (Zonotrichia leucophrys) and Song Sparrows (Melospiza melodia) tend to support the contention that migratory populations of these species are less likely to have dialects than resident populations.

I conducted playback experiments with towhees on Long Island with songs of towhees recorded from New York, California, and Guatemala; with songs of Common Yellowthroats (Geothlypis trichas), White-crowned Sparrows and Green-tailed Towhees (Pipilo chlorurus); with one song of an acoustically isolated male and with variously isolated parts of songs recorded on Long Island. Towhees did not respond to broadcasts of song of other species nor to the song of the Rufous-sided Towhee from California. The song of the acoustically isolated male and individual syllables of song evoked weak responses while complete songs and songs consisting of either a note-complex or trill phrase elicited moderate to strong responses. The results from these experiments suggest that towhees recognize song of conspecifics on the basis of a combination of syntax, frequency and temporal features of song. This redundancy is probably necessary to allow for identification of individuals and to allow for locally distributed environmental factors which may differentially distort or attenuate different properties of song.

One male towhee raised in acoustic isolation from the egg failed to develop song typical of wild towhees. The sequence of syllables of the song was not as predictable as the sequence of syllables of free-living towhees and the tempo of the songs was slower than songs of wild birds. The isolated male had no songs containing a trill, unlike wild towhees, where every individual I recorded had at least one song-type containing a trill.

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Dr. Alvin Liberman allowed me to use the sound synthesizer at the Haskins Laboratories in New Haven, Conn. My colleagues at the American Museum of Natural History assisted in many and diverse ways through their friendship and their willingness to share their knowledge and experience.

I thank Gilbert Bergen, formerly of the Connetquot River State Park, for generously allowing me access to the Connetquot River State Park. Permission to use Tobay Beach was through the courtesy of the town superviser of Oyster Bay. Dr. Wesley E. Lanyon gave me access to the Kalbfleisch Field Research Station. I thank him, Vicki Lanyon, Cynthia (Lanyon) Duncan, Scott Lanyon, James Mansky and the late Edward Szaly for making my visits there such a pleasure. Ivy Kuspit encouraged me, particularly in the last stages of writing.

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INTRODUCTION

The study of song in birds has provided a great deal of information on the processes that affect acoustic communication and how and why these systems develop. In only a few species however, most notably the Indigo Bunting (Passerina cyanea), has enough information been gathered to begin to understand how song is used to broadcast information and how the received information is used by other conspecifics. Yet, it is difficult to generalize the results from these studies to species having more complex repertoires. Thus, in this dissertation I present data on various aspects of song in the Rufous-sided Towhee (Pipilo erythrophthalmus), a species where most individuals have several song-types, many of which are individually-specific, in an attempt to understand why the repertoire of this species is so complex. Here I report on the variation of song within and between populations, the response of birds to playback experiments, and the development of song. Each section is presented as a separate paper. The results from each section are interwoven into the discussions of other sections so that no final conclusion is presented.

Geographical variation in avian song has received much attention (for most recent reviews see Thielcke, 1969; Lemon, 1975), but the factors governing the occurrence and maintenance of dialects remain poorly understood. Although the interaction of dispersal and learning is important in determining whether dialects occur, few hypotheses predict when dialects should occur based on this interaction and other aspects of singing behavior and the environment. In this paper I assess one aspect of dispersal on the formation of dialects by comparing the results of studies of song from migratory and resident populations of the Rufous-sided Towhee (Pipilo erythrophthalmus) with other species. Based on these data, I explore the possibility that increased dispersal, as a corollary of migration, may inhibit the formation of dialects. I relate these data to the hypothesized functions of dialect, and discuss how generally these conclusions may be applied.

This paper is largely based on geographical variation in the song of the Rufous-sided Towhee at three localities on Long Island, New York. At one of these localities I studied song of color-banded males over a seven-year period to see whether locally distributed features of song remained in the population over several breeding seasons. The analysis of micro-geographical variation in song and of year to year variation in song at one locality has not appeared in most studies of geographical variation in song.

METHODS AND MATERIALS

I recorded songs of Rufous-sided Towhees from 1969 through 1975 at the Kalbfleisch Field Research Station, Huntington, Suffolk County, New York (40° 50′N, 73°20′W), during 1973 at Connetquot River State Park, Islip, Suffolk County, New York (40°46′N, 73°09′W), and in 1972 at the J.F. Kennedy Sanctuary (Tobay Beach) on the barrier beach in Nassau County, New York (40°37′N, 73°27′W) (see Fig. 1). The straight line distance between Kalbfleisch and Connetquot is about 11 miles (15 km), between Kalbfleischhand Tobay Beach 16.5 miles (19 km), and between Connetquot and Tobay Beach 20 miles (28 km). Towhees at Kalbfleisch inhabited deciduous woodland dominated by oak (Quercus spp.), Flowering Dogwood (Cornus florida), and Red Maple (Acer rubrum), that was interspersed with shrubby woodlands of birch (Betula populifolia and B. lenta), oak, bayberry (Myrica pensylvanica) and other trees and shrubs. The dense ground and vine cover at Kalbfleisch was dominated by catbriar (Smilax rotundifolia) and poison ivy (Rhus radicans). At Connetquot oak and pitch pine (Pinus rigida), with an understory of Vaccinium spp. occurred in most towhee territories. At Tobay Beach dense thickets of 10- to 15-foot (3 to 4 m) wild cherry (Prunus serotina), chokeberry (Pyrus spp.), bayberry and poison ivy grew between the leeward side of a barrier beach and a salt marsh. Towhees selected these thickets for their territories.

I analyzed 441 songs of 166 individuals from the three localities. Practically all territorial males at Kalbfleisch were recorded during each of the seven years, where I recorded a total of 39 birds. I recorded 13 males at Tobay Beach. Approximately 11% of the territorial males (one pair per 1.25 hectares, 1225 hectares of habitat, 114 of an estimated 980 males present) were recorded at Connetquot. The location of the territories of individuals at Kalbfleisch during 1969 through 1975 are depicted in Figs. 2 through 8 and at Connetquot in Fig. 9. Data on the occurrence of individuals at Kalbfleisch from 1969 through 1977, including banding data, are presented in Appendix 1 . The number of different song-types and different syllables per individual, along with a list of different song-types recorded from each individual and the location on tape from which a sonogram was made are presented in Appendices 2, 3, and 4.

Banding methods. At Kalbfleisch I banded males, some females, and as many nestlings and fledglings as possible with United States Fish and Wildlife Service bands and with unique combinations of three plastic bands of various colors. Males were attracted to mist nets and captured by broadcasting song from a speaker placed under a net. In some cases a mummified male towhee was mounted on a tripod and placed near the center of the net. Because females did not respond to playback they could be banded only if nestlings were located in nests on the ground, or if fledglings could be captured. A trap could then be placed over the nest or fledgling and the female captured as she came to the nest or to feed the young. This technique was also used to capture males feeding young. The birds recorded at Connetquot and Tobay Beach were not banded.

<u>Sampling methods</u>. Individuals at Kalbfleisch were observed at different times of the day and breeding season, and I monitored these birds until no familiar songs were heard or recorded. All song-types were sung throughout the breeding season. Birds at Connetquot and Tobay Beach were usually recorded on only one day for periods ranging from 15 to 45 minutes, although some birds subjected to playback experiments were recorded on two days.

I believe I tape recorded the complete repertoires of 31 individuals at Kalbfleisch (see Table 1) and 37 individuals at Connetquot (see Table 2). Seventeen birds at Kalbfleisch were recorded for two or more breeding seasons to determine whether repertoires were stable from year to year. Of these individuals (see Table 1), I recorded six that had no repertoire changes from year to year (K7,K17,K23,K38, K39,K40), two where I recorded fewer song-types only during the second year of four years recording (K2,K32), and eight where I recorded more song-types for up to two years after the first year of recording (K1,K3,K18,K19,K22,K30,K31,K42). In these cases only new song-types were added to the repertoire previously recorded. I recorded K37 for only two years and recorded fewer song-types during the second year. I believe this variation is due to uneven recording efforts from year to year and does not indicate annual changes in repertoire size. Consequently, calculation of repertoire size for each individual is based on the maximum repertoire size observed even though not all song-types may have been recorded each year.

The data from the Kalbfleisch population are largely based on color-banded birds but also include unbanded birds recorded continually in one area that were recorded four or more days during a breeding season. The unbanded birds were recognized by associating particular song-types with specific locations. Repertoire size of birds from Connetquot is based on those birds recorded two or more days, usually just prior to and after playback experiments. None of the Connetquot birds were banded and I associated a set of song-types with a territory site to identify individuals.

Instrumentation. I made tape recordings with a Uher 4000-L tape recorder with a Uher M512 microphone mounted at the focal point of a 24-inch parabolic reflector made of fiberglas. A Uher preamplifier was used. Most recordings were followed by recording the 440 Hz fundamental of a pitch pipe to check the relative accuracy of recordings made at different times. Sonograms were made with a Kay Electric Co. Model 6061-B Sonograph using the FL-1 filter. I made sonograms with both the wide and narrow band filters to obtain temporal and frequency characteristics, respectively, for each song.

Terminology. The terminology used here largely follows

Mulligan (1966) and Kroodsma (1974), with minor modifications (see Fig. 10). A comprehensive review of terminology used to describe bird song has been made by Shiovitz (1975).

Note. A continuous trace on the sonogram.

Syllable. A note or group of notes identified as a discrete component of a song; syllables forming part of the trill are designated by numbers, and all other syllables are designated by letters.

Trill. Consecutive rendition of the same syllable three or more times.

Phrase. A section of a song, either a note-complex (that part of the song composed of unrepeated syllables or those repeated once only) or trill (that part of the song composed of syllables repeated two or more times).

Song-type. A stereotypic sequence of phrases repeated in a consistent manner in the repertoire of an individual.

Bout. A series of songs, usually of the same song-type, separated by silent intervals of at least 60 secs from another series of songs.

Geographical variation. Used in the broad sense of variation in song at different localities and <u>without</u> the connotation of Nottebohm (1969) that refers to "differences in song over long distances and between populations which normally do not mix."

Dialect. Variation "appearing as a consistent difference in the predominant song type between one population and another of the same species" (Marler and Tamura, 1962).

I felt that other definitions of dialect (for example, Harris and Lemon, 1972) were ambiguous. Much of this ambiguity arises when a song-type or syllable, occurring in two or more localities but not in the songs of most individuals at any one locality, is used to designate dialect areas. In such cases it is possible that the distribution of different song-types or syllables would not be concordant; the delineation of dialect areas then becomes a subjective impression of relative similarity. I believe, then, that those definitions of dialect requiring only that there be some geographical localization of syllables are too inclusive and consequently I use the term in the relatively strict sense of Marler and Tamura (1962).

Classification of Notes and Syllables. Notes and syllables were traced from the sonograms onto tracing paper. I then arranged them in different groups based on their frequency, temporal and shape characteristics; notes on a gradient were designated by the same code. Thus, similar but non-identical notes or syllables could be designated by the same code. I re-examined my arrangement twice before I made the final classification of notes and syllables. This classification of syllables is essentially subjective and these data on the distribution of notes and syllables must be considered only an approximation of the differences between populations.

Statistical Analysis. Most data were analyzed using the SPSS packages at the CUNY/University Computer Center of the City University of New York. Some data were analyzed with the Hewlett-Packard 9810A calculator, using programs available with it. The .05 significance level was used for testing null hypotheses.

Time measurements were taken from the sonograms by drawing perpendicular lines to the base line at the beginning and end of each component of song. In a very few cases the limits of a part of song were so indistinct or faint on the sonogram that no measurements could be made. Measurements were made to the nearest tenth of a millimeter and multiplied by 0.007 to convert the measurements to time in seconds. I measured frequency to the nearest tenth of a kilohertz.

For this analysis of geographical variation in song and repertoire size I analyzed (1) temporal characteristics of song (length of song, length of note-complex and trill phrases and syllables, the time between syllables and phrases) and frequency characteristics of song (the maximum, minimum and frequency range of a song and its phrases and syllables) using univariate F-tests and t-tests and the multivariate technique of discriminant analysis ; (2) the number of syllables per phrase; (3) the rate of delivery of syllables in each phrase; (4) the organization of song into various combinations of note-complex and trill phrases; (5) the distribution of syllables of the note-complex and trill phrases and of shared song-types within and between populations; and (6) the repertoire size of Kalbfleisch and Connetquot populations.

RESULTS

Differences in song between localities have been expressed in several ways, the most common method being that of delineating geographical areas where distinctive song-types or portions of song-types occur. In this study I analyze song with this method in addition to comparing other aspects of song between the three Long Island localities.

Repertoire size. The number of different song-types per individual averages 3.5 and was not significantly different between years at Kalbfleisch (df=6; Kruskal-Wallis H=8.63; $p > .05$) or between Kalbfleisch and Connetquot (df=7; Kruskal-Wallis H=10.14; $p > .05$). At Tobay Beach estimated repertoire sizes were two to six, which is identical to the range of repertoire sizes at Kalbfleisch and very similar to that at Connetquot, but incomplete sampling methods at Tobay Beach do not permit a more detailed comparison. These data suggest that repertoire size does not vary geographically on Long Island.

The repertoire size of Rufous-sided Towhees averages more than one song-type per individual throughout the range of the species, but different sampling techniques make it difficult to compare the repertoire sizes of other populations with the Long Island populations. Kroodsma (1971) reported that of four color-banded males of the subspecies oregonus recorded on five or more mornings, two had repertoires of seven song-types and one each had a repertoire of eight and nine song-types. Three less intensively studied males had repertoires of four, five and six song-types. Molnar (1977) found that repertoire sizes of three to eight ($\bar{x} = 4.5$) occurred among six males of the subspecies erythrophthalmus in New Jersey. One individual from Florida was reported to have eight song-types (Borror, 1959a) and another from Ohio had 22 song-types (Borror, 1972), although Borror probably used different criteria for defining a song-type than I used in this study. Davis (1958), who did not tape record songs, stated that "there are five basic types of song in the repertoire of most individuals" thus implying that the repertoire size of at least one California population of the race <u>megalonyx</u> was at least five. Bent (1968) stated that one bird of the race <u>montanus</u>, of the southern Rocky Mountains and northern Mexico, sang six song-types during 42 minutes of singing in one morning. Another Rufous-sided Towhee recorded in Chihuahua, Mexico had five basic song-types (Marler and Isaac, 1960a). In central Mexico, Sibley (1950) determined that at least two Rufous-sided Towhees had two or more song-types and he believed that some birds at San Felipe, Mexico had only one song-type. Cody and Brown (1970) however, implied that Rufous-sided Towhees at San Felipe had up to two or three song-types. Neither Sibley nor Cody and Brown provided documentation for their conclusions and no investigators, except Kroodsma and Molnar, worked with individually marked birds. These fragmetary data indicate however that repertoires of Rufous-sided Towhees are typically larger than one, perhaps being at least five along the Pacific coast of the United States. Samples are too small to warrant generalizing on the size of the repertoire in other areas away from the New York City area.

<u>Organization of song</u>. Song is organized into note-complex and trill phrases (see Fig. 10). There are only minor differences on Long Island in the proportion of song-types in each population containing songs of each of four categories: (1) only a note-complex

phrase; (2) one or more trill phrases but no note-complex phrase; (3) one note-complex phrase followed by one trill phrase; or (4) other combinations of note-complex and trill phrases (see Table 3). Approximately 88% of the song-types in all three populations have one note-complex phrase followed by one trill phrase and all other categories of song are rare (11.6%). Thus, the three populations on Long Island can not be differentiated by these features of song. These data are similar to those of Borror (1975), who found that only 134 of 765 song-types (17.5%) of the race erythrophthalmus were not of the one note-complex phrase followed by one trill phrase sequence. However, individuals of other races of the Rufous-sided Towhee, particularly those in the western United States, frequently have songs with reduced note-complex phrases or with only trill phrases (Kroodsma, 1971; Borror, 1975).

Number and rate of delivery of syllables. There were no significant differences (one-way analysis of variance) in the average number of syllables per note-complex phrase (df=6,32; F=1.90; $p > .05$) or per trill phrase (df=6,32; F=1.20; $p > .05$) or in the average rate of delivery (syllables/sec) of syllables of the note-complex phrase (df=6,32; F=1.19; $p > .05$) or trill phrase (df=6,32; F=0.97; $p > .05$) between years at Kalbfleisch. These results are based on the average number and rate of delivery of syllables per phrase for all songs of a bird and where each bird was included in the analysis only during the first year of its appearance at Kalbfleisch. Consequently these populations were treated as one population. Variation in the number of syllables per phrase and the rate of delivery of syllables per phrase within one song-type of one individual were not rigorously analyzed.

There were no significant differences between Kalbfleisch, Tobay Beach and Connetquot in the average number of syllables in the note-complex phrase (df=2,163; F=2.60; $p > .05$) or in the trill phrase (df=2,163; F=2.67; $p > .05$). These results are summarized in Table 4. Borror (1975) reported that the race erythrophthalmus has an average of 2.3 syllables (range 1 to 7; N=323 songs) per introductory (=note-complex) phrase and 7.3 syllables (range 1 to 18; N=232 songs) per trill phrase. These data, although based on the characteristics of every song rather than the average characteristics of song of different individuals, are similar to those of Kalbfleisch.

Individuals of the three populations differed in the rate at which they sang syllables of the note-complex phrase (df=2,153; F=13.41; $p < .005$) but not in the rate at which they sang syllables of the trill phrase (df=2,163; F=2.34; $p > .05$). Birds at Tobay Beach sang syllables of the note-complex phrase at a significantly faster rate than birds at both Kalbfleisch (df=49; t=5.30; $p < .001$) and Connetquot (df=115; t=4.62; $p < .001$), while birds at Kalbfleisch and Connetquot were not significantly different from each other (df=142; t=0.82; $p > .05$). The rate of delivery of syllables of the trill phrase for the race erythrophthalmus was reported to be 11.3 syllables/sec (range 4.4 to 40; N=232) by Borror (1975), which is considerably slower than the Long Island populations sampled (see Table 4). The rate of delivery of syllables of the note-complex phrase was not summarized in Borror (1975).

Sharing of song-types. Few song-types were shared among towhees on Long Island. Of 21 song-types (5.13% of 409 song-types and their variants) occurring in the repertoires of two or more birds, 19 were restricted to birds of one locality. Six song-types were shared by neighboring birds within a population, two were shared by both neighboring and non-neighboring birds within a population, eight were shared by non-neighbors within a population and three song-types occurred in the repertoires of different individuals that were found at the same locality in different years (see Table 5). Only three song-types were shared by three or more birds (see Table 5). Forty-six individuals (27.2% of birds recorded) sang song-types shared with other birds. There is then, little basis for delineating dialects on the basis of the distribution of shared song-types.

The proportion of song-types shared among birds seems to vary geographically. Borror (1975) found that 118 of 950 (12.4%) song patterns (= song-types) of an estimated 492 birds recorded throughout the United States and in Ontario, but largely from the northeastern United States, were shared by two or more birds. Within one locality, Blendon Woods, Franklin County, Ohio, 20.8% of the song-types were shared among birds but only 1.8% to 6.9% of the Blendon Woods song-types occurred in areas as close as other parts of Franklin County, Ohio to as far away as North

Dakota (see Table 6; Borror, pers. comm.). Four of 274 Blendon Woods song-types occurred in other states (Maine, Virginia, North Carolina, and North Dakota; Borror, pers. comm.). Kroodsma (1971) found that 26 of 31 song-types recorded from four color-banded males in Oregon that held adjacent territories were shared between them, including three song-types that all four banded males possessed. Seven of 11 song-types (63.5%) of near neighboring males were similar to song-types of the four banded males in contrast to only 10.7% of 32 song-types of more distant males found up to 2 km away.

Data from Borror on the distribution of shared song-types seems to be similar to Long Island data. In both areas a small proportion of song-types were shared between birds and these song-types usually were shared between only two individuals of one population. The data from Kroodsma differs in that a much larger proportion of song-types were shared among several birds. Thus, there appears to be more homogeneity in song in Oregon compared to equivalently sized areas in Ohio and Long Island.

Sharing of syllables. From 441 songs of 166 individuals I defined 79 distinct syllables in the note-complex phrase and 62 distinct syllables in the trill phrase. These syllables are illustrated in Figs. 11 and 12 respectively. Examples of the variation occurring within designated syllables are shown in Fig. 13. The distribution of syllables of both note-complex and trill phrases is listed in Appendices 5 and 6 respectively. These data indicate that approximately 60% of all syllables were endemic to a single locality, about 22% were found in two of the three localities and 18% were found in all three localities (see Table 7).

At least some syllables found in all three Long Island populations occur outside Long Island. Of the 11 syllables of the trill phrase that were most widespread in all three Long Island populations, 10 occurred in the songs of birds in areas sampled by Borror (1959a; see Table 8). Nine of the 10 syllables occurred in Ohio where Borror did most of his recording while a small proportion of these 10 were recorded in Maine, West Virginia, North Carolina, Florida and Michigan. Only trill syllable 51 (illustrated in Figs. 10 and 12) was widespread on Long Island but not recorded by Borror (1959a). The syllable sequence of V followed by D (illustrated in Fig. 10), which is included in the note-complex phrase of more birds on Long Island than any other sequence of syllables, also occurs in Ohio and Michigan (see Fig. 27 of Plate 2 and Table 1 of Borror, 1959a). Except for syllable 51, then, syllables that occur in a relatively large proportion of birds from Long Island are also found outside Long Island. Thus, the Long Island population is not strongly differentiated from other populations of the subspecies erythrophthalmus on the basis of its most widely distributed syllables.

For any one locality on Long Island endemism varied from 24% to

52% for the syllables of the note-complex phrase (see Table 9) and 12% to 48% for the syllables of the trill phrase (see Table 10). The population at Connetquot had more endemic syllables than either Kalbfleisch or Tobay Beach but because the number of endemic syllables increases with sample size I believe this difference is an artifact of sample size.

The distribution of syllables shared between localities indicates that Kalbfleisch and Connetquot birds share proportionately more syllables with each other than either does with Tobay Beach (see Tables 9 and 10). Tobay Beach birds appear to share more syllables with Connetquot birds than with Kalbfleisch birds. Thus, the towhees on this barrier beach off Long Island seem to have developed a relatively distinct set of syllables compared to the populations on the mainland of Long Island.

Of the 85 syllables endemic to one population, 52 (61.2%) occurred in the repertoire of only one bird, 28 syllables (32.9%) occurred in the repertoires of two to five birds of a population and only five syllables (5.9%) occurred in the repertoires of six or more birds (see Table 11). All five syllables found in the repertoires of six or more birds were recorded at Connetquot. Four of these five syllables (J,TTT,38, and 46) were found in either six or seven birds (5.3% and 6.2% of Connetquot birds) and one syllable (31) was found in 15 birds (13.4% of Connetquot birds). Thus, syllables endemic to a single population tended to be found in only a few individuals in each population.

In contrast, syllables found in two or more populations usually occurred in more birds in each population than endemic syllables (see Table 12). These data suggest that syllables endemic to a population are frequently restricted to one individual and can not serve to characterize populations, while syllables that are more widespread geographically also tend to be more common within a population.

Sharing of syllables between individuals whose complete repertoires were recorded at Kalbfleisch suggests that an individual is as likely to share syllables with neighboring birds as it is with non-neighbors. For 30 individuals from Kalbfleisch (see Table 1 for a list of these individuals; K16 not included in this analysis) about 15.4% of the syllables in the repertoires of neighboring birds were shared and 14.6% of the syllables of non-neighboring birds were shared. On the basis of sharing of syllables, then, towhees at Kalbfleisch differ from those in Oregon, where syllables are more likely to be shared between neighbors compared to non-neighbors (Kroodsma, 1971).

The distribution of the 71 syllables recorded at Kalbfleisch through the seven year period shows that some syllables were present all seven years while others appeared in fewer years. The occurrence of the different syllables at Kalbfleisch varied in the number of years a given syllable was present and in the proportion of birds having the syllable in different years (see Tables 13 and 14). Many syllables appeared only in the repertoire of one individual and were present only as long as that individual returned to Kalbfleisch but the proportion of individuals having other syllables steadily increased through successive years (see Tables 13 and 14).

Of the 22 syllables restricted to Kalbfleisch, however, only one syllable of the note-complex phrase (CCC) and one syllable of the trill phrase (17) were present for five or more years, and these two were never part of the repertoires of more than two of the approximately 11 territorial males present in any given year. Consequently, the particular characteristics of a syllable probably could not be used efficiently by birds to identify the towhee population at Kalbfleisch over periods as short as several breeding seasons.

Temporal and Frequency Characteristics of Song

Univariate methods. Univariate F-tests demonstrated that only two of 63 variables were significantly different among all three populations: the minimum frequency of the trill phrase (df=2,397; F=12.63; p <.001) and the length of the trill phrase (df=2,401; F=23.91; p < .001). Yet, these same variables also were significantly different between at least two different years at Kalbfleisch (df=6,109; F=4.12; p < .001; df=6,113; F=4.29; p < .001, respectively). Thus, these data suggest that no single variable of the song could be used by birds to distinguish any of the three populations from each other.

Multivariate methods. Although no single variable may be used to associate song with a particular locality, birds may use a combination of variables simultaneously to associate songs with a particular locality. Consequently, I used a stepwise, multiple discriminant program described by Klecka (1975), which maximally separates groups on the basis of the variables entered in the analysis. This was done to determine which set of variables would have the highest probability of being associated with a population. This analysis of 13 variables of song, the length of song, and its' note-complex and trill phrases, the length of time betwen the note-complex and trill phrase, and the minimum and maximum frequency and frequency range of the song and its note-complex and trill phrases, showed that only three variables, the length of the note-complex phrase (INTRP1TI), the length of the trill phrase (TRLP1TIM), and the minimum frequency of the note-complex phrase (INTPMIF), contributed significantly to the separation of the populations. The results of this analysis are based on the average value of each of these three variables for all songs of each individual. The mean ± standard deviation of these values for each population are presented in Table 15.

Table 16 shows which populations differed significantly from each other based on these three variables. Individuals first appearing at Kalbfleisch in any given year were usually more similar in their characteristics of song to newly-appearing birds in other years at Kalbfleisch then they were to birds from Connetquot or Tobay Beach (see Table 16). The Tobay Beach and Connetquot populations differed from each other and from most Kalbfleisch populations.

These data suggest that birds from different localities differed more from each other than birds which appeared in different years at Kalbfleisch. Thus, some continuity of features of song occurred in the populations from Kalbfleisch.

Of the three discriminant functions derived, two contributed significantly to the separation of the populations (see Table 17). The relative loadings of each of the three variables to the two significant standardized discriminant functions are shown in Table 18. These two functions accounted for 91% of the total variance (see Fig. 14). The minimum frequency of the note-complex phrase (INTPMIF) contributed most to the first function and served to separate Connetquot, which had the lowest minimum frequency of the note-complex phrase (see Table 15). The length of the note-complex phrase (INTRP1TIM) contributed most to the second function, and it separated Tobay Beach, which had the shortest note-complex phrase, from all other populations. The length of the trill phrase (TRLP1TIM) contributed most to the third function. Thus, the Connetquot and Tobay Beach populations and, to a lesser extent, the 1969 Kalbfleisch population, could be distinguished relatively well from each other and from the other Kalbfleisch populations on the basis of these three variables of song, whereas the 1970-1975 Kalbfleisch populations were relatively similar to each other and clustered together.

The classification of the groups using these discriminant functions shows, however, that the individuals could be classified into their correct group only about 55.4% of the time (see Table 19). This poor discrimination seems to be a result of the tight clustering of the group centroids coupled with a large amount of intrapopulational variation in song. The centroid for each group, which is the group mean along each of the discriminant functions, are tightly clustered for most of the Kalbfleisch populations so that songs from each population would have to be extremely similar to each other for these populations to be discriminated. Where the songs of the populations are variable, then, discrimination would be poor. The data indicate there is considerable variability of song (see Table 15) and individuals of groups that cluster together are frequently not classified to either their own population or to populations that cluster with it (see Table 19). Thus, these three characteristics of song are relatively variable within each group, so that birds could associate song with a specific population with only about 55% accuracy, on the average. Where sample sizes were reasonably large, those populations that were classified more accurately also tended to be separated most clearly along the first two discriminant axes.

Dispersal and Population Dynamics

Dispersal and population dynamics data are available only from the population at Kalbfleisch, where towhees are present from late April through October. Banding data from Kalbfleisch demonstrate that about 60% of adult males (AHY) return the subsequent year (based on observations of color-banded males during this study) and these individuals live an average of 2.4 years (range one to seven years; based on returns of birds banded during their hatching year). Although no banded nestlings of known parentage have returned to Kalbfleisch, about 7% of the males banded as juveniles at Kalbfleisch returned to Kalbfleisch as adults (see Table 20). Most juveniles probably die prior to breeding but the dispersal of surviving juveniles that do not return to Kalbfleisch remains largely unknown. There have been only two foreign recoveries of birds banded as juveniles at Kalbfleisch; one female (65-185394) banded at Kalbfleisch 4 September 1964 was recovered one mile (1.7 km) from Kalbfleisch on 17 May 1966 and another female (68-103506) banded 15 July 1965 at Kalbfleisch was found dead 13 miles (21.7 km) from Kalbfleisch at Westbury, New York on 15 May 1966. Although most Long Island towhees are on territory by mid-May, it is possible these birds were not yet on territory. However, these data suggest that female juveniles, and presumably males, which do not return to Kalbfleisch, may become established at relatively short distances from Kalbfleisch.

The number of young produced per year at Kalbfleisch is difficult to evaluate but is important for determining whether production of young males is sufficient to replace those that die, and thereby determine whether it is possible for song traditions to be maintained over time. Males are monogamous, except for one male (K23) that was polygamous during one of its seven breeding seasons. Parasitism by Brown-headed Cowbirds (_Molothorus ater_) is uncommon but may reduce productivity slightly. Clutch sizes at Kalbfleisch vary from three to six, with most late nestings being due to the failure of earlier nests. Assuming that each female raises one brood, that the average clutch size at Kalbfleisch is 3.5 eggs, and that the sex ratio of the eggs is 1:1, the expected number of males produced annually by the 11 pairs is 19. Since only about 7% of these 19 return to Kalbfleisch, and about 5 of the established males die each year, it appears that only one male can be recruited from the Kalbfleisch population to replace the loss of established males. Thus, it would be difficult to maintain a dialect. These results are concordant with the song data; there is some continuity of song characteristics but little persistence of endemic elements.

Song Development

Rufous-sided Towhees probably learn most of their songs by copying songs, or parts of songs, from other male towhees. This interpretation is supported by an analysis of the repertoires of two males that were banded as juvenile males at Kalbfleisch in years when I recorded the repertoires of all males at Kalbfleisch. These two males, K23 and K30, had a large proportion of the syllables of their repertoires, 71.4% and 60.0% respectively, composed of syllables found in the repertoires of Kalbfleisch birds that were present during the year they hatched. This suggests that these birds copied parts of song from other males in the Kalbfleisch population during their first summer and incorporated these components in their songs. The ability of towhees to copy songs and calls and incorporate them into song is demonstrated by the fact that a very small proportion of towhee songs contain songs and calls of other species (Borror, 1977; Richards, MS; Greenlaw, pers. comm.; Ewert, pers. obs.), including those of the Common Flicker (Colaptes auratus), Tufted Titmouse (Parus bicolor), Carolina Wren (Thryothorus ludovicianus), American Robin (Turdus migratorius), and Field Sparrow (Spizella pusilla). Additionally, one young towhee, raised in captivity with an Ortolan Bunting (Emberiza hortulana) developed at least one song similar to the Ortolan Bunting but lacked any songs resembling that of the towhee (Anon., 1900). Another male, raised in acoustic isolation, developed an aberrant song-type that failed to elicit responses from territorial males (Ewert, in prep.), suggesting that towhees need to hear towhee song for normal development of song to occur.

However, the relatively low rate of sharing of song-types and of syllables may reflect the occurrence of imprecise copying, improvisation (Borror, 1975) or the dispersal of young from hatching sites may be so great that few instances of sharing of song-types are observed. All three factors may contribute to the variation of song seen in Rufous-sided Towhees, although the relative importance of each of these factors to song variation probably varies geographically.

DISCUSSION

Local differences in some temporal and frequency features of song on Long Island occur at localities no more than 30 km apart and appeared to consistently differentiate the Kalbfleisch populations from the Tobay Beach and Connetquot populations. However, song-types are rarely shared between birds and no syllables endemic to a population occurred in more than 14% of the birds of a population. Of those syllables endemic to Kalbfleisch, few remained in a population for several years. Consequently, dialects can not be delineated either spatially or temporally for Rufous-sided Towhees on Long Island. Thus, there is variation in song over short distances, with some continuity of features of song at one locality over time, but differences in song are insufficient to distinguish most birds of one locality from other localities.

Dispersal and variation in song on Long Island. This variation in song is consistent with data on dispersal of towhees on Long Island. Apparently enough young males return to a particular locality so that some continuity of features of song persists, but young birds from other localities, presumably having repertoires different from birds in the area in which they establish territories, replace some of the males which fail to return, so that no dialects result. The overall similarity in song between birds from Kalbfleisch and Connetquot compared to Tobay Beach may be a result of more exchange of first year individuals between Kalbfleisch and Connetquot. This may occur not only because Kalbfleisch and Connetquot are closer together than either is to Tobay Beach, but also because the oak and oak/pine habitats at Kalbfleisch and Connetquot, respectively, are more similar to each other than either is with the _Myrica_ and _Rhus_ dominated thicket habitat on the barrier beach at Tobay Beach. Consequently, birds returning to breed for the first time and unable to establish territories at their home localities, may select nearby areas with similar habitats. Such dispersal, coupled with a system where song is learned from the father or from nearby males during a bird's first summer or fall, could account for the geographical variation of song observed on Long Island.

Variation in song in other populations of Rufous-sided Towhees. Geographical variation in song of migratory and resident populations of Rufous-sided Towhees has been extensively studied by Borror (1959a, 1975), while Kroodsma (1971) intensively studied song of four individuals of a resident population in Oregon. Borror (1972) found no evidence of dialects in the Rufous-sided Towhee, although most areas were not sampled intensively. At Blendon Woods, Franklin Co., Ohio, where Borror has recorded 274 song-types (Borror, pers. comm.)

over a period of several years, only a small proportion of the song-types, introductory (= note-complex) and trill phrases occurred in two or more birds and were endemic to Blendon Woods (see Table 6). This indicates that dialects are absent from populations of towhees in central Ohio. Data from other areas sampled by Borror suggest that dialects do not occur elsewhere in the eastern United States but more intensive recording of individually marked birds in more populations is required to clarify this point. However, populations from Long Island and Blendon Woods do not have dialects because so few components of song are shared among individuals within a population. In contrast, Kroodsma (1971) found considerable sharing of song-types among neighboring males with "a continuous but relatively rapid change in song structure over short distances", suggesting that highly localized dialects may occur. However, sampling more males over a larger area is needed to determine whether dialect regions could be delineated.

Variables affecting the occurrence of dialects in towhees. Of the three areas sampled where data are sufficient to characterize populations for the presence or absence of dialects, the migratory populations of Long Island and Franklin County, Ohio, do not have dialects while the resident population in Oregon has a dialect, or at least approaches the stereotyped variation in song seen in dialects. At least three variables, the presence or absence of migration, the density of the population, or the distribution of available habitat, could influence where young birds establish territories and hence whether dialects occur. This discussion assumes that the chronology of the development of song does not vary between the populations.

Two variables, population density and habitat distribution, do not seem to vary between the eastern and western populations. Territory size on Long Island averages 1.25 ha., and towhees are abundant and widespread. Although data on population densities of the subspecies *oregonus* in Oregon are lacking, towhees are reported to be very common permanent residents in western Oregon, where they inhabit second-growth (Gabrielson and Jewett, 1940). At Point Reyes, California densities of male towhees of the subspecies *falcifer* are reported to range from 20 males/40.5 ha. to 45 males/40.5 ha. in chaparral and from 20 to 26 males per 40.5 ha. in mature Douglas Fir (*Pseudotsuga menziesii*) forest (American Birds, 25-29 (6)). This is equivalent to an average territory size of 0.99 ha. in chaparral and 1.72 ha. in mature Douglas fir forest, assuming each of the territories lay completely within the study site and all areas of the study sites were occupied by towhees. Towhees are apparently common and widespread on both the east and west coasts of the United States, and differences in population density or the distribution of favorable habitat do not account for the differences in geographical variation in song.

The third variable, the migratory habits of the populations, is the most obvious difference between the population from Oregon and the populations from Long Island and Ohio, that might affect dispersal of young birds. The non-migratory and presumably less mobile population from Oregon (see Kroodsma, 1971 for data on movement of birds from Washington) has characteristics of a dialect while the migratory populations do not. Presumably this is because many young of migratory populations of birds fail to re-locate their natal site and thus disperse over a relatively wide area (Kendeigh, 1974; p. 280), as seems to be the case with Song Sparrows (Melospiza melodia; Nice, 1937; Johnston, 1956). If this holds true for towhees, migration might affect local dispersal of young sufficiently to contribute to the differences in variation of song observed between the migratory and non-migratory populations. Thus, given the present data, the differences in migration provide the simplest mechanism or explanation that can be cited to account for differences in the occurrence of dialects between these populations of towhees.

Dialects may not serve an important communicatory function in the Rufous-sided Towhee. Where repertoire sizes are relatively large, as in the Oregon population, each individual may have too large a repertoire for shared song-types to be associated with a particular locality. Probably the identification of a locality by song is least ambiguous when one song-type is shared among all birds of one population. The occurrence of larger repertoire sizes suggests that other selection pressures become important in governing the compostion of the repertoire of a bird. Towhees from Oregon have repertoires where it may be possible to associate several song-types with one locality but this could simply be a non-adaptive result of the interaction between short distance dispersal and the timing of song development. Further, the absence of dialects may not be adaptive. DeWolfe _et al_ (1974) postulated that individuals of migratory populations of White-crowned Sparrows (_Zonotrichia leucophrys_) are under strong selective pressure for characteristics of song that facilitate individual recogntion, so that energy is conserved in re-establishing territories and attracting mates each breeding season. Thus, selection would favor individually-specific song within a migratory population and a repertoire size skewed toward one. While migratory populations of towhees have a smaller average repertoire size, and have a higher proportion of components of song that are individually specific than the resident population, the variation in song is still complex enough that recognition of individuals would involve associating up to six song-types with an individual. These data do not suggest that there is strong selective pressure for a simplified repertoire among individuals of migratory populations. Thus, the absence or occurrence of dialects in towhees are probably not a result of selection pressure to permit birds to associate particular localities with particular song-types but may be an artifact of how individuals of a population disperse.

It is not known, however, whether dialects serve an adaptive function in populations of towhees from the west coast of the United

States. While populations that are comprised of individuals that are permanent residents may be more likely to have dialects than migratory populations, other factors, not yet determined, may correlate with or contribute to the occurrence of dialects. Further study of the singing behavior and response of towhees to song are needed to determine if localized features of song serve a specific function. Such studies could determine whether dialects have an adaptive function or are a secondary and non-adaptive result of other selective pressures or are some combination of both factors. It remains speculative, then, whether the occurrence or absence of dialects in towhees is a result of selective pressure acting on the association of song with a specific locality or habitat.

Other species where geographical variation in song has been described for migratory and resident populations

Data on geographical variation of song of other species where both resident and migratory populations have been studied show that most populations of one species either have or lack dialects and that intrapopulational variation in song tends to be greatest in migratory populations. These species include three emberizine finches, the White-crowned Sparrow, Rufous-collared Sparrow, and Song Sparrow and a cardueline finch, the House Finch (*Carpodacus mexicanus*).

White-crowned Sparrow. Geographical variation in song of White-crowned Sparrows has received more attention than that in any other species. Song has been studied in migratory populations of the subspecies gambelii in Alaska (DeWolfe et al, 1974), in oriantha in California (Orejuela and Morton, 1975) and Colorado (Baker, 1975) and in pugetensis (Baptista, 1977). Song variation of resident populations of the race nuttalli has been described by Marler and Tamura (1962), Baker (1974, 1975) and Baptista (1975). Most individuals of these populations have one song-type per individual and one trill phrase is shared by most members of a population. White-crowned Sparrows have much less variation in song than Rufous-sided Towhees, even where populations are not reported to have dialects.

Dialects were not reported by DeWolfe et al in migratory populations of gambelii in Alaska or by Baker (1975) for a migratory population of oriantha. However, Baker found that approximately 60 males from the East River watershed in Colorado shared a similar song-type that differed from song-types recorded from a disjunct population of birds occurring 16 km away at Kebler Pass. More extensive sampling may reveal that dialects occur in White-crowned Sparrow populations in Colorado (Baptista, pers. comm.). DeWolfe et al noted that most birds of a population shared a similar trill phrase but other parts of the song, the whistle and warble, showed considerable variation within populations. The relative abundance of two of the warbles changed in one population from 1967 to 1971. White-crowned Sparrows in Alaska have enough variation in song within a population that DeWolfe et al did not consider these populations to have dialects.

Baptista (1974, 1977) found dialects in migratory populations of _pugetensis_ from Oregon to British Columbia but stated that "the trained eye can distinguish a greater amount of individual variation in the songs of local populations of _pugetensis_ than in any population of _nuttalli_ so far described" (Baptista, 1974). In a more recent analysis of dialects of _pugetensis_, Baptista (1977) delineated two dialects that were considered to be part of a northern theme group. The two theme groups were differentiated primarily by the sequence of the buzz, complex syllables and trills following the introductory whistle while different dialects were defined primarily by the distribution of terminal trills. Some local populations within a dialect could be distinguished from each other by their complex syllables. From these data, Baptista concluded that migratory populations of _pugetensis_ have dialects that are not as localized as those of _nuttalli_, but that intrapopulational variation in song was similar to _nuttalli_ in five of the six dialects except in the area sampled in British Columbia where it was apparently greater. Orejuela and Morton (1975) found that most populations of the migratory subspecies _oriantha_ in the Sierra Nevada of California had dialects, except at Lassen National Park, where no dialects occurred. They found the greatest amount of intrapopulational variation in song among small populations in suboptimal habitat and that dialects were best defined where habitat barriers separated large populations. Thus, both Baptista and Orejuela and Morton delineated dialect regions in migratory populations of White-crowned Sparrows, in contrast to DeWolfe et al. These data suggest that at least some migratory populations exhibit greater variation in song than resident populations, and that the characteristics of song of some migratory populations are not stable over time. Further, the occurrence of dialects is effected by the size and stability of populations and the distribution of favorable habitat.

All resident populations of the subspecies nuttalli that have been studied are reported to have dialects (Marler and Tamura, 1962; Baker, 1974, 1975; and Baptista, 1975). These dialects may arise by chance because some young males who become established in recently disturbed habitat before development of song is completed, develop a slightly different song-type from that of birds from their natal site (Baker, 1975). The boundaries between dialects are well defined (Baker, 1975; Baptista, 1975), do not always coincide with habitat differences or physiographic discontinuities (Baker, 1975; Baptista, 1975) and these dialects appear to be stable over time where environments remain stable (Marler and Tamura, 1962; Baptista, 1975). Occasionally an individual of a dialect area is observed that has a song typical of another dialect, including that of another subspecies, or an individual may have a song which has components of song from two dialects (summarized in Baptista, 1977). This usually occurs at the boundary between dialects or in areas where recent habitat disturbance has occurred (Baptista, 1975). Thus, the dialects of nuttalli are relatively well delineated and seem to be stable over periods of two to ten years, suggesting that resident populations have better defined dialects than some migratory populations in the White-crowned Sparrow.

Rufous-collared Sparrow. The song of the Rufous-collared Sparrow has been most extensively studied in Argentina where most birds have one song-type (Nottebohm, 1969; Nottebohm and Selander, 1972; King, 1972; Handford and Nottebohm, 1976) although Nottebohm (1975a) has also reported on song variation outside Argentina. Dialects have been described for these populations, most of which are resident. The only possible migratory populations that have been studied for geographical variation in song are those from the Andes near Tafi del Valle (Nöttebohm and Selander, 1972; Handford and Nottebohm, 1976).

The results of these studies have demonstrated that the boundaries of dialects, defined by the rate of delivery of trills, usually coincide with changes in life-zones, or with changes in altitude. Changes in dialects may be abrupt or gradual. Where there are habitat differences within a life-zone, contiguous populations of capensis may have a significantly different proportion of different themes (King, 1972). The data suggest that differences in song between habitats occur irrespective of the migratory status of the population. Thus, Rufous-collared Sparrows appear to have a system of dialects where the distribution of different song-types coincides with differences in habitat, the dialects are not as sharply defined as they are in White-crowned Sparrows, and the occurrence of dialects cannot be correlated with migratory habits. However, data from migratory populations are required to determine whether these populations typically have dialects.

Song Sparrow. Geographical variation in the song of Song Sparrows has been studied in migratory (Borror, 1965; Harris and Lemon, 1972) and resident (Mulligan, 1966; Eberhardt and Baptista, 1977) populations. The results of these studies demonstrate that Song Sparrows have such large repertoires (five to 14 in the east; 5 to 23 in the west) and exhibit so much individual variation in song that dialects can not be delineated like those of White-crowned Sparrows or Rufous-collared Sparrows. Although intrapopulational variation in song may be greater in migratory populations of Song Sparrows than in resident populations, this interpretation is tentative since the treatment of data are considerably different in these four studies.

Borror (1965), working with migratory populations in Maine, found that relatively few syllables and only 12 of 544 song-types were shared between birds and these were usually shared between birds in the same population or in nearby populations. Harris and Lemon (1972) reported that no song-types were shared between birds from three localities in Quebec but found that 20% to 40% of the syllables were shared between birds, with birds from the same locality being much more likely to share syllables than birds from different localities. Thus, Borror (1965) and Harris and Lemon (1972) found that those features of song shared by two or more birds are more likely to be shared between birds from one locality and consequently they called these areas dialects. However, it is not clear if these localized differences in song distinguish most members of any population from another population as they do in White-crowned Sparrows.

Resident populations studied in California by Mulligan (1966) and Eberhardt and Baptista (1977) also have considerable individual variation in song but many individuals shared one to three song-types with other individuals, frequently that of their neighbor. Eberhardt and Baptista found that some individuals did not share any song-types with other individuals but 85% to 100% of the syllables in the repertoire of each of nine individuals were shared with others. However, no syllables were shared by all members of a population. Mulligan found that more syllables were shared between birds than were song-types. Thus, a higher proportion of song-types and syllables seem to be shared between birds in resident populations of Song Sparrows in California than in migratory populations from northeastern North America.

House Finch. Song of the House Finch has been studied in the New York City area by Mundinger (1975) and in the Los Angeles area by Bitterbaum and Baptista (MS). House Finches have more than one song-type per individual, are resident in California and at least partially migratory in the New York City area. The song of House Finches is complex so that the variation in song is comparable to that in towhees.

Mundinger found that small discrete dialects occurred in the New York City area with most individuals of each population having a repertoire of songs that distinguished them from any other population. These dialects are stable over time and boundaries between dialects are relatively sharp. A few birds, usually near the boundaries of dialects, had repertoires containing elements of two adjacent dialects. Thus, these populations of House Finches have dialects.

Bitterbaum and Baptista (MS) reported that House Finches do not have dialects in the Los Angeles area they sampled. Although many syllables within a population were shared between birds, they found no evidence that complete song-types were shared between birds. Consequently, it appears that dialects do not occur among these resident populations of House Finches.

These results are in contrast to the towhee, White-crowned Sparrow and Song Sparrow, where intrapopulational variation in song was greater in migratory than in resident populations. Part of this difference may be explained by the unusual population dynamics of the introduced populations of the House Finch in eastern North America. At least some House Finches that summer together in the New York area have been found away from New York at the same locality during the winter (Mundinger, 1975), so that group cohesiveness could be maintained throughout the year. Consequently, increased dispersal of young birds would not necessarily result from migration. With such a social system, dialects might be expected in the eastern populations, particularly since the founding colonies may have been established from several populations whose repertoires may have been different from each other. It is also possible that the recently established populations of House Finches are below the carrying capacity so that young birds can establish territories near their natal site, in contrast to populations of House Finches in Los Angeles where high population densities may force young birds to disperse over relatively long distances to establish a territory. However, the results from the west coast are clearly not consistent with expected results based on the effects of migration.

Geographical variation in song of those species where only migratory or resident populations have been studied. Data from other species where only migratory or resident populations have been studied make it even more difficult to separate the effect of migration from other variables which affect the occurrence of dialects. However, the effect of dispersal on the formation of dialects can be examined indirectly by comparing those species where geographical variation in song of either resident or migratory populations has been studied. I have treated these data cautiously since the term dialect has not been used consistently nor have standardized sampling methods been employed. In some cases, I reclassified a species as having or not having a dialect, *contra* the original author, to conform with the definition of dialect I have used in this paper.

Thus, the data cited are useful as a crude comparison with those species discussed in detail. The species characterized as having or lacking dialects are listed in Table 21. These data are summarized in Table 22. A chi-square analysis showed that neither the migratory (df=1; $X^2=1.5$; $p > .05$) nor the non-migratory populations (df=1; $X^2=0$; $p > .05$) had a tendency to either have or lack dialects.

Geographical variation of song of other species compared to the Rufous-sided Towhee. Migratory populations of Rufous-sided Towhees, White-crowned Sparrows, and Song Sparrows seem to have more intrapopulational variation in song than resident populations, the difference being most pronounced in towhees and least in the White-crowned Sparrow. On the other hand, House Finch populations that are partially migratory have dialects while a resident population lacks dialects. The scanty data on migratory populations of Rufous-collared Sparrows suggests that both migratory and resident populations have dialects. Thus, of these five species, three are consistent with the observation that migration, as a corollary of increased dispersal, reduces the frequency of occurrence of dialects. Of the other species, more data on the song of the Rufous-collared Sparrow are needed, while the rapid colonization of eastern North America by House Finches, along with their complex post-breeding dispersal, makes it difficult to compare migratory populations with resident populations of that species. For those species where only a migratory or resident set of populations have been studied, it does not appear that proportionately more resident populations have dialects than migratory populations. Thus, it is obvious that other selective pressures also affect whether dialects occur.

Why do dialects occur ? The results of studies on geographical variation in song allow few generalizations on why dialects occur except that the occurrence of dialects must be a complex problem that centers primarily around when song is learned (the "sensitive period"), where, when and why young birds disperse from their natal site, and perhaps on the structural complexity of song. Migration is one factor that may contribute to or correlate with increased dispersal of young birds, but the previously overlooked effects of migration on the formation of dialects may vary between species because of differences in population structure, the distribution of the favored habitat of a species, the function of song, or the chronology of song development. Hence, how migration affects the dispersal of young birds and consequently the occurrence of dialects is difficult to evaluate.

Migration and development of song. Migration itself is caused by ecological factors so migration can only be a proximate correlate with a reduction in dialects. Thus, factors which affect dispersal of young will partially determine whether dialects occur by determining from whom song is learned and where birds establish territories. In populations which do not migrate, young should disperse to nearby unoccupied habitat favorable for that species, and attempts to establish territories should begin when that site is found. This can occur soon after young birds become independent in Bewick's Wrens (Kroodsma, 1974) and Song Sparrows (Nice, 1937). This should lead to increased selective pressure for any behavior that enchances a bird's ability to defend a territory, such as development of song at an early age. Thus, dialects might be a result of selection for early development of song. Dialects, in these cases, will not be selected for a specific function. This interaction of dispersal and song development may also account for the relatively high rate of song sharing observed among neighboring birds in non-migratory populations of birds that do not have dialects, such as the Bewick's Wren (Kroodsma, *op. cit.*), Carolina Wren (Borror, 1965) and Mockingbird (*Mimus polyglottos*; Howard, 1974). Migratory populations however, would not be under such strict pressure, since territories could not be established until the following spring. Consequently, song could be learned either in the fall or early in the following spring, or both. This could lead to greater variability of song of individuals that would be compounded by birds dispersing over a large area. Consequently, dialects would be less likely to occur, although neighbors might share song-types if song is learned in the spring (see Thompson, 1970). However, studies are required to determine whether there are differences in the period when song is learned in resident and migratory populations of the same species.

Other correlates of dialects. Other correlates of dialects will be briefly discussed although it is evident that any dialect system will be a consequence of a complex interaction of at least some of these variables. More complete discussions of the variables affecting dialects have been presented elsewhere (Thielcke, 1969; Lemon, 1975; Payne, unpubl.). Table 23 represents a synopsis of these variables. The more complete discussion of migration in this paper is not meant to imply that migration plays a larger role in the formation of dialects than any other variable.

The function of song may be primarily to attract females and/or repel males. Where individual recognition is important, dialects are less likely to occur but where song is used to attract females, and females search for males with a song-type that is associated with a locality or habitat where the female was raised and where her fitness is presumably greatest, dialects should result. Songs, once learned, should not change appreciably from year to year in these areas, but where song expresses male dominance, especially in colonial species, songs may vary from year to year to resemble those of the alpha male (Payne, unpubl.).

Colonial species, or species inhabiting isolated patches of habitat, may have little intrapopulational variation in song because young birds may be exposed to relatively few song-types. This may contribute to the occurrence of dialects in Phaethornis (Wiley, 1971), Vidua spp. (Payne, 1973), Ammodramus sandwichensis beldingi (Bradley, 1977), Dolichonyx oryzivorus (Avery and Oring, 1977), and Certhia brachydactyla in Spain (Thielcke, 1976), although these dialects are probably a result of different selective pressures. In Ammodramus, Dolichonyx, and Certhia dialects may be used to maintain a deme but for Phaethornis and Vidua, which are lek species, it is more likely that the dialect is a result of selective pressure related to sexual selection. However, regardless of the function of the dialect, a tendency to have dialects might be re-enforced where numbers are stable from year to year so that recruitment comes from the home colony every year, and where colonies are far enough apart so movement of individuals from colony to colony is reduced (see Table 23). The same selective pressures effect non-colonial species but dialects might be less likely to occur since there would be fewer opportunities to learn song from individuals with similar song-types. This might result in individuals copying song from other individuals less accurately, or favor birds developing new song-types ("improvising"). However, data are not consistent for even the simple case of populations from islands. Song of some species on islands diverges from song on the mainland (Marler, 1952; Mirsky, 1976; Chappuis, 1976) but in other species song does not change (Thielcke, 1974; Chappuis, 1976). Thus, it becomes difficult to identify those selective pressures which regulate the occurrence of a dialect system.

Function of dialects. While there are no data to suggest that dialects serve a function in towhees, they may be functional with other species. Dialects may function to reduce the complexity of song to simplify its' communicative properties (Thielcke, 1969), or they could simply be a consequence of environmental constraints on song (Chappuis, 1971; Morton, 1975). Dialects may also be used by birds to associate a specific song-type with a locality since males of at least some species can distinguish songs from different populations and respond selectively to song from their own population (see Milligan and Verner, 1971; Lemon, 1967, 1974; Kreutzer, 1974b; Harris and Lemon, 1974; however, for those species where many song-types are individually-specific it is important to determine whether different song-types from the same population elicit different responses before responses to songs of different localities can be evaluated). Further Baptista and Wells (1975) reported that one first year male Zonotrichia leucophrys nuttalli had one song-type like some pugetensis from Oregon and was not mated when observed on 5 June 1974 although it was not known if song played a role in preventing this bird from obtaining a mate. However, Baptista (1973, 1974) found that females of Zonotrichia leucophrys nuttalli will mate with males having song-types of the race pugetensis and Payne (1973) reported that Vidua finches do not distinguish songs of their dialect from other dialects. These observations suggest that dialects may not serve to isolate some populations. Attempts have been made to see whether the distribution of dialects coincides with the distribution of population demes by correlating the distribution of dialects with the distribution of enzyme polymorphisms. Thus far the results are ambiguous. Nottebohm and Selander (1972) and Handford and Nottebohm (1976) found no correlation in the distribution of enzyme polymorphisms with dialects of Zonotrichia capensis. However, Baker (1975) found a boundary between two dialects of the White-crowned Sparrow in California that coincided with a change in enzyme polymorphisms. As Baker pointed out, this could be a consequence of dispersal patterns and not of any function of dialects. Thus, the functional aspects of dialects remain conjectural.

Finally, I believe that dialects are simply a result of strong selective pressure for stereotyped song within a population. This may be a result of any number of variables, and may or may not be selected so that one song-type, phrase, or syllable can be associated with a specific locality or habitat. The study of geographical variation in song requires concomitant study of the function of song, dispersal, song development, and the social system of a population before the function of dialects can be understood. Dialects are not as simplistic as they have been frequently portrayed.

TABLE 1. THE NUMBER OF SONG-TYPES RECORDED BY YEAR FOR INDIVIDUALS FROM KALBFLEISCH.

Individual	Number of song-types recorded in						
	1969	1970	1971	1972	1973	1974	1975
K1	1	3	4	4			
K2	5	3	5	5			
K3	1	3	3	3			
K4	2	2					
K5	5						
K7	2	2					
K16		6					
K17	0	2	2				
K18		2	4				
K19		2	4				
K22	0	3	4	4	4		
K23		2	2	2	2	2	2
K24			3				
K25			2				
K26				4			
K27				3			
K28				4			
K29				4			
K30				1	2		
K31				4	4	5	5
K32				3	1	3	3
K34					2		
K36					3		
K37					2	1	
K38						4	4
K39					0	3	3
K40						4	4
K42						4	6
K44							4
K45							5
K46							5

TABLE 2. NUMBER OF SONG-TYPES PER INDIVIDUAL FROM CONNETQUOT FOR BIRDS WHOSE COMPLETE SONG REPERTOIRES WERE RECORDED.

Number of song-types	Individual(s)
1	C84.
2	C39,49,74,90,95.
3	C1,8,22,57,58,64,70,76,80,92,100.
4	C2,4,12,19,29,53,62,66,71,73,79,81,82,106.
5	C75,77,86,115.
6	C28,93.

TABLE 3. NUMBER (PERCENT) OF SONG-TYPES BY DIFFERENT PHRASE SEQUENCES AT THREE LONG ISLAND LOCALITIES.

		Phrase sequence			
Locality	N	Note-complex phrase only	Trill phrase(s) only	One note-complex phrase followed by one trill phrase	Other sequences of note-complex and trill phrases
Kalbfleisch	125	8 (6.4)	0	112 (89.6)	5 (4.0)
Tobay Beach	40	0	0	35 (87.5)	5 (12.5)
Connetquot	276	6 (2.2)	5 (1.8)	243 (88.1)	22 (7.9)
Grand Total	441	14 (3.2)	5 (1.1)	390 (88.4)	32 (7.3)

TABLE 4. NUMBER AND RATE OF DELIVERY OF SYLLABLES OF NOTE-COMPLEX AND TRILL PHRASES OF SONG IN THREE POPULATIONS FROM LONG ISLAND.[1]

	Number of syllables		Rate of delivery (syllables/sec.)	
Locality, year(s)	Note-complex phrase	Trill phrase	Note-complex phrase	Trill phrase
Kalbfleisch 1969-1975	2.1 ± 0.58 (39)	8.0 ± 1.90 (39)	4.3 ± 0.77 (39)	16.5 ± 3.03 (39)
Tobay Beach 1972	1.9 ± 0.46 (13)	8.8 ± 2.65 (13)	5.9 ± 1.35 (12)	20.3 ± 6.26 (13)
Connetquot 1973	2.0 ± 0.45 (114)	9.6 ± 4.24 (114)	4.4 ± 1.02 (105)	18.5 ± 7.02 (114)

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[1] Data given as mean ± standard deviation; number of individuals in parentheses.

TABLE 5. SONG-TYPES SHARED BY TWO OR MORE INDIVIDUALS.

Song-type	Individual	
C,EE-25	C13, C14	Neighbors
E-25	K25, C6	
EE-44	C40, C100	Non-neighbors
I,V,D-51	K23, K40	Neighbors
MM,S,D-40	C2, C4	Non-neighbors
S,D-39	C56, C57	Neighbors
S,H-24	C25, C40	Non-neighbors
V,D-1	C48, C93	Non-neighbors
V,D-25	C18, C55, C73, C76, C90	Non-neighbors
V,D-39 *	C11, C98	Non-neighbors
V,D-39 *	K36, C29	
V,D-39 *	C80 with C81, C82, C83 C81 with C80, C82, C83 C82, C83	Non-neighbors Non-neighbors Neighbors
V,D-49	C8, C29	Non-neighbors
V,D-51 *	C58, C59	Neighbors
V,D-51 *	K31, K37 K31, K46. K7 with K31, K37, K46 K37 (1973, 1974), K46 (1975)	Neighbors Non-neighbors
V,D-52	K2 (1969-1972), K38 (1974, 1975)	
Z,D-29	K32, K44	Neighbors
Z,V,D-17	K12 (1969), K18 (1970, 1971)	
Z,V,D-53	K25 (1971), K33 (1973)	
Z,C-40-13	C106, C122	Non-neighbors
1-FF-50	T1, T3	Neighbors

* Variations of one song-type

TABLE 6. OCCURRENCE OF SONG-TYPES FOUND IN TWO OR MORE RUFOUS-SIDED TOWHEES AT BLENDON WOODS, OHIO (after Borror, pers. comm.; data through 1976).

Location	Note-complex	Trill	Song-type	Miles away
Blendon Woods (number)	126	80	274	
Blendon Woods (per cent of each type of phrase and song-type, respectively)	49.2	66.2	27.4	
Per cent found:				
In 2 or more Blendon Woods birds only	7.9	8.8	14.6	
In 2 or more Blendon Woods birds, and also elsewhere	22.2	33.8	6.2	
Also in Blacklick Woods	23.0	31.2	6.9	10-11
Also elsewhere in Franklin County	23.0	31.2	3.3	up to 20
Also in the Delaware Wildlife Area	6.4	10.0	2.6	20-25
Also in Clear Creek Valley	9.5	15.0	2.2	35-40
Also in northern or southern Ohio	11.9	26.2	2.6	50-120
Also in adjacent states	13.5	15.0	2.6	125-330
Also farther away	13.5	27.5	1.8	400-2000

TABLE 7. SHARING OF SYLLABLES BY PHRASE BETWEEN LOCALITIES.

Phrase	Number of different syllables	Number (percent) of syllables Endemic	 Shared by Two localities	 All localities
Note-complex	79	48 (60.8)	14 (17.7)	17 (21.6)
Trill	62	37 (59.7)	11 (17.7)	14 (22.6)

TABLE 8. SYLLABLES OF THE TRILL PHRASE, ILLUSTRATED IN BORROR (1959a) THAT OCCUR ON LONG ISLAND.

Syllable	Equivalent syllable in Borror (1959a) (Plate #, Fig. # respectively)	Occurence outside Long Island
1	33 (5,85), 34 (5,86; 5,87), 35 (5,88; 6,89), 36 (6,90), 40 (6,93)	Maine, West Virginia, Ohio
9	31 (5,83), 47 (6,105), 54 (6,116)	Ohio, Michigan, Florida
13	5 (5,57; 5,58)	Ohio, North Carolina
19	9 (5,62), 53 (6,115)	Ohio, West Virginia
25	43 (6,96)	Maine
28	50 (6,110)	Maine, Ohio
39	47 (6,102; 6,103; 6,104)	Ohio
40	17 (5,70), 18 (5,71), 19 (5,72), 26 (5,79)	Maine, Ohio, West Virginia
45	22 (5,75), 23 (5,76), 24 (5,77)	Ohio

TABLE 9. SHARING OF SYLLABLES OF THE NOTE-COMPLEX PHRASE BETWEEN THREE LONG ISLAND LOCALITIES.

		Number of syllables (per cent)				
				Shared with		
Locality	N*	Endemic	All	Kalbfleisch	Tobay Beach	Connetquot
Kalbfleisch	36	10 (27.8)	14 (39.9)	-	2 (5.6)	10 (27.8)
Tobay Beach	28	7 (25.0)	14 (50.0)	2 (7.1)	-	5 (17.9)
Connetquot	60	31 (51.7)	14 (23.3)	10 (16.7)	5 (8.3)	-

* N is the number of different syllables found in each locality.

TABLE 10. SHARING OF SYLLABLES OF THE TRILL PHRASE BETWEEN THREE LONG ISLAND LOCALITIES.

		Number of syllables (percent)				
				Shared with		
Locality	N*	Endemic	All	Kalbfleisch	Tobay Beach	Connetquot
Kalbfleisch	35	13 (37.1)	11 (28.6)	-	1 (2.9)	10 (31.4)
Tobay Beach	17	2 (11.8)	11 (64.7)	1 (5.9)	-	3 (17.6)
Connetquot	46	22 (47.8)	11 (23.9)	10 (21.7)	3 (6.5)	-

* N is the number of different syllables found at each locality.

TABLE 11. SYLLABLES ENDEMIC TO ONE OF THE LONG ISLAND LOCALITIES.

Number of birds having syllable	Kalbfleisch	Tobay Beach	Connetquot
1	A,II,JJ,RR,XX,DDD, FFF,GGG,11,14,26, 33,34,36,41,55,58	KK,LL,LLL,QQQ,RRR, 42,57	B,K,M,N,Q,X,CC,HH,QQ,NNN,VVV,WWW, XXX,YYY,ZZZ,AAAA,DDDD,7,10,12,16, 18,20,21,27,35,54,60
2 to 5	CCC(3)*,HHH(2), 15(2),17(3),29(2), 56(2)	MMM(2),PPP(2)	P(3),R(4),W(2),DD(4),MM(2),NN(2), ZZ(2),BBB(2),SSS(5),UUU(3),BBBB(2), CCCC(5),4(3),24(4),30(5),37(2), 43(2),48(2),61(3),62(4)
6 or more	-	-	J(7),TTT(6),31(15),38(7),46(6)

* Number of birds having each syllable.

TABLE 12. MEAN PERCENT OF INDIVIDUALS HAVING SYLLABLES ENDEMIC TO A LOCALITY COMPARED WITH SYLLABLES FOUND IN TWO OR MORE POPULATIONS.

		Percent of individuals having each syllable [2]	
Locality	N [1]	Endemic to one population	Found in two or more populations
Kalbfleisch	39	3.4	13.5
Tobay Beach	13	9.5	19.2
Connetquot	114	2.2	9.8

[1] Number of birds from each locality.

[2] Average for all syllables in each population for each category.

TABLE 13. PERCENT OF INDIVIDUALS AT KALBFLEISCH WITH EACH NOTE-COMPLEX SYLLABLE IN THEIR REPERTOIRE.

	No. years	Year	1969	1970	1971	1972	1973	1974	1975
Syllable	recorded	No. ind.	10	11	10	12	10	9	10
D	7		70.0	90.9	100.0	100.0	100.0	100.0	100.0
F	7		10.0	9.1	10.0	25.0	10.0	11.1	10.0
H	7		40.0	54.5	40.0	66.6	40.0	33.3	40.0
S	7		40.0	45.4	20.0	33.3	20.0	44.4	60.0
V	7		70.0	90.9	100.0	100.0	90.0	100.0	100.0
Z	7		40.0	45.4	50.0	50.0	40.0	55.5	70.0
E	6		10.0	18.2	10.0	-	10.0	11.1	20.0
I	6		-	18.2	10.0	8.3	10.0	22.2	30.0
WW	6		-	18.2	20.0	8.3	10.0	11.1	30.0
CCC	6		-	9.1	10.0	8.3	10.0	22.2	30.0
C	5		10.0	18.2	20.0	16.7	10.0	-	-
FF	5		10.0	18.2	10.0	8.3	-	-	10.0
AAA	5		-	9.1	10.0	8.3	-	11.1	10.0
PP	4		-	9.1	10.0	-	-	11.1	20.0
HHH	4		-	-	-	8.3	10.0	11.1	10.0
Y	3		20.0	-	-	-	-	22.2	20.0
YY	2		-	9.1	10.0	-	-	-	-
U	2		-	9.1	10.0	-	-	-	-
RR	2		-	9.1	10.0	-	-	-	-
SS	2		-	9.1	10.0	-	-	-	-
TT	2		-	9.1	10.0	-	-	-	-
VV	2		-	9.1	10.0	-	-	-	-
XX	2		-	9.1	10.0	-	-	-	-
III	2		-	-	-	8.3	10.0	-	-
JJ	2		-	-	-	-	-	11.1	10.0
A	1		10.0	-	-	-	-	-	-
AA	1		-	18.2	-	-	-	-	-
EE	1		-	-	10.0	-	-	-	-
II	1		-	-	10.0	-	-	-	-
DDD	1		-	-	10.0	-	-	-	-
EEE	1		-	-	10.0	-	-	-	-
FFF	1		-	-	10.0	-	-	-	-
UU	1		-	-	-	8.3	-	-	-
GGG	1		-	-	-	8.3	-	-	-
L	1		-	-	-	-	10.0	-	-
JJJ	1		-	-	-	-	10.0	-	-

TABLE 14. PERCENT OF INDIVIDUALS AT KALBFLEISCH WITH EACH TRILL SYLLABLE IN THEIR REPERTOIRE.

	No. years	Year	1969	1970	1971	1972	1973	1974	1975
Syllable	recorded	No. ind.	10	11	10	12	10	9	10
1	7		10.0	36.4	30.0	41.7	20.0	44.4	60.0
17	7		10.0	9.1	10.0	8.3	10.0	11.1	10.0
39	7		10.0	9.1	10.0	33.3	30.0	55.5	60.0
49	7		10.0	9.1	10.0	16.6	10.0	11.1	10.0
51	7		20.0	36.4	20.0	50.0	60.0	55.5	50.0
52	7		20.0	9.1	10.0	16.6	10.0	11.1	10.0
13	6		30.0	27.3	30.0	25.0	-	11.1	20.0
40	6		20.0	18.2	10.0	16.6	10.0	-	10.0
9	5		10.0	36.4	30.0	16.6	10.0	-	-
25	5		10.0	18.2	20.0	16.6	10.0	-	-
15	4		-	18.2	20.0	16.6	10.0	-	-
23	4		-	9.1	10.0	8.3	10.0	-	-
44	4		-	9.1	10.0	8.3	10.0	-	-
29	4		-	-	-	8.3	10.0	11.1	20.0
3	4		10.0	9.1	10.0	8.3	-	-	-
2	3		-	18.2	10.0	8.3	-	-	-
8	3		10.0	9.1	10.0	-	-	-	-
56	3		-	18.2	20.0	8.3	-	-	-
32	2		-	9.1	-	-	10.0	-	-
53	2		-	-	10.0	-	10.0	-	-
14	2		-	-	-	-	-	11.1	10.0
41	2		-	-	-	-	-	11.1	10.0
47	2		-	-	-	-	-	11.1	10.0
50	2		-	-	-	-	-	11.1	10.0
55	2		-	-	-	-	-	11.1	10.0
59	2		20.0	9.1	-	-	-	-	-
58	1		10.0	-	-	-	-	-	-
28	1		-	-	10.0	-	-	-	-
33	1		-	-	10.0	-	-	-	-
36	1		-	-	10.0	-	-	-	-
26	1		-	-	-	8.3	-	-	-
5	1		-	-	-	-	10.0	-	-
22	1		-	-	-	-	10.0	-	-
11	1		-	-	-	-	-	-	10.0
34	1		-	-	-	-	-	-	10.0

TABLE 15. MEANS ± S.D. FOR THE VARIABLES OF SONG USED IN A DISCRIMINANT ANALYSIS OF THE POPULATIONS.

Population	N	Variable INTRP1TI (secs)	TRLP1TIM (secs)	INTPMIF (kHz)
Grand Mean	164	0.48 ± 0.160	0.53 ± 0.081	2.1 ± 0.32
Kalbfleisch				
1969	9	0.49 ± 0.207	0.47 ± 0.061	2.6 ± 0.41
1970	6	0.45 ± 0.098	0.50 ± 0.091	2.4 ± 0.24
1971	2	0.68 ± 0.245	0.48 ± 0.013	2.2 ± 0.42
1972	7	0.49 ± 0.172	0.56 ± 0.082	2.4 ± 0.17
1973	7	0.53 ± 0.178	0.53 ± 0.040	2.3 ± 0.18
1974	5	0.68 ± 0.239	0.45 ± 0.078	2.2 ± 0.23
1975	3	0.53 ± 0.040	0.48 ± 0.081	2.3 ± 0.25
Tobay Beach	13	0.34 ± 0.116	0.45 ± 0.066	2.2 ± 0.33
Connetquot	112	0.48 ± 0.147	0.55 ± 0.077	1.9 ± 0.25

TABLE 16. F MATRIX FOR POPULATIONS FROM KALBFLEISCH (BY YEAR OF FIRST APPEARANCE), TOBAY BEACH (T), AND CONNETQUOT (C) BASED ON THREE VARIABLES OF SONG (INTPMIF, INTRP1TI, TRLP1TIM). D.F. = 3,153.

	1969	1970	1971	1972	1973	1974	1975	T
1970	1.03							
1971	1.49	1.14						
1972	2.24	0.87	1.28					
1973	2.22	0.67	0.64	0.31				
1974	3.04	2.31	0.05	3.16	1.73			
1975	0.91	0.25	0.40	1.01	0.46	0.66		
T	6.20*	2.27	3.21	6.87*	5.79*	6.37*	1.61	
C	16.82*	4.81*	2.23	6.35*	4.32*	6.22*	2.17	13.37*

* Significant difference at the .05 level.

TABLE 17. DISCRIMINATORY ANALYSIS OF THREE FEATURES OF SONG FROM 164 INDIVIDUALS FROM THREE LOCALITIES ON LONG ISLAND.

Disriminant Axis	Chi-square	Relative %	Degrees of Freedom	Probability
1	119.52	67.93	24	.000
2	42.92	23.37	14	.000
3	12.17	8.70	6	.058

TABLE 18. LOADING OF THE THREE VARIABLES OF SONG ON THE STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS (DISCRIMINANT AXES). ONLY THE FIRST TWO DISCRIMINANT FUNCTIONS CONTRIBUTE SIGNIFICANTLY TO THE SEPARATION OF THE POPULATIONS.

Variable	1	2	3
INTRP1TI	0.13086	0.91794	0.44893
TRLP1TIM	-0.25120	0.67002	-0.78911
INTPMIF	0.90055	0.31055	-0.46284

TABLE 19. CLASSIFICATION OF INDIVIDUALS FROM KALBFLEISCH (BY YEAR OF FIRST APPEARANCE), TOBAY BEACH (T), AND CONNETQUOT (C) BASED ON DISCRIMINANT ANALYSIS OF THREE TEMPORAL AND FREQUENCY CHARACTERISTICS OF THEIR SONGS.[1]

Pop.	N	1969	1970	1971	1972	1973	1974	1975	T	C
1969	9	44.4	0	11.1	0	0	11.1	11.1	22.2	0
1970	6	33.3	0	0	16.7	16.7	0	11.1	16.7	16.7
1971	2	0	0	50.0	0	0	0	0	0	50.0
1972	7	0	0	0	71.4	14.3	14.3	0	0	0
1973	7	14.3	0	14.3	14.3	28.6	0	0	14.3	14.3
1974	5	0	0	0	20.0	0	60.0	0	20.0	0
1975	3	33.3	0	0	33.3	0	0	33.3	0	0
T	13	15.4	7.7	0	0	0	7.7	0	69.2	0
C	114	0.9	4.4	5.3	7.0	4.4	2.6	3.5	3.5	59.6

---

[1] INTPMIF, INTRP1TI, TRLP1TIM

TABLE 20. RATE OF RETURN OF JUVENILES TO KALBFLEISCH.

	Number banded *	Number returned	% return
Males	172	12	7.0
Females	185	16	8.6
Total	357	28	7.8

* Birds banded on or before 1 September plus those completing prebasic molt or rectrix molt after 1 September.

TABLE 21. LIST OF SPECIES CHARACTERIZED AS HAVING OR LACKING DIALECTS.

Species	M^1	N	Dialect	Location(s) of sample(s)	Reference
Phaethornis longuemareus		X	Yes	Trinidad	Wiley, 1971
Thryomanes bewickii		X	No	Oregon	Kroodsma, 1974
Thryothorus ludovicianus		X	No	s.e. U.S.A., Ohio	Borror, 1956
Troglodytes troglodytes		X	Yes	France	Kreutzer, 1974a
Turdus iliacus	X		Yes	Norway	Bjerke, 1974
Acrocephalus palustris	X		Yes	Belgium	Lemaire, 1975
Parus carolinensis		X	No	s.e. U.S.A.	Ward, 1966
Certhia brachydactyla		X	No ?	Europe, except Spain	Thielcke, 1973a, 1976
		X	Yes	Spain	Thielcke, 1973a, 1976
Nectarinia coccinigaster		X	Yes	Ghana	Grimes, 1974
Emberiza hortulana	X		Yes	Germany	Conrads, 1976
E. schoeniclus	X		No	Belgium	Ghiot, 1976
Zonotrichia albicollis	X		No	Canada, U.S.A.	Borror and Gunn, 1965
	X		No	New Brunswick	Lemon and Harris, 1974
Junco hyemalis		X	No	California	Konishi, 1964a
		X	No	California	Williams and MacRoberts, 1977
J. phaeonotus		X	No	Mexico	Marler and Isaac, 1961

TABLE 21 (continued).

Species	M	N	Dialect	Location(s) of sample(s)	Reference
Ammodramus sandwichensis beldingi		X	Yes	Calif., Mexico	Bradley, 1977
Spizella passerina[2]	X		No	n.e. U.S.A.	Borror, 1959b
		X	No	Mexico	Marler and Isaac, 1961
S. pusilla	X		No	Ohio	Goldman, 1973
	X		No	Michigan	Heckenlively, 1976
Amphispiza bilineata		X	No	New Mexico	Heckenlively, 1970
Pipilo fuscus		X	No	Calif., Mexico	Marler and Isaac, 1960a
Cardinalis cardinalis		X	Yes	Ontario	Lemon, 1966
Passerina cyanea	X		No	e. U.S.A.	Shiovitz and Thompson, 1970
P. amoena	X		No	w. U.S.A.	Thompson, 1976
Vermivora pinus	X		No[3]	Michigan, New York	Gill and Murray, 1972
Seiurus aurocapillus	X		No	Ontario	Weeden and Falls, 1959
Geothlypis trichas	X		No	U.S.A.	Borror, 1967
Dolichonyx oryzivorus	X		Yes	Minn., N.Dak.	Avery and Oring, 1977
Fringilla coelebs		X	Yes	Belgium	Metzmacher and Mairy, 1974
Vidua spp.		X	Yes	Africa	Payne, 1973

TABLE 21 (continued).

[1] M = migratory; N = non-migratory

[2] Sample sizes too small to compare with other species where song has been studied in both migratory and non-migratory populations.

[3] Song-type I

TABLE 22. THE NUMBER OF TAXA THAT HAVE DIALECTS BY MIGRATORY STATUS.*

	Migratory	Non-migratory
Dialect	4	7
No dialect	8	7

---

* Excludes _Certhia brachydactyla_ and _Spizella passerina_.

TABLE 23. FACTORS THAT MAY AFFECT THE OCCURENCE OF DIALECTS IN PASSERINES THAT LEARN SONG FROM CONSPECIFIC INDIVIDUALS AND WHOSE REPERTOIRE IS FIXED ONCE LEARNED (partially after Payne, unpubl.).

FAVOR DIALECTS	INHIBIT DIALECTS
Learn song before becoming independent of parents	Learn song after becoming independent of parents
Young disperse short distances from natal site	Young disperse relatively long distances from natal site.
Species locally distributed	Species generally distributed
High density populations	Low density populations
Species found in stable environment	Species found in relatively unstable environment
Small repertoire	Large repertoire
Ability to copy song precisely	Imprecise copying or much improvising
Ability to recognize dialects	Unable to recognize dialects

FIG. 1. Location of study sites on Long Island, New York. Stippling represents that portion of New York City on Long Island.

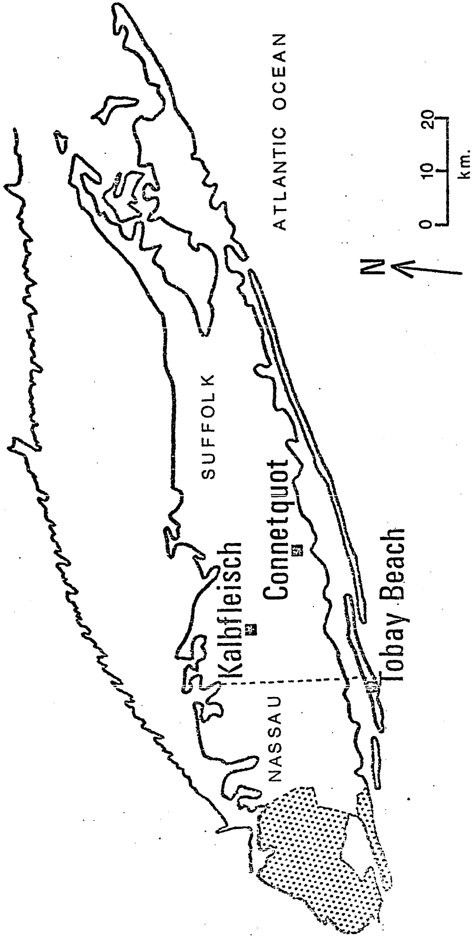

ATLANTIC OCEAN
SUFFOLK
NASSAU
Kalbfleisch
Connetquot
Tobay Beach
N
0
10
20
km.

FIG. 2. Location of towhee territories at the Kalbfleisch Field Research Station in 1969. Stippled areas represent fields or other habitats not occupied by towhees.

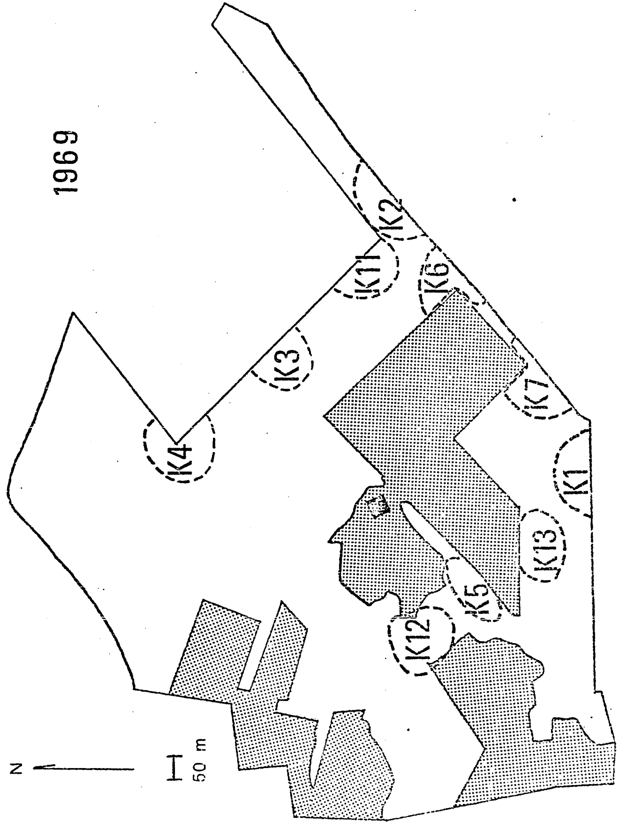

1969
K1
K2
K3
K4
K5
K6
K7
K11
K12
K13
N
50 m

FIG. 3. Location of towhee territories at the Kalbfleisch Field Research Station in 1970.

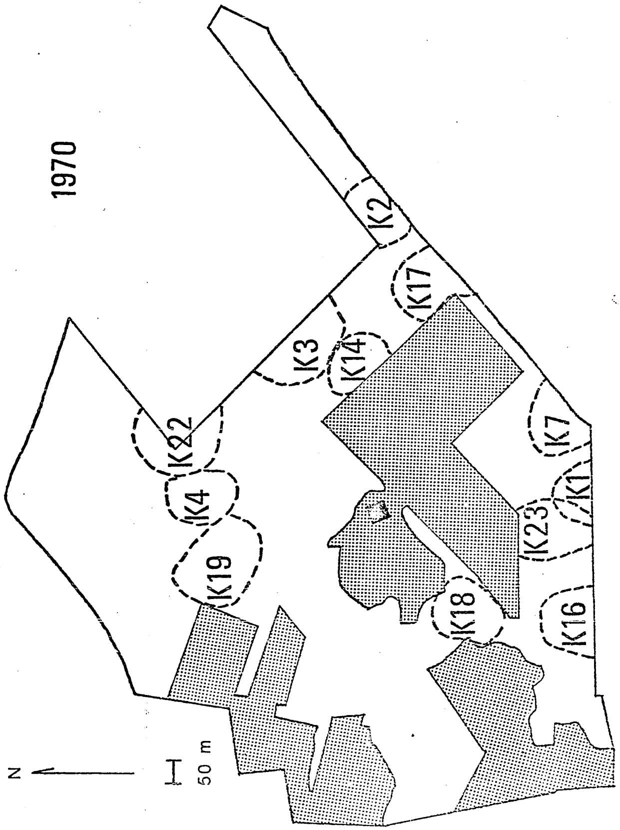

1970
K2
K17
K3
K14
K22
K4
K19
K7
K1
K23
K18
K16
N
50 m

FIG. 4. Location of towhee territories at the Kalbfleisch Field Research Station in 1971.

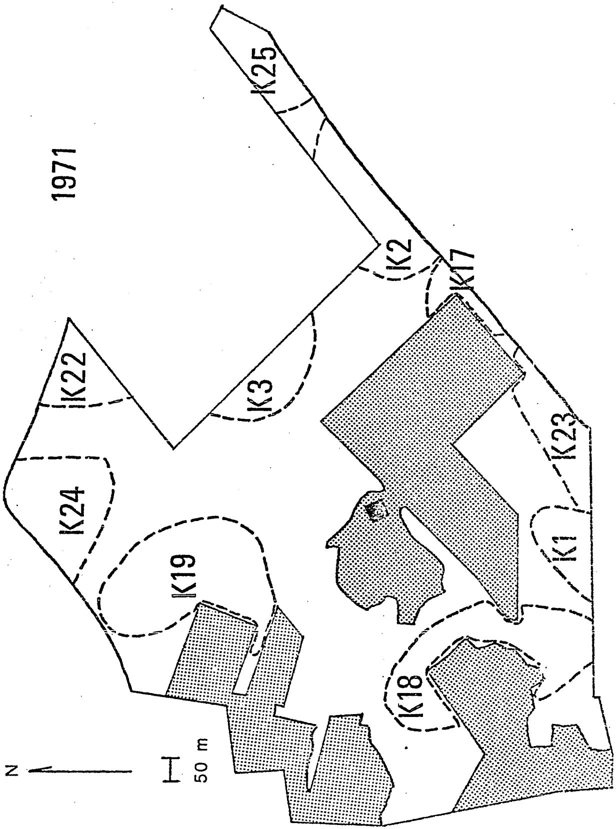

1971
K25
K2
K17
K22
K3
K23
K24
K1
K19
K18
N
50 m

FIG. 5. Location of towhee territories at the Kalbfleisch Field Research Station in 1972. K29 was last observed on 18 May; K3 was last observed on 21 May; K31 first appeared on 26 May.

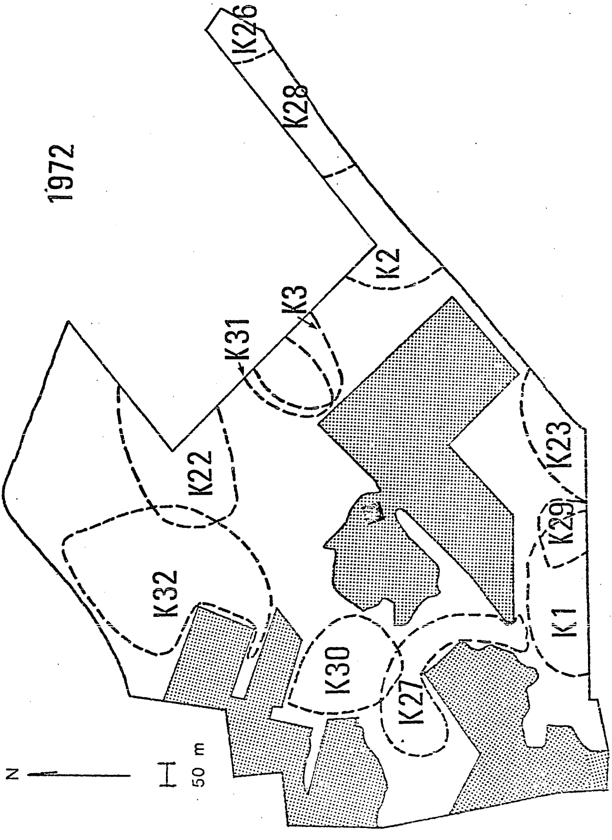

1972
K26
K28
K2
K3
K31
K22
K23
K29
K32
K1
K30
K27
N
50 m

FIG 6. Location of towhee territories at the Kalbfleisch Field Research Station in 1973.

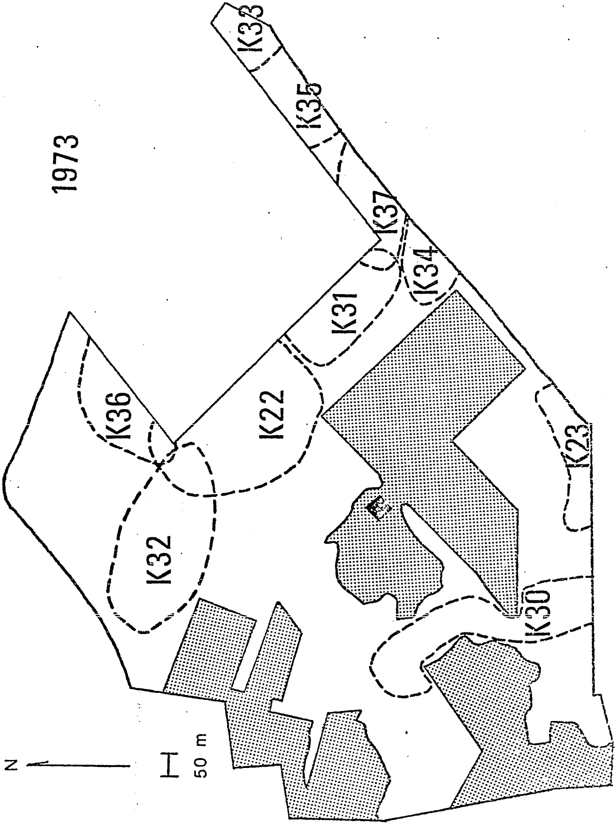

1973
K33
K35
K37
K34
K31
K36
K22
K32
K23
K30
N
50 m

FIG. 7. Location of towhee territories at the Kalbfleisch Field Research Station in 1974.

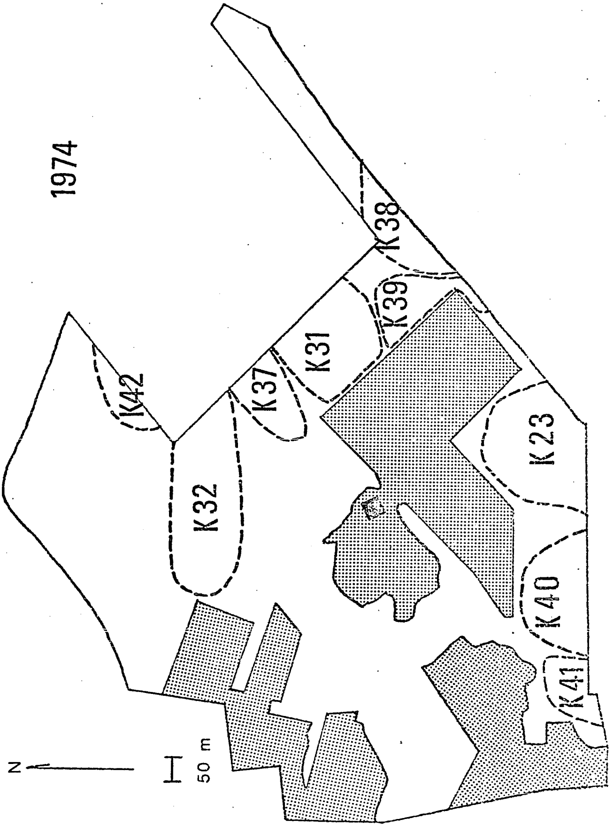

1974
K38
K39
K31
K37
K42
K32
K23
K40
K41
N
50 m

FIG. 8. Location of towhee territories at the Kalbfleisch Field Research Station in 1975.

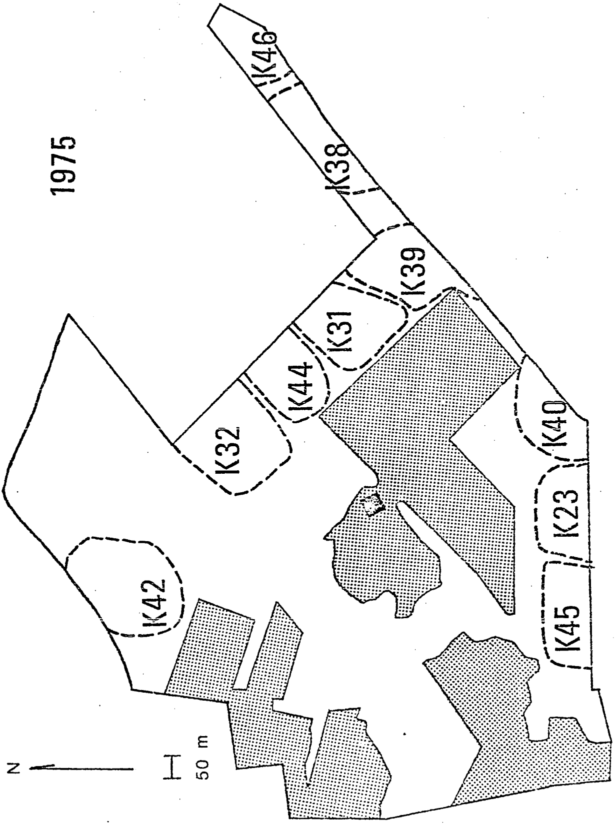

1975
K46
K38
K39
K31
K44
K32
K40
K23
K42
K45
N
50 m

FIG. 9. Map of territories of towhees recorded at Connetquot River State Park in 1973. The numbers on the map represent the location of the territories and correspond with the Connetquot birds listed in Appendix 4. The location of some territories was not noted but their approximate location is indicated on the map (6,7,11,15,25,26,43,48,52,122). The location of the territory of 118 is not known.

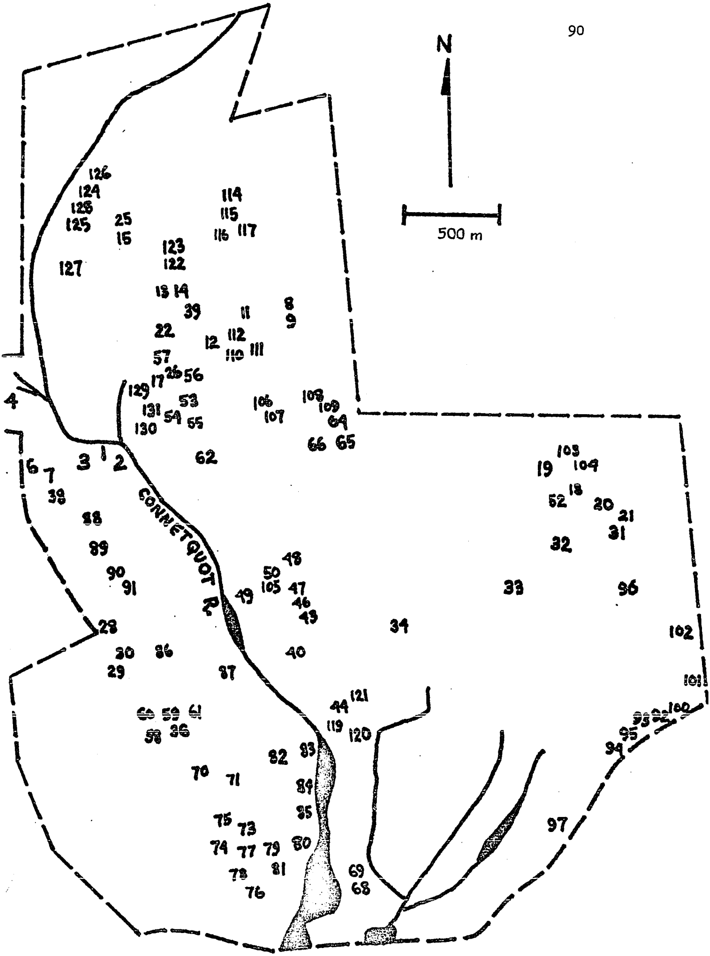

N
500 m
126
124
128
125
25
15
127
114
115
116
117
123
122
13
14
39
11
8
9
22
12
112
110
111
57
26
17
56
129
53
131
54
55
130
106
107
108
109
64
66
65
4
6
7
3
1
2
62
38
CONNETQUOT R.
88
89
90
91
103
19
104
18
52
20
21
31
32
48
50
105
47
49
46
43
33
96
28
34
102
30
86
40
29
87
101
121
44
60
59
61
58
36
119
120
93
92
100
95
94
82
83
70
71
84
85
97
75
73
74
77
79
80
81
78
76
69
68

FIG. 10. Sonogram of a song of a towhee recorded on Long Island used to illustrate terminology used in text. See text for a description of the terms illustrated here.

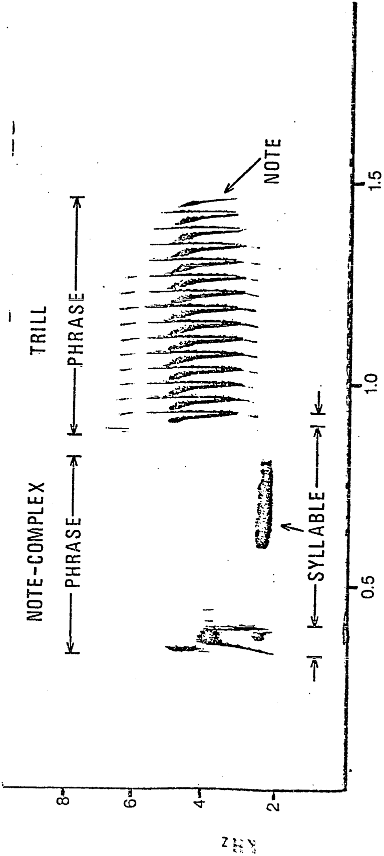
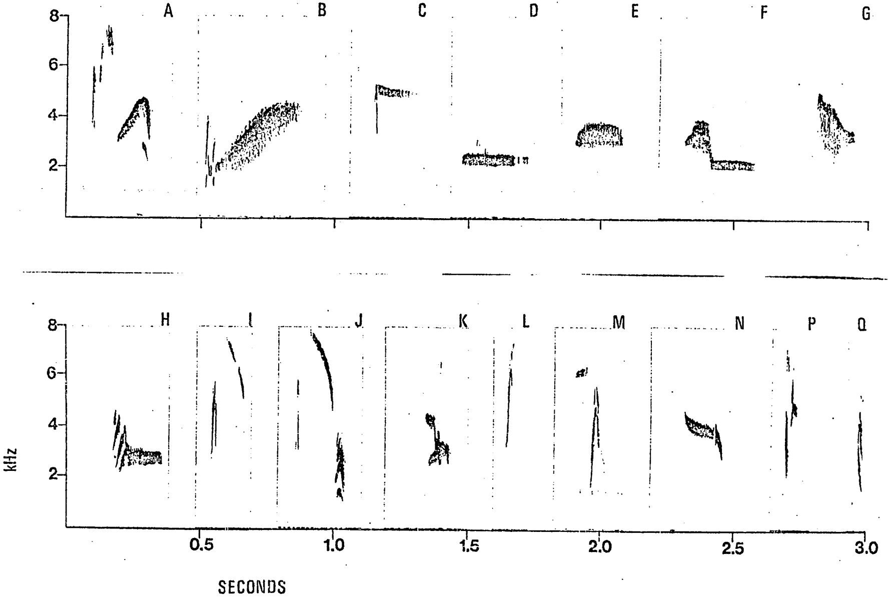
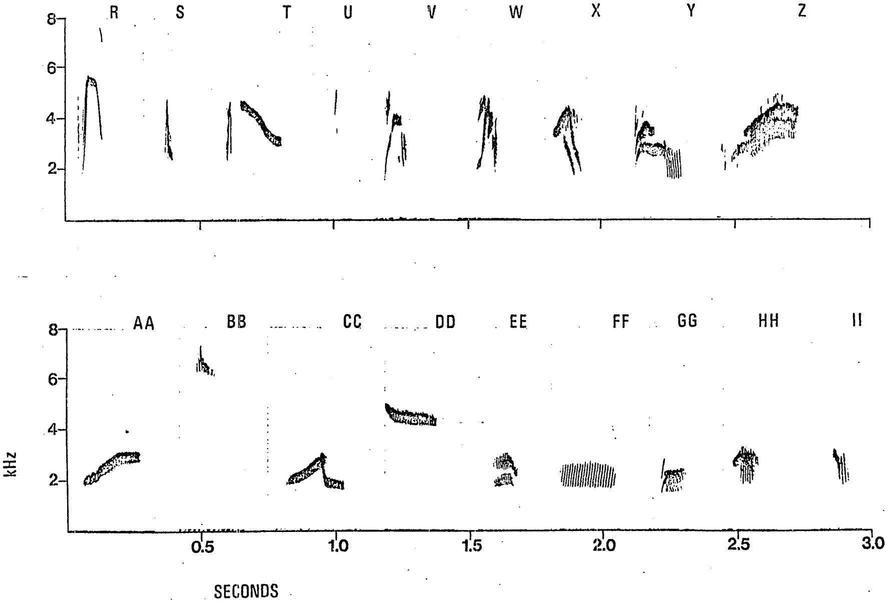
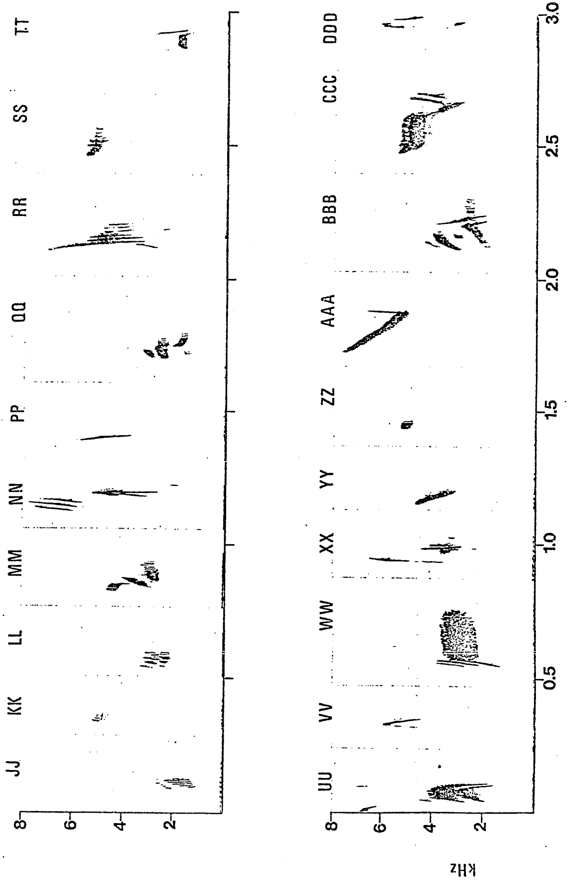
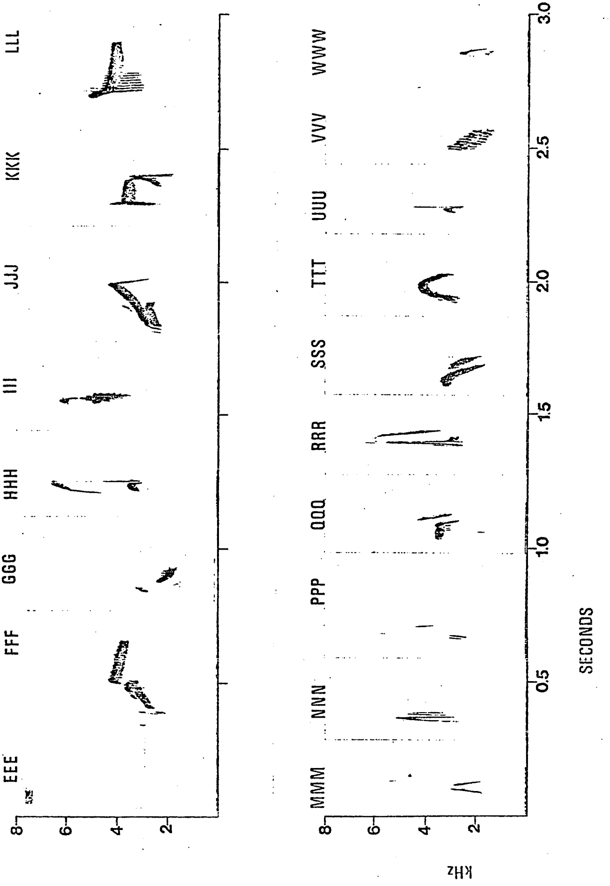

NOTE-COMPLEX
PHRASE
TRILL
PHRASE
NOTE
SYLLABLE
SYLLABLE
SECONDS
0.5
1.0
1.5
8
6
4
2
KHZ

FIG. 11. Illustration of the syllables of the note-complex phrase.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
P
Q
8
6
4
2
kHz
0.5
1.0
1.5
2.0
2.5
3.0
SECONDS


R
S
T
U
V
W
X
Y
Z
AA
BB
CC
DD
EE
FF
GG
HH
II
8
6
4
2
kHz
0.5
1.0
1.5
2.0
2.5
3.0
SECONDS


JJ
KK
LL
MM
NN
PP
QQ
RR
SS
TT
UU
VV
WW
XX
YY
ZZ
AAA
BBB
CCC
DDD
8
6
4
2
KHz
0.5
1.0
1.5
2.0
2.5
3.0
SECONDS


EEE
FFF
GGG
HHH
III
JJJ
KKK
LLL
MMM
NNN
PPP
QQQ
RRR
SSS
TTT
UUU
VVV
WWW
8
6
4
2
KHz
0.5
1.0
1.5
2.0
2.5
3.0
SECONDS

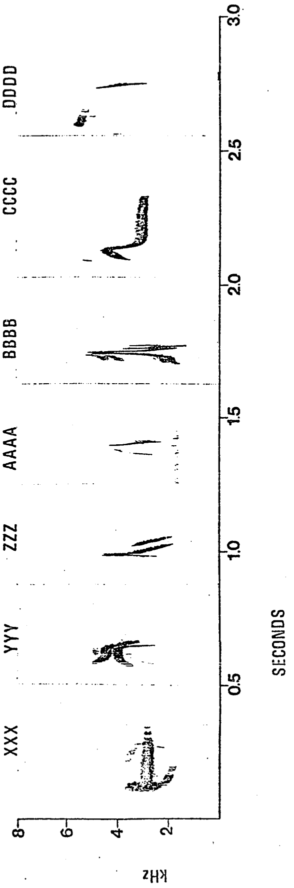
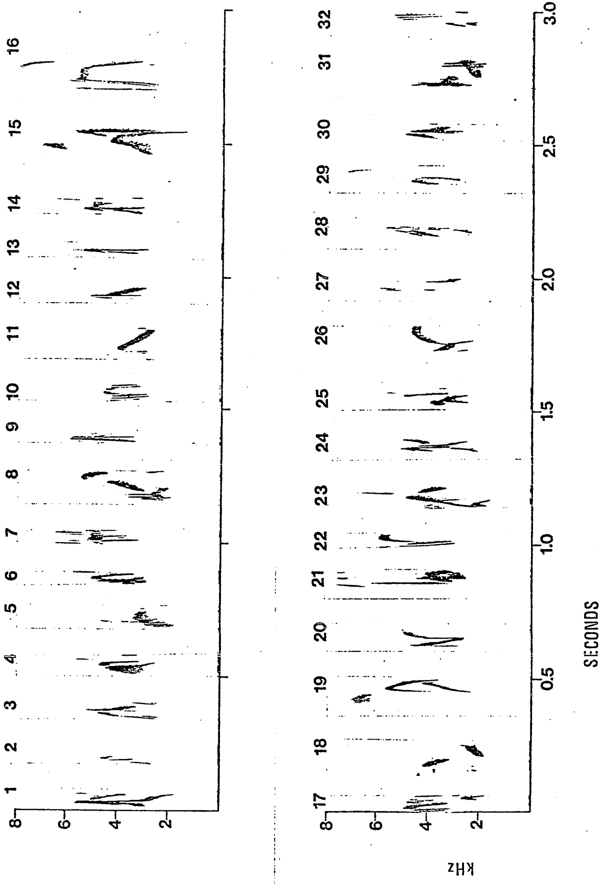

XXX
YYY
ZZZ
AAAA
BBBB
CCCC
DDDD
8
6
4
2
KHz
0.5
1.0
1.5
2.0
2.5
3.0
SECONDS

FIG. 12. Illustration of the syllables of the trill phrase.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
8
6
4
2
kHz
0.5
1.0
1.5
2.0
2.5
3.0
SECONDS

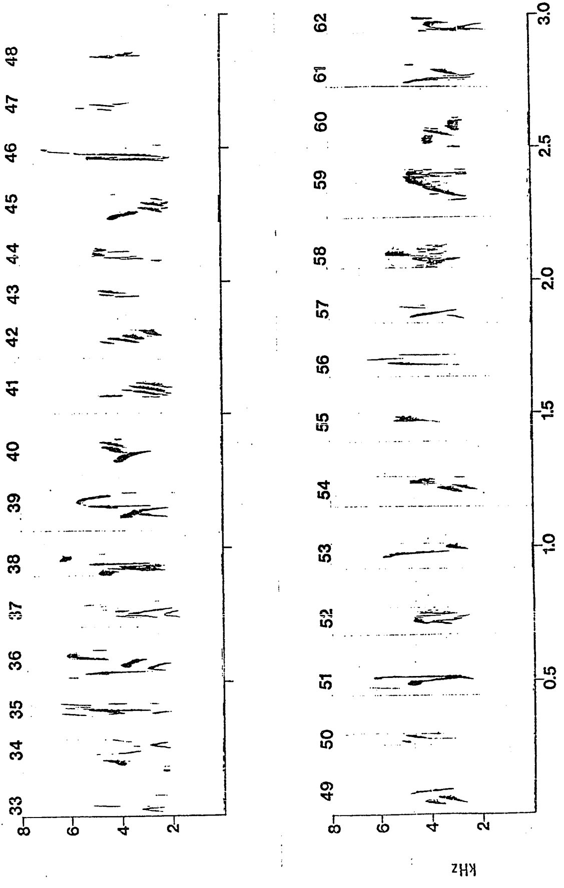

33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
8
6
4
2
KHz
0.5
1.0
1.5
2.0
2.5
3.0
SECONDS

FIG. 13. Illustration of the variation within syllables C, F, H, 1, 25, and 40.

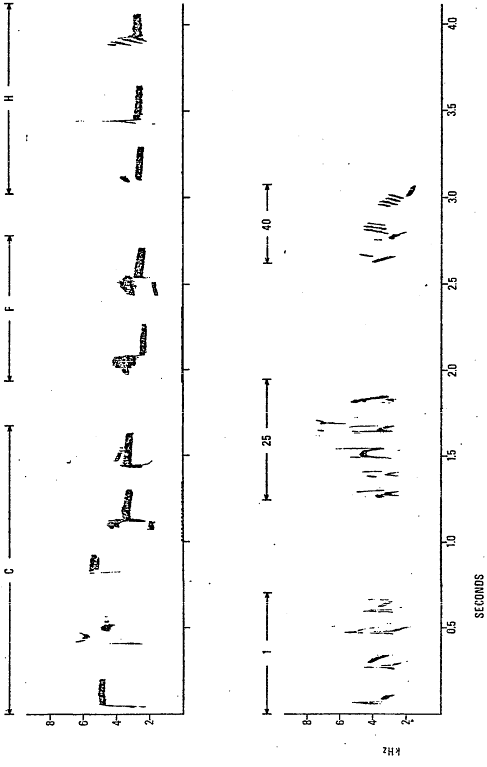
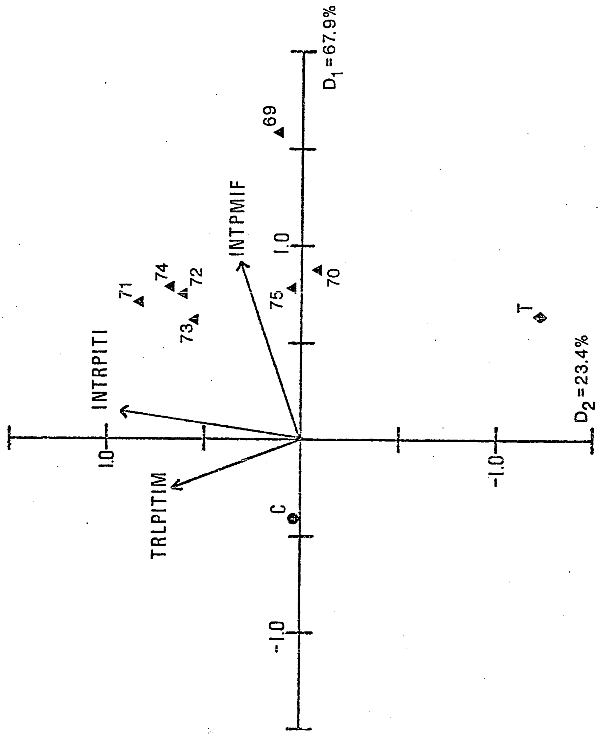

C
F
H
1
25
40
8
6
4
2
KHz
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
SECONDS

FIG. 14. Multiple discriminant analysis of three variables of song from different years at Kalbfleisch (1969-1975), and from one year each at Tobay Beach (T) and Connetquot (C), Long Island, New York. Mean of each population is shown in the first (D_1 = 67.9%) and second (D_2 = 23.4%) discriminant axes. Standardized coordinates are represented by the direction of each vector coming from the grand mean. The length of each vector represents one standard deviation of the measurement. INTRP1TI = length of the note-complex phrase; INTPMIF = minimum frequency of the note-complex phrase; TRLP1TIM = length of the trill phrase.


D$_1$=67.9%
D$_2$=23.4%
INTPMIF
INTRPITI
TRLPITIM
69
70
71
72
73
74
75
T
C
1.0
-1.0
1.0
-1.0

How parts of song identify a male as a conspecific to other males of its species has been studied experimentally with the European Nightjar (*Caprimulgus europaeus*; Abs, 1963), Wood Lark (*Lullula arborea*; Tretzl, 1965), Winter Wren (*Troglodytes troglodytes*; Bremond, 1968a, 1976a), Gray Catbird (*Dumetella carolinensis*) and Brown Thrasher (*Toxostoma rufum*; Boughey and Thompson, 1976), European Robin (*Erithacus rubecula*; Bremond, 1965, 1967, 1968c), Willow Warbler (*Phylloscopus trochilus*; M. Schubert, 1971), Chiffchaff (*P. collybita*, G. Schubert, 1971), Bonelli's Warbler (*P. bonelli*; Bremond, 1972a, 1976b), Wood Warbler (*P. sibilatrix*; Bremond, 1968b, 1972a), Goldcrest (*Regulus regulus*) and Firecrest (*R. ignicapillus*; Becker, 1976), Yellowhammer (*Emberiza citrinella*; *in* Thielcke, 1976), White-throated Sparrow (*Zonotrichia albicollis*; Falls, 1963, 1969), Field Sparrow (*Spizella pusilla*; Goldman, 1973), Indigo Bunting (*Passerina cyanea*; Emlen, 1972; Shiovitz, 1975), Golden-winged Warbler (*Vermivora chrysoptera*; Ficken and Ficken,1973), Ovenbird (*Seiurus aurocapillus*; Falls, 1963), Common Yellowthroat (*Geothlypis trichas*; Wunderle, 1976), and Chaffinch (*Fringilla coelebs*; Bremond, 1972b).

These studies, typically done with birds having a single song-type, have revealed that the song of each species has its own set of features that it contains to be recognized by conspecific males. However, there has been little work on how songs of conspecifics are recognized in bird species that have more than a single song-type per individual, except for the studies of the Yellowhammer (*in* Thielcke, 1976) and the Gray Catbird and Brown Thrasher (Boughey and Thompson, 1976). Thus, I undertook the present study to determine what components of song contribute to species-recognition in the Rufous-sided Towhee (*Pipilo erythrophthalmus*), a species in which males have at least two song-types (Borror, 1959a, 1972, 1975; Kroodsma, 1971; Richards, MS; Ewert, in prep.). The results of this study are then compared with results of playback experiments done with species that are sympatric with the Rufous-sided Towhee over large areas of eastern North America. With this type of comparison it is possible to outline the features of song that are most likely to facilitate identification of conspecific song within a community of species.

METHODS AND MATERIALS

Playback experiments were conducted during May, June and July from 1972 through 1977 at the Kalbfleisch Field Research Station of the American Museum of Natural History, Huntington, Suffolk County, New York; Connetquot River State Park, Islip, Suffolk County, New York and Nissequoque River State Park, Smithtown, Suffolk County, New York. I usually ran experiments in the morning except when it was cool or cloudy, when experiments were conducted throughout the day.

Territories were delimited by observation or by broadcasting tape recordings of towhee song to delineate the area defended by an individual. When I broadcast recordings of towhee song to define territorial limits I played a tape only a few times to minimize a bird's experience with playback. Experiments were done near the center of a territory and the breeding status of the birds was noted whenever possible. With few exceptions, only males responded to playback of song and the analysis of the data is based solely on the responses of males. Playback experiments were done with Uher Report-L-4000 tape recorders connected by 50 foot (15.2 m) cables to Electrovoice speakers placed on the ground.

Most playback tapes were made to determine how the syntax of song affects recognition of song. A few tapes were made to study the role that temporal and frequency aspects of song play in song recognition. Playback tapes were made by recording a song at 1 7/8 ips (4.8 cm/sec) from another recording (see Appendix 7). I did any required splicing of these tapes, and constructed a tape loop. Each loop was constructed so there was one vocalization broadcast every six seconds, the usual amount of time between songs of towhees. I then recorded a five-minute long playback tape at 7 1/2 ips (19 cm/sec) from the loop. I filtered out extraneous sounds on the tape loop below and above the frequency range of the taped vocalization with a Krohn-Hite filter, Model 310-AB. Fourteen different tapes, representing rearrangements and parts of towhee songs, songs of different individuals from home and foreign localities, one song of an acoustically isolated male, and one song of a Green-tailed Towhee (Pipilo chlorurus) were used in these experiments. These vocalizations are described and illustrated in Table 24 and Fig. 15 respectively.

Synthesized song made with the pattern synthesizer (described by Cooper et al, 1951) at Haskins Laboratory, New Haven, Conn., failed to evoke responses from towhees.

Procedures for experiments. Playback procedures were modified from those described by Lanyon (1963). Two tapes were played simultaneously from two separate speakers placed approximately 100 feet (30.4 m) apart near the center of a territory. This allowed each bird to choose to respond to one of the two tapes. No mounts were used. After a bird approached and remained within 30 feet (9 m) of one of the speakers for 45 seconds, cables connecting the recorders with the speakers were switched so that each of the taped sounds was broadcast from the other speaker; this insured that the response was independent of the location of the speaker. I conducted three successive experiments with each bird. Approximately 10 minutes of silence elapsed between each of the five-minute experiments. Each bird was tested with two pairs of test tapes and one pair of control tapes. Four different test tapes were usually played to each individual, to minimize effects of habituation, and I began the series of experiments with the pair of tapes I thought would evoke the weakest response. This was done so that habituation or residual effects from tapes eliciting strong responses would not bias responses to tapes eliciting weak responses. The control tapes were played at the end of the series of experiments and each bird received only one series of three experiments. Not every combination of tapes was played. Attempts were made to use pairs of tapes that could provide tests for hypotheses concerning song recognition.

I evaluated the response of a bird by counting the number of times it approached each of the two tapes. If there was no approach to within 30 feet (9 m) of either tape I concluded that the tapes elicited little or no response. If the bird approached both tapes an equal number of times I interpreted the results to mean that both tapes had the same stimulus value. If one tape was approached one more time than the other I considered the response to be equivocal but with a tendency to react more strongly to that tape; if there were two or more approaches to one tape over the other I considered this to be positive discrimination of that tape over the other.

I conducted 41 dual-speaker experiments with six birds at Kalbfleisch during June 1971 but those data are not directly comparable with data collected after 1971, because I used a mount of a Rufous-sided Towhee at each speaker; I conducted more than three experiments with a bird; I switched cables only once during each experiment and I did not have a control set of tapes following each series of experiments. Consequently, these experiments are cited only for comparison with data obtained in subsequent years.

Data were analyzed with the Wilcoxon Signed-Rank Matched-Pairs Test (Siegel, 1956) using a .05 significance level and a two-tailed test. The raw data are presented in Appendix 8.

Description of song. On Long Island, most songs consist of a note-complex phrase of one to five (usually two) syllables followed by a trill consisting of three or more identical syllables uttered in rapid succession (see Fig. 10). A few songs lack either a note-complex or a trill phrase or have the note-complex phrase following the trill phrase. Most syllables are composed of several notes and many syllables have a wide frequency range, particularly those occurring in the trill phrase. A list of several features of song of towhees from Long Island is presented in Table 25. Most males on Long Island have two to six song-types, most of which are unique to that male. Approximately 29.2% of the individuals recorded shared one or more song-types with other males. Dialects do not occur among populations of towhees in the northeastern United States (Borror, 1975; Ewert, in prep.) but a relatively high proportion of song-types are shared between birds in Oregon (Kroodsma, 1971; Heinemann, pers. comm.)

RESULTS

The results from every pair of tapes used in this study are presented in Table 26. These results were used to rank the tapes. The ranking of the tapes was made to estimate the relative stimulus value of the tapes, and to infer the relative stimulus value of tapes that were not played together. The ranking of the tapes is summarized in Table 27. It was obtained by determining if there were statistically significant differences in the number of approaches to each tape of a pair of tapes. By using this method of analysis for every pair of tapes that was played together a ranking of these tapes was derived. I then determined if the average number of approaches to a tape was consistent with the number of experiments that the tape elicited more response than the tape it was played against (see Table 26). This was particularly useful when differences in response to tapes were not significantly different. In only one case did the average number of approaches to a tape not agree with the number of times that it elicited more response than the other tape (see Table 26; Tapes 29,31). Thus, these methods of analysis resulted in a consistent ranking of these tapes.

I roughly classified the tapes into five categories to facilitate the interpretation of Table 27; these categories do not serve an analytic purpose. The (1) control tape (Tape 1, see Fig. 15;1) elicited the most response, followed in order of decreasing response, by (2) an unaltered song lacking a trill (Tape 4; Fig. 15;4) and the control song spliced such that the trill phrase preceded the note-complex phrase (Tape 28; Fig. 15;8); (3) then by a Guatemala song (Tape 5; Fig.15;5), and the note-complex (Tape 2; Fig. 15;2) and trill phrases (Tape 3; Fig. 15;3) of Tape 1; (4) by two different syllables (Tapes 29, 32; Fig. 15;9 and 12 respectively) presented alone, the trill phrase of the Guatemala song (Tape 33; Fig. 15;13), the song of a male kept in sound isolation (Tape 31; Fig. 15;11) and where the time interval between syllables of Tape 2 was increased by about five times (Tape 34; Fig. 15; 14) and finally by (5) the second syllable of Tape 2 (Tape 30; Fig. 15; 10), a song recorded from California (Tape 27; Fig. 15;7), and a song of a Green-tailed Towhee (Tape 26; Fig. 15;6).

Species recognition. The results of these experiments indicate that Rufous-sided Towhees can distinguish their own song, or even parts of it, from that of the Green-tailed Towhee, which also has a song composed of both note-complex and trill phrases. Playback experiments done in 1971 with one song each of the White-crowned Sparrow (Zonotrichia leucophrys), recorded at Moosonee, Ontario, and the Common Yellowthroat, recorded on Long Island, New York, showed that Rufous-sided Towhees did not respond to these songs, even though the song of the White-crowned Sparrow is composed of note-complex and trill phrases. Thus, towhees seem to respond only to the song of their own species. This seems to be true even when the song of a towhee is like that of another species (Richards, MS).

Population recognition. Rufous-sided Towhees on Long Island responded less vigorously to a towhee song recorded in Guatemala than to songs from Long Island, and only a few birds responded (very weakly) to a song from California. The response to the Guatemala song was moderately strong but less than that to complete songs or a complete note-complex or trill phrase from Long Island, but more than to tapes consisting of single syllables of the note-complex phrase. This moderate response to Guatemala song is probably due to the similarity of the structure of the Guatemala song to most Long Island songs, both of which consist of a note-complex phrase followed by a trill phrase. The structure of the California song is, however, different from that of any song recorded on Long Island, since it is a rapidly modulated trill with no note-complex phrase and it sounds much "buzzier" than any song I recorded on Long Island.

These results suggest that towhees might be able to recognize and respond less strongly to songs from different localities, as do Winter Wrens (Kreutzer, 1974b), Cardinals (_Richmondena cardinalis_; Lemon, 1967), and White-crowned Sparrows (Milligan and Verner, 1971), and perhaps Song Sparrows (_Melospiza melodia_; Harris and Lemon, 1974). Similarly, Thielcke (1973a) found that Short-toed Treecreepers (_Certhia brachydactyla_) from Germany did not respond to song of _brachydactyla_ recorded in Morocco. However, it is difficult to determine whether these differences in response are a consequence of the properties of a particular song, when there is as much individual variation in song as there is in towhees and Song Sparrows. A lack of response to some songs of conspecifics should be expected where characteristics of song are quite variable within, and particularly between localities.

Song recognition. Towhees apparently recognize several features of song to identify another male towhee. At least the syntax of song (the arrangement or ordering of syllables within a song), and the time interval separating parts of song and perhaps the frequency range of the song may contribute to song recognition, as discussed below. But, the fact that a tape consisting of a single syllable could evoke a response suggests that the song of towhees contains additional sources of information for species-recognition. Thus, the problem becomes one of determining whether any of these variables are more important for species-recognition than others.

Syntax of song. The syntax of the song of a towhee affects whether a song is recognized by other towhees. This is suggested by the fact that as more of the song of Tape 1 was omitted from playback tapes the weaker the response became, and that when the sequence of phrases was reversed the response was less than that evoked by normal song. In order from strongest to weakest response, the tapes were ranked as follows: (1) normal song consisting of two syllables in a note-complex phrase followed by a trill phrase (Tape 1; Fig. 15;1); (2) song of Tape 1 changed so that the trill phrase preceded the note-complex phrase (Tape 28; Fig.15;8); (3) the trill phrase of Tape 1 played alone (Tape 3; Fig. 15;3); (4) the note-complex phrase of Tape 1 played alone (Tape 2;Fig. 15;2); (5) the first syllable of the note-complex phrase of Tape 1 (Tape 29; Fig. 15;9); and (6) the second syllable of the note-complex phrase (Tape 30; Fig. 15;10) alone (see Table 27).

The results obtained with Tape 1 and its parts, suggest that towhees most readily recognize song consisting of two phrases, especially when a note-complex phrase is followed by a trill phrase. A song containing both phrases elicits a stronger response than a song containing only one phrase even if the sequence of phrases is reversed. If only one phrase is present, the trill phrase apparently elicits a stronger response than the note-complex phrase. Complete note-complex or trill phrases, in turn, evoke stronger responses than a single syllable taken from that phrase. These results are consistent with the fact that 88% of the towhee songs I recorded from Long Island consisted of one note-complex phrase followed by one trill phrase and that every male I recorded had at least one song-type with a trill phrase.

However, results from other tapes are somewhat different from those of Tape 1, and its variously isolated components. Although isolated syllables taken from other songs evoked responses similar to those isolated from Tape 1, and were ranked similarly, two complete songs were ranked differently than would have been expected from results obtained by manipulating the song on Tape 1. Tape 4, a song without a trill phrase (see Fig. 15;4), elicited a stronger response than Tape 28 (see Fig. 15;8). Thus, at least one song lacking a trill evokes a stronger response than a song having both note-complex and trill phrases in reverse order. Tape 5 (Fig. 15;5), a song recorded in Guatemala and having a note-complex phrase followed by a trill phrase, elicited less response than tapes having a note-complex phrase alone (Tape 2; Fig. 15;2) or a trill phrase alone (Tape 3; Fig. 15;3). These results suggest that responses to songs having a particular syntax are modified by other characteristics of song.

Time. The duration of song probably has little influence on species-recognition of song in towhees, since a single syllable can elicit a fairly strong response, even though the coefficient of variation of the duration of song is fairly low. Other temporal features of song were found to affect response to playback, however. When the time interval between two syllables of the note-complex phrase was increased by about five times, the response to that tape was significantly less than to the same note-complex phrase with a normal time interval between syllables. This suggests that relatively long time intervals between components of song reduce the response to song. It is not known if increasing departures from the average rate of delivery of trill components (17.0 syllables/sec) result in decreased responses.

Frequency. The frequency range may play a role in recognition of conspecific song by towhees. One nearly pure-tone syllable (see Fig. 15;10) from the note-complex phrase of Tape 1 elicited virtually no response. Other syllables (see Fig.15 ;9,12), having frequency ranges more than 2.3 kHz, elicited stronger responses than the nearly pure-tone syllable; although the response to these tapes was relatively weak. Experiments done in 1971 with another nearly pure-tone syllable (frequency 5.5 to 6.0 kHz), also elicited no response. Thus, these data suggest that there may be a minimum frequency range necessary for species-recognition, but because syllables having different structures were used in these experiments this remains conjectural.

Song of isolate male. The song of the isolate male elicited very little response from wild territorial male towhees. This suggests that learning of song may be essential for the development of a song that would be effective in defending a territory, at least early in the breeding season. These results are similar to those from playback experiments done with Coal Tits (Parus ater; Thielcke, 1973b), Wood Thrushes (Hylocichla mustelina; Lanyon, MS), and Indigo Buntings (Shiovitz, 1975), where there was little response to song of acoustically isolated males by wild territorial males, except for one Kasper Hauser song of an acoustically isolated male Brown-headed Cowbird (Molothrus ater), that elicited more response from captive females than normal song (King and West, 1977).

DISCUSSION

The results of these experiments indicate that towhees use several characteristics of song to recognize songs of conspecific males, although some songs of towhees may elicit no response because they lack characteristics of song associated with towhee song at that locality. At least some species, then, may have so much geographical variation in song that the characteristics of song used to identify conspecifics vary geographically. For towhees in eastern North America the syntax of song and the time interval between syllables of the note-complex phrase of the song play a part in facilitating recognition of conspecifics. There might also be a minimum frequency range necessary for species-recognition but this remains to be determined. Features of the song not investigated, such as frequency and amplitude modulation and more detailed aspects of temporal and frequency features of the song may also contribute to species recognition. This might include the time interval between the note-complex and trill phrases and the maximum frequency and frequency range of the trill phrase, which did not differ significantly between individuals. However, towhees apparently use several features of song to identify song of conspecific males and the minimal requirements for song recognition can be present in one syllable of a song.

These results are similar to other findings (for examples see Falls, 1963; Emlen, 1972; Shiovitz, 1975; Boughey and Thompson, 1976; Wunderle, 1976) where it was shown that each species uses more than one feature of song to identify song of conspecifics. Thus, there may not be any single species-specific characteristic which permits identification but each species may have a distinctive set of features of song, which may vary geographically, that it relies upon to accurately distinguish their own song from song of sympatric species. This redundancy is probably necessary to permit individual recognition of song and to allow for locally distributed environmental factors that influence efficient transmission of different sounds.

The set of characteristics of song which permit species identification should differ from the characteristics of song that identify other species if song facilitates species-identification. Additionally, the structure of song presumably reflects the constraints imposed on it by what sounds can be produced and by characteristics of the air medium and vegetation structure which affect transmission of sound (see Morton, 1975; Chappuis, 1971; Marten and Marler, 1977; Marten et al, 1977; Wiley and Richards, in press). Here I focus on how songs of species of birds sympatric with the Rufous-sided Towhee in eastern North America are distinguished from each other. Only those species of birds in which playback experiments have been designed to study species-recognition aspects of song will be discussed. Consequently, the lack of data from other species that are sympatric with towhees limits the scope of this discussion.

Playback experiments designed to find "species-specific" characteristics of song have been conducted with six species of birds that are extensively sympatric with Rufous-sided Towhees. The characteristics of the song of these species and of the Rufous-sided Towhee are presented in Table 28 and the results of playback experiments with these species are presented in Table 29.

As Emlen (1972) noted, the characteristics of song that ornithologists cite as being characteristic of a species may not be essential for birds to recognize song of conspecifics. Thus, the repetition of a syllable is not required for species-recognition in Indigo Buntings or Brown Thrashers, although the repetition of similar or identical syllables facilitates species recognition in Brown Thrashers. Nor is the organization of song into two phrases in Rufous-sided Towhees or the increasing loudness toward the end of song of the Ovenbird essential for species-recognition. In the Field Sparrow however, the increasing tempo of the song seems to be critical for species-recognition.

Since these distinguishing properties of song of different species are frequently not essential or perhaps important for species-recognition, other variables of song must be used by birds to distinguish conspecific song from song of other species. The tempo of song appears to be an important cue in species-recognition. The available data suggest that the time interval between syllables of song differs between each of these species (see Table 28). Altering the silent interval between syllables of a song has resulted in reduced responses compared to control songs by Ovenbirds, Common Yellowthroats, Indigo Buntings, Rufous-sided Towhees and Field Sparrows. Changing the time interval between syllables of normal song by as little as 0.05 sec resulted in significantly reduced responses by Indigo Buntings and Common Yellowthroats. Thus, the tempo of song may be an important cue to the species identity of a singer with this group of sympatric species. This is consistent with the fact that birds may be able to resolve differences in time as small as 1 to 10 msec (Konishi, 1969a; Wilkinson and Howse, 1975), so that the small differences in the inter-syllable time interval of these seven species could be an important and efficient method of coding species-identity in song. Thus, birds in one area may be able to focus on one feature of song for species-identification. Where two species have songs with a similar tempo other features of song would become important for species-identification. In other areas, or even among other taxonomic groups of birds other than mimids, parulids and emberizines, the tempo of the song may not be an important cue to species-identity (see Emlen, 1972).

Details of syllables seem to play an important role in species-recognition of song by Ovenbirds, Common Yellowthroats, and Indigo Buntings (Falls, 1963; Wunderle, 1976; Emlen, 1972, respectively). The sequence of notes or components of each syllable seems to be important in eliciting responses to song by Indigo Buntings and Ovenbirds but it is not known what aspect of the syllable structure is used in recognizing conspecific song. In Yellowthroats minor details of syllables ("hooks") are not important species-identification cues but the syllables must be repeated at least twice and each syllable should consist of two notes, one an upslur, the other a downslur.

Other aspects of song apparently play a role in eliciting species-specific responses. Single syllables of towhee song with a relatively wide frequency range elicit more response than those with a narrow frequency range. Yellowthroats responded less to songs where the frequency range had been compressed and the absolute frequency range had been lowered compared to normal song. But, since most songs of most species occurring with towhees fall within a frequency range of 2.0 to 7.0 kHz, it may be that song of species that inhabit this second-growth habitat must be within these limits to minimize distortion and attentuation. Thus, although certain frequency variables of song may be relatively unimportant for species identity there may be critical properties of the frequency of a song that a song must have to minimize degradation during trasmission in particular habitats (Morton, 1975; Wiley and Richards, MS).

The results of playback experiments with Rufous-sided Towhees and six sympatric species illustrate the variety of acoustical cues birds use to associate song with conspecific individuals. Each species relies on several cues to identify a conspecific singer and the tempo of song may be especially important for species identification of song among this group of species. Much remains to be learned however, since few precise statements can be made concerning how a species is able to distinguish its song from song of other species. Further, it is extremely difficult to determine what parts of song are primarily evolved for individual recognition or, whether song is selected to communicate only some of this information.

The interpretation of the behavior of the birds can also be difficult to evaluate. Aside from the usual problems of estimating intensity of behavioral responses and designing experiments to minimize responses to stimuli independent of those created by an experiment, it is essential to know what sounds birds are capable of responding to. Konishi (1969b) found that the hearing threshold curve of three species of passerines roughly correlated with the highest frequency of their vocalizations but these same species did not produce sounds below 1 kHz even though they could hear sound below 1 kHz. Using more elaborate procedures, Leppelsack and Vogt (1976) demonstrated that neurons of the caudal neostriatum of Starlings (Sturnus vulgaris), respond to a variety of sounds, including some that are species-specific. Different neurons responded to a single variable, different combinations of variables, or to all the variables that constitute a sound. Thus, based on playback results and the results of Leppelsack and Vogt, it seems that sounds produced by birds have co-evolved with the ability to selectively respond to these same sounds. Species that have large and diverse repertoires might respond to a large variety of stimuli to insure that song of conspecifics would be recognized. Or, a "species-specific" sound may occur in different parts of song to allow for variation in song. More experimental data are needed to determine how species-identity of song occurs.

TABLE 24. DESCRIPTION OF TAPES USED IN THE PLAYBACK EXPERIMENTS.

Tape #	Description of playback tape	Length of vocalization (secs)	Time between syllables of Phrase 1 (secs)	Time between syllables of Phrase 2 (secs)	Frequency Max. (kHz)	Frequency Min. (kHz)	Frequency Range (kHz)
1	"Drink-your-tea" song of K23.	1.06	0.19	0.02	8.0	2.4	5.6
2	Note-complex phrase of song on Tape 1.	0.53	0.19	-	5.2	2.4	2.8
3	Trill phrase of song on Tape 1.	0.43	0.02	-	8.0	3.1	4.9
4	Song of K23 that lacks trill phrase.	0.77	0.18	-	5.6	2.7	2.9
5	Guatemala song.	0.93	-	0.03	5.5	2.1	3.4
26	Green-tailed Towhee song.	1.60	-	-	7.2	2.3	4.9
27	Rufous-sided Towhee song from Calif.	0.50	0.01	-	5.9	2.0	3.9
28	Song of Tape 1 altered so trill appears before note-complex phrase.	0.92	0.02	0.19	8.0	2.4	5.6
29	First syllable of note-complex phrase on Tape 2.	0.08	-	-	5.2	2.4	2.8
30	Second syllable of note-complex phrase on Tape 2.	0.27	-	-	2.6	2.4	0.2
31	Song of isolate male.	1.38	0.24	-	7.1	1.7	5.4
32	First syllable of song of C74.	0.24	-	-	4.4	2.0	2.4
33	Trill phrase of song on Tape 5.	0.64	0.03	-	5.5	3.0	2.5
34	Like Tape 2 but silent interval between syllables increased by factor of 4.6.	1.23	0.88	-	5.2	2.4	2.8

TABLE 25. FEATURES OF SONG OF THE RUFOUS-SIDED TOWHEE FROM LONG ISLAND, NEW YORK.

Variable	Mean ± S.D. (N)	Range	C.V. [1]
Temporal features (secs)			
Song length	1.11 ± 0.217 (441)	0.44-1.92	20.38
Note-complex phrase length[2]	0.48 ± 0.202 (412)	0.02-1.74	42.26
Trill phrase length[2]	0.53 ± 0.097 (404)	0.22-0.59	18.41
Time between note-complex[2] and trill phrase	0.10 ± 0.039 (399)	0.02-0.42	39.80
Length of first syllable of note-complex phrase	0.13 ± 0.075 (437)	0.01-0.29	59.06
Length of second syllable of note-complex phrase	0.18 ± 0.073 (353)	0.01-0.40	41.01
Length of syllable of[2] trill phrase	0.06 ± 0.025 (427)	0.01-0.13	43.86
Time between syllables[2] of trill phrase	0.02 ± 0.015 (426)	0 -0.11	88.88
Time between syllables[3] of note-complex phrase	0.18 ± 0.068 (351)	0.01-0.47	38.57
Frequency features (kHz)			
Highest freq. of song	6.4 ± 1.03 (441)	4.4 - 8.6	16.23
Lowest freq. of song	2.0 ± 0.39 (441)	1.2 - 3.5	19.16
Freq. range of song	4.3 ± 1.10 (441)	2.3 - 7.1	25.37

[1] Coefficient of variation (C.V.) = $(s/\bar{x})\ 100$.

[2] Data from songs having either one note-complex phrase/song or one trill phrase/song or one note-complex and one trill phrase.

[3] Time between first and second syllables of note-complex phrase only.

TABLE 26. RESULTS OF DUAL-SPEAKER PLAYBACK EXPERIMENTS.

Tape		N^1	Mean Number of Approaches ± S.D.		T^2	P	Number of experiments where ^{3}					
a	b		a	b			a>b	a≥b	a=b	a≤b	a<b	No response
1	2	7	2.0 ± 0.82	0.1 ± 0.38	0	.02	5	2	0	0	0	0
1	3	7	2.9 ± 0.90	0.7 ± 0.95	0	.02	5	2	0	0	0	0
1	4	7	3.3 ± 1.38	0	0	.02	7	0	0	0	0	0
1	5	7*	4.0 ± 1.83	0.1 ± 0.38	0	.02	6	1	0	0	0	0
1	26	7*	3.0 ± 1.00	0.1 ± 0.38	0	.02	7	0	0	0	0	0
1	28	7*	2.0 ± 1.15	0.3 ± 0.49	0	.05	3	3	1	0	0	0
1	29	1*	5.0	0	0	-	1	0	0	0	0	0
1	31	5	3.2 ± 1.48	0.2 ± 0.45	0	.06	4	1	0	0	0	0
2	3	16*	1.0 ± 1.10	1.2 ± 1.34	43.5	-	4	1	1	4	6	0
2	4	10	1.0 ± 0.82	2.4 ± 1.90	4.0	.03	0	2	1	1	6	0
2	5	11	1.6 ± 1.21	0.7 ± 0.79	11.0	-	4	2	2	2	1	0
2	28	11*	0.9 ± 0.83	1.9 ± 1.38	11.5	-	1	2	1	2	5	0
2	29	12*	1.5 ± 0.90	0.4 ± 0.67	8.5	.03	4	6	1	0	1	0
2	30	8	1.8 ± 1.28	0	0	.02	4	3	0	0	0	1
2	31	7	2.6 ± 0.98	0	0	.02	6	1	0	0	0	0
2	32	8	1.5 ± 1.31	0.1 ± 0.35	2.0	.05	4	2	0	1	0	1
2	34	7	2.1 ± 1.07	1.1 ± 0.69	0	.06	1	4	2	0	0	0
3	4	10*	1.0 ± 1.33	1.7 ± 1.06	10.0	-	1	1	2	2	4	0

TABLE 26. RESULTS OF DUAL-SPEAKER PLAYBACK EXPERIMENTS (continued).

Tape		N	Mean Number of Approaches ± S. D.		T	P	Number of experiments where					
a	b		a	b			a>b	a≥b	a=b	a≤b	a<b	No response
3	5	22	2.2 ± 1.33	1.4 ± 1.40	78.5	-	12	3	0	3	4	0
3	26	7	2.1 ± 1.68	0.1 ± 0.38	0	.02	3	4	0	0	0	0
3	28	8	0.9 ± 1.13	3.0 ± 2.00	3.0	.04	0	2	0	0	6	0
3	29	9	1.9 ± 1.69	0.6 ± 0.73	2.0	.05	4	2	1	1	0	1
3	30	7*	2.3 ± 1.50	0.6 ± 1.51	6.0	-	5	1	0	0	1	0
3	31	8	3.2 ± 1.04	0.2 ± 0.46	0	.01	8	0	0	0	0	0
3	33	7	2.1 ± 0.90	0.3 ± 0.49	0	.05	4	2	1	0	0	0
3	34	7	2.4 ± 1.51	0.3 ± 0.49	1.0	.06	5	0	1	1	0	0
4	5	21*	1.1 ± 1.09	0.7 ± 0.96	59.0	-	4	7	3	6	1	0
4	26	9*	0.9 ± 1.05	0.1 ± 0.33	2.5	-	2	3	0	1	0	3
4	27	8	2.2 ± 2.38	0.4 ± 0.52	0	.06	5	0	0	0	0	3
4	28	7	1.9 ± 1.35	0.7 ± 0.95	3.5	-	4	1	1	0	1	0
4	31	15	1.5 ± 1.55	0.6 ± 0.83	22.0	-	5	4	2	3	1	0
5	26	6*	1.8 ± 0.75	0.8 ± 0.75	0	.05	0	6	0	0	0	0
5	27	7*	1.6 ± 1.40	0	0	.06	3	2	0	0	0	2
5	28	8*	0.4 ± 0.74	2.4 ± 1.41	3.5	.05	1	0	0	1	6	0
5	29	7	1.6 ± 1.27	0.6 ± 0.79	6.0	-	4	1	0	1	1	0

TABLE 26. RESULTS OF DUAL-SPEAKER PLAYBACK EXPERIMENTS (continued).

Tape		N	Mean Number of Approaches ± S.D.		T	P	Number of experiments where					
a	b		a	b			a>b	a≥b	a=b	a≤b	a<b	No response
5	31	8	1.5 ± 1.31	0.1 ± 0.35	2.0	-	4	2	0	1	0	1
5	33	7	1.9 ± 1.46	0.3 ± 0.49	1.5	.08	4	1	0	1	0	1
5	34	7	0.7 ± 0.49	0.4 ± 0.79	10.0	-	0	5	0	1	1	0
26	27	1	0	0	-	-	0	0	0	0	0	1
26	29	1*	0	3.0	0	-	0	0	0	0	1	0
27	30	7	0.6 ± 0.53	1.1 ± 0.90	7.0	-	0	2	0	4	1	0
27	31	8	0	0.8 ± 1.04	0	-	0	0	0	3	1	4
27	32	8	0.2 ± 0.46	0.6 ± 0.74	6.0	-	0	2	0	3	1	2
29	30	8*	1.6 ± 1.19	0.5 ± 0.76	2.0	.09	3	2	1	1	0	1
29	31	9	0.9 ± 1.05	1.0 ± 2.00	16.0	-	2	3	0	1	2	1
29	32	9	1.0 ± 1.12	0.6 ± 0.73	6.5	-	2	2	1	1	1	2
29	33	7	2.0 ± 0.82	1.0 ± 1.15	0	-	2	2	3	0	0	0
29	34	8	0.6 ± 0.74	1.0 ± 1.20	4.0	-	0	2	1	1	2	2
30	31	7	0.3 ± 0.49	1.4 ± 1.40	2.5	-	0	0	1	1	3	2
30	32	11	0.2 ± 0.40	0.4 ± 0.50	7.0	-	0	2	0	4	0	5
31	32	7	0.6 ± 0.79	0	0	-	1	2	0	0	0	4
32	33	4	0.5 ± 0.58	1.2 ± 1.26	2.0	-	0	1	0	2	1	0
33	34	4	0.5 ± 0.58	1.8 ± 0.50	0	-	0	0	0	3	1	0

TABLE 26. RESULTS OF DUAL-SPEAKER PLAYBACK EXPERIMENTS (continued).

[1] Where the value of N is followed by an asterisk, this indicates that at least one experiment was not done under standardized conditions.

[2] T is the smaller of the sums of the like-signed ranks of the Wilcoxon matched-pairs signed ranks test. Probabilities are given only where significant differences (.05 level) between tapes occur or are approached (two-tailed test). The sample size for the Wilcoxon test for a given pair of tapes may be less than the total sample size (N) if tie scores occurred (a = b; no response).

[3] Tape a > b is used to mean there were at least two more approaches to a than b; a $\geq$ b means there was one more approach to a than b; and a = b means both tapes received the same number of approaches.

TABLE 27. RESULTS OF PLAYBACK EXPERIMENTS BY PAIRED TAPES IN ORDER OF THOSE THAT ELICITED THE STRONGEST RESPONSE TO THOSE THAT ELICITED THE WEAKEST RESPONSE. * INDICATES THAT THE TAPE OF THE COLUMN ELICITED SIGNIFICANTLY MORE RESPONSE (.05, two-tailed, Wilcoxon Signed-Rank Matched-Pairs Test) THAN THE TAPE OF THE ROW. + INDICATES THE TAPE OF THE COLUMN ELICITED MORE RESPONSE THAN THE TAPE OF THE ROW, BUT NOT SIGNIFICANTLY. = INDICATES THAT THE TAPE OF THE COLUMN ELICITED THE SAME RESPONSE AS THE TAPE OF THE ROW.

	1	4	28	3	2	5	34	29	33	31	32	30	27
1													
4	*												
28	*	+											
3	*	+	*										
2	*	*	+	+									
5	*	+	*	+	+								
34				+	+	+							
29	+			*	*	+	+						
33				*		+	+	+					
31	+	+		*	*	+		(+)[a]					
32					*			+	+	+			
30				+	*			+		+	+		
27	*	+				+				+	+	+	
26	*	+		*		*		+					=

[a] The average number of approaches to 31 was greater than 29 but 29 elicited a greater response in more experiments than 31.

TABLE 28. MEAN VALUES OF CHARACTERISTICS OF SONG OF THE RUFOUS-SIDED TOWHEE AND OF FIVE SPECIES OF BIRDS SYMPATRIC WITH TOWHEES.

Species	Recorded From	Song Length (secs)	Length of Syllables[1] (secs)		Time between Syllables (secs)		Freq. range of Song (kHz)
			Phrase 1	Phrase 2	Phrase 1	Phrase 2	
Gray Catbird[2]	Mich.	0.27	0.27	-	0.19	-	~1.75 to 7
Brown Thrasher[3]	Mass.	0.64	~0.17	-	~0.08	-	1.6 to 5.5
Common Yellowthroat[4]	Long Is., New York	1.89	0.11	-	0.05	-	3.0 to 6.3
Indigo Bunting[5]	Ithaca, New York	2.31	0.18	-	0.10	-	2.4 to 7.3
Rufous-sided Towhee[6]	Long Is., New York	1.11	0.15	0.06	0.17	0.01	2.0 to 6.4
Field Sparrow[7]	Ohio Mich.	~2.75 2.65	~0.14	~0.10	~0.09	~0.05	~3.2 to 4.3 2.8 to 4.2

[1] Syllables of different phrases were treated separately if songs consisted of two distinct parts or phrases.

[2] Data from Thompson and Jane (1969), I used the terms song length and syllable synonymously with their term syllable pattern.

[3] Data from Boughey and Thompson (1976); my use of song length and syllable equal their terms group length and figure respectively; data on syllables were taken from Fig. 4 of their paper and are approximate.

[4] Data from Wunderle (1976); syllable = note of Wunderle.

TABLE 28. (continued).

[5] Data from Emlen (1972); syllable = figure of Emlen.

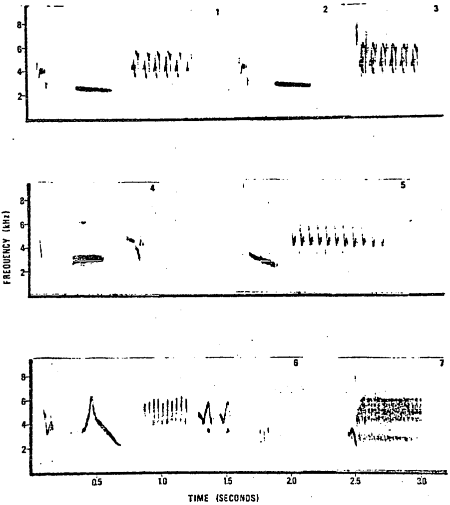
[6] This study.

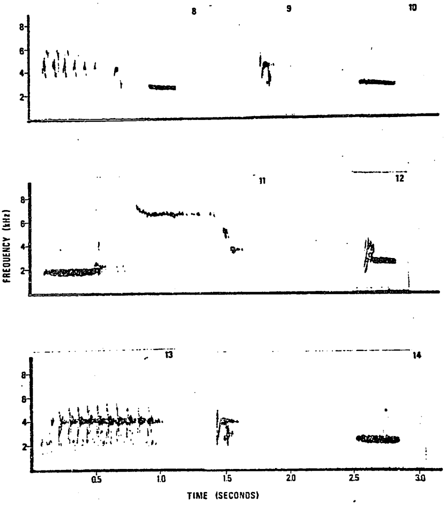
[7] Data from Ohio from Goldman (1973); syllable = note of Goldman, data taken from Fig. 1 are approximate; data from Michigan from Heckenlively (1976).

TABLE 29. FEATURES OF SONG BELIEVED TO CONTRIBUTE TO SPECIES RECOGNITION IN RUFOUS-SIDED TOWHEES AND SIX OTHER SPECIES.

Species	Important "species-specific" features	Other distinctive features of song
Gray Catbird	? (repetition rate not important)	Unpaired figures, continuous song.
Brown Thrasher	Repetition of syllables twice	Paired figures, continuous song.
Ovenbird	Specific tempo Specific sequence of notes	Increasing loudness of song.
Common Yellowthroat	Repeated two-noted upslur and downslur phrases; 0.05 sec between notes. Frequency 2.0 to 7.0 kHz Frequency range at least 2.1 kHz	Repetition of same phrase throughout song at same rate.
Indigo Bunting	Time between figures about 0.10 sec Time between components of figures Sharp increase in frequency followed by sharp decrease around an inflection point for each figure. Length of phrase? Frequency range?	Paired figures, discontinuous song.
Rufous-sided Towhee	Time between syllables Frequency range at least 0.5 to 2.5 kHz? Sequence of phrases?	Song divided into two distinct parts.
Field Sparrow	Decreasing note length toward end of song	Increasing tempo of song toward end of song.

FIG. 15. Sonograms of songs, and their components, used in playback experiments. Sonograms 1 through 5 are graphs of songs and their components of Tapes 1 through 5, respectively. Sonograms 6,7,8,9,10,11, 12,13, and 14 are graphs of songs and their components on Tapes 26,27,28,29,30,31,32,33, and 34 respectively. See Table 24 for a description of these tapes.


1
2
3
4
5
6
7
8
6
4
2
FREQUENCY (kHz)
0.5
1.0
1.5
2.0
2.5
3.0
TIME (SECONDS)


8
9
10
11
12
13
14
8
6
4
2
FREQUENCY (kHz)
0.5
1.0
1.5
2.0
2.5
3.0
TIME (SECONDS)

Passerine birds raised in acoustic isolation or deafened at an early age typically develop songs which are more variable, "buzzier", and less well organized than songs of wild conspecific birds (Marler, Kreith and Tamura, 1962; Konishi, 1964b Konishi and Nottebohm, 1969; Marler <u>et al</u>, 1972; Nottebohm, 1975b). Few researchers however, have studied song development in passerine birds raised from the egg, either with foster parents (for exceptions see Mulligan, 1966; Kroodsma, 1977) or without foster parents (see Lanyon, 1976; Lanyon, MS). Because embryos of some non-passerines are sensitive to sound (Gottleib, 1966) and because passerines can selectively respond to (but not necessarily learn to repeat) specific sounds when they are three days old (Messener in Thielcke, 1976), it is preferable to study song development with acoustically isolated birds that have been raised from the egg. I raised one male Rufous-sided Towhee (<u>Pipilo erythrophthalmus</u>) to maturity from an egg, recorded its song and conducted playback experiments with the song. This report represents the first study of development of song in the Rufous-sided Towhee. Results from the playback experiments will be presented elsewhere (Ewert, MS).

METHODS AND MATERIALS

I collected three eggs from a nest at the Kalbfleisch Field Research Station, Huntington, Long Island, New York on 15 July 1974. The eggs were approximately nine days old when taken from the nest. They hatched 18 July 1974 in a sound isolation chamber. The two males and one female were kept together in the sound isolation chamber until 11 August 1974 when each male was transferred to its own sound isolation chamber at the American Museum of Natural History, and the female was kept in a cage in an office. The birds were not deafened and could hear themselves. I moved them at night in a car so they would not hear other birds during the move. One male died shortly after being placed in a sound chamber. Following establishment of the surviving male in the chamber I periodically monitored and tape recorded the bird. Recordings were made with a Uher 4000-L tape recorder and a Uher M512 microphone. The photoperiod was adjusted to roughly correspond with the natural photoperiod except in early spring when I lengthened the photoperiod to induce singing by early April.

The male was first heard singing subsong (terminology follows Nottebohm, 1975b) on 28 August 1974, when he was 42 days old. "Warble" song was heard by 17 February 1975 and "plastic" or full song on 13 April 1975. Recordings used for this analysis of song development were made on 8 September 1974 (subsong), 13 April and 1 June 1975 ("plastic" or full song), and 10 and 25 May 1976 ("plastic" or full song). I analyzed 111 songs for this study. In Appendix 9 these songs are listed in the order in which they were sung. The terminology used to describe song follows Kroodsma (1974). A continuous spectrum analyzer (described by Hopkins, Rossetto, and Lutjen, 1974) was used to graph the songs from tapes played at one-quarter speed. Measurements were taken from photographic paper copies of the graphs of the recordings. Because the within variance of songs of the isolate male is not comparable to the variance of eight songs of eight males from Kalbfleisch, it was not possible to test for significant differences between the songs of the isolated male and the eight free-living males.

RESULTS

Song morphology and organization

At least 23 syllables could be defined from tape recordings of subsong made on 8 September 1974. These syllables were given consistently throughout the recording period but were not organized into songs. Some of these syllables may have been homologues to the eight syllables that appeared in "plastic" or full song (illustrated in Fig. 16), but because so few recordings were made this is not certain. The number of syllables in the repertoire of the "plastic" or full song of the isolated male is similar to that of wild birds having repertoires of three songs. The number of syllables in the repertoire of a bird, then, appears to be species-specific for a given repertoire size, as it is in other species. Like other passerines, the number of syllables that occurred in subsong of this towhee was greater than the number of syllables that occurred in later stages of song development (Nottebohm, 1975b), and these syllables were more variable than syllables of wild birds.

Although too few recordings were made to determine whether the acoustically isolated male ever developed full song, "plastic" song may have been the final stage of song development achieved because songs were so variable from one recording session to another, even when the bird was two years old. On each of the four days when I recorded the male, a different song variant (a unique sequence of syllables) was sung proportionately more than other variations of song, and none of the 39 different song variants were recorded on all four days (see Table 30). The most frequent song variant of the isolate male recorded on each of the four days is illustrated in Fig. 17 . Only one of the song variants that prevailed on one of the four days was tape recorded another day. The songs of this bird may then differ from individually isolated Red-winged Blackbirds (Agelaius phoeniceus), Western Meadowlarks (Sturnella neglecta), and Song Sparrows (Melospiza melodia) and deafened Dark-eyed Juncos (Junco hyemalis oregonus) and Yellow-eyed Juncos (J. phaeonotus), in which songs developed by their first spring remained relatively stable (Marler et al, 1972; Lanyon, pers. comm.; Kroodsma, 1977; Konishi, 1964b respectively). Songs of one year old wild towhees also differ from those of the isolate male in that the sequence of syllables of each song-type is relatively stereotypic and each song-type is repeated in a sequence of songs (a song bout) that is separated from a bout of another song-type by several minutes of silence (Ewert, unpubl.).

Although the most common variant of three of the four days consisted of only three syllables, the number of syllables in other song variants ranged from one to eight. Certain syllables however, tended to occur in specific parts of song (see Table 31). Syllables 1 and 6 occurred more often at the end of song than the beginning of song whereas syllables 2 and 3 were found at the end of song much more often than the beginning of song. Syllable 3 occurred at the end of 18 of 39 of the song variants and the modal song of each day ended with syllable 3. Syllable 3, which had the highest pitch of any syllable I recorded, always appeared at the end of song except in two song variants where it was the penultimate syllable. Syllable 1 was at the beginning of more song variants (23) than the total number of song variants (16) that began with syllables 2,4,6, and 7, the only other syllables that were at the beginning of song. On days when I heard, but did not record the towhee, songs that resembled songs having a syllable sequence of 1,2,3 or 6,8,3 were frequently heard. Thus, there was a tendency for this bird to initiate songs with syllable 1 and to terminate songs with syllable 3 but other syllables could be interspersed between these two syllables or, occasionally, other syllables were used at the beginning or ending of song.

In the 37 song variants composed of two or more syllables the sequence of syllables was not random (see Table 32). The expected number of times a given sequence of two syllables should occur randomly was calculated using the expression (from Chatfield and Lemon, 1970): $e_{ij} = N_2\ P(i)\ P(j)$, where N_2 = total number of pairs, $P(i)$ = probability of encountering i, and $P(j)$ = probability of encountering j. The probability of encountering each syllable independently of all othersyllables is listed in Table 33. Comparing the expected occurrence of pairs of syllables with the observed values showed that syllable 1 tended to be followed by syllables 2 and 4 and syllable 2 was frequently followed by syllable 3. The sequence of syllables 4,1 and 4,2 occurred more than expected but did not deviate from expected values as much as the sequences 1,2; 1,4; or 2,3. Comparisons of expected with observed sequences with syllables 5,6,7 and 8 was not possible because expected values are so small. These results demonstrate however, that the sequence of syllables in the song of the isolate male are not independent events and thus fit a first order Markov model. To determine whether a second order Markov model fits any sequence of syllables in songs of the isolate male I compared the frequency of observed values of different series of three syllables (triplets) with expected values. Expected values were calculated using the formula (from Lemon and Chatfield, 1973):

$$e_{ijk} = \frac{N_3 \, n_{ij} \, n_{jk}}{N_2 \, n_j}$$

where N_2 and N_3 equal the total number of pairs and triplets respectively and n_{ij} and n_{jk} equal the frequency in the ith row and jth column, and the jth row and kth column respectively of the transition matrix and n_j equals the sum of the jth row of the transition matrix. Although this formula underestimates the expected values and is only approximate (Lemon and Chatfield, 1973), the results indicate that the sequence of syllables 1,1,2 and

1,2,3 occur much more than expected while the sequences of 4,1,1 and 4,1,2 seem to occur less than expected (see Table 34). Some songs then, are structured to fit at least a second order Markov model. Thus, the sequence of syllables in songs of the isolate male follows a general order where song begins with syllable 1, ends with syllable 3 and the sequence of syllables are not independent of each other. There is however, considerable variation in the sequence and location of syllables so that the sequence of syllables in songs of the isolate male are less predictable than in songs of free-living males.

No songs of this isolate male contained trills (rendition of the same syllable three or more times in rapid succession), unlike wild towhees, where every individual I recorded had at least one song-type that had a trill phrase. Although songs of some wild birds lack a trill, the isolate male was the only individual I recorded where at least one song of the individual did not have a trill. As in wild towhees, some syllables occurring in song were also given as calls. Syllable 7, which was given as an alarm call, appeared in several songs on 10 May 1976.

Quantitative Features of Song

Characteristics of four songs of the isolate male (the most frequent song of each of the four days that I recorded the male) were compared with the same characteristics of eight songs that lacked a trill phrase that I recorded from eight individuals at Kalbfleisch (see Table 35). The raw data are presented in Appendices 10 and 11.

Although sample sizes were small, consistently large differences occurred in the length of the longest syllable in a song, in the average number of notes per syllable, and in the rate of delivery of syllables of the song, with the isolate male having longer syllables, fewer notes per syllable, and a slower rate of delivery than wild birds. Less consistent or smaller differences were found between the isolate male and the wild males in the duration of song, the frequency range, maximum and minimum frequency of the song and in the duration of the syllables. The tempo of songs of the isolate tended to be slower than those of the wild males because both the song and its syllables were relatively long. The frequency range of the songs of the isolate was relatively compressed because the maximum frequency of its songs tended to be lower than in wild birds.

DISCUSSION

The results of this experiment indicate that auditory feedback from other singing conspecific males is necessary for normal development of song to occur in the Rufous-sided Towhee. Although certain characteristics of song of the isolate male were similar to songs of free-living males that lacked a trill phrase, other characteristics of song, such as the longer length of the longest syllable of the song, the reduced number of notes per syllable, and the slower rate of delivery of song, seemed to distinguish song of the isolate male from song of wild birds. These differences, coupled with the harsh sound of the isolate song, and the variability of successive songs, easily distinguished songs of the isolate male from songs of wild birds. Thus, while the songs of the isolate towhee exhibited some aspects of normal song they lacked the precision and complexity of song of wild birds. And, the repertoire of the isolate male differed from that of all free-living males that I recorded on Long Island in that it had no song variants with a trill phrase.

These data are consistent with findings from the development of song of other species of finches (see Table 2 of Kroodsma, 1977), where the song of individually isolated males differed from the song of wild birds in that their syllables had relatively few notes, were relatively long and were sung at a relatively slow rate and their songs had a relatively narrow frequency range. Similarly both individually isolated Song Sparrows and towhees produced song that was relatively long, that had a narrow frequency range, that had a low maximum frequency, that sang at a slow rate and that had longer syllables or notes compared to song of wild birds (see Table 1 of Kroodsma, 1977). However, songs of the isolate male towhee had fewer phrases and a lower minimum frequency than songs of the wild males in contrast to Song Sparrows where songs of isolates had more phrases per song and a higher minimum frequency than songs of wild males. Larger sample sizes with acoustically isolated towhees under a variety of experimental conditions will be required to determine if the similarities and differences in isolate and wild song of each species represent real differences in song development between these species.

TABLE 30. NUMBER OF SONGS OF EACH SYLLABLE SEQUENCE BY DATE.

	Number of songs			
	1975		1976	
Syllable sequence	13 April (n=21)	1 June (n=56)	10 May (n=17)	25 May (n=17)
1	6	5		
1,1	1			
1,1,2	1			
1,1,2,3		1		
1,1,4	2		1	
1,1,7,4			1	
1,2	1			
1,2,3	7	2		
1,3		21		
1,3,3		2		
1,4	2	6		
1,4,1,1,2		1		
1,4,1,1,2,3		1		
1,4,1,1,3,2		1		
1,4,1,1,4,1,2,3		1		
1,4,1,2		1		
1,4,1,2,3		1		
1,4,2		1		
1,4,2,3		1		
1,4,3		2		
1,4,4,5		1		
1,4,6,1,2,3		2		
1,6,1,1,2,3		1		
2,3	1			
4			1	
4,1,1,2		2		
4,1,2,3			2	
4,1,4,2,3			1	
4,2			1	
4,2,3			6	
4,4,2,3			1	
6,1				1
6,1,1,2		1		
6,1,1,2,3		1		
6,1,1,4,1,1,2		1		
6,8				2
6,8,3				14
7,4			1	
7,4,4,1,2			1	

TABLE 31. OCCURRENCE OF SYLLABLES AT THE BEGINNING OR ENDING OF SONG.

Syllable	Number of times Begin	 End	Binomial probability
1	22	2	.0054
2	1	11	.0054
3	0	18	.0000
4	6	4	.2344
5	0	1	.5000
6	6	0	.0156
7	2	0	.2500
8	0	1	.5000

TABLE 32. THE NUMBER OF TIMES THAT A SYLLABLE FOLLOWS ANOTHER SYLLABLE FOR ALL POSSIBLE PAIRS OF SYLLABLES IN 37 SONG VARIANTS (see text for calculation of expected values).

		1		2		3		4		5		6		7		8		Row Total	
		O*	E*	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E
1		15	15.89	17	7.11	3	5.68	16	8.21	0	0.29	1	2.29	1	0.86	0	0.57	53	40.9
2		0	7.11	0	3.18	14	2.54	0	3.67	0	0.13	0	1.02	0	0.38	0	0.26	14	18.3
3		0	5.68	1	2.54	1	2.03	0	2.93	0	0.10	0	0.82	0	0.31	0	0.20	2	14.6
4		12	8.21	6	3.67	1	2.93	3	4.24	1	0.15	1	1.18	0	0.44	0	0.30	24	21.1
5		0	0.29	0	0.13	0	0.10	0	0.15	0	0.01	0	0.04	0	0.02	0	0.01	0	0.7
6		6	2.29	0	1.02	0	0.82	0	1.18	0	0.04	0	0.33	0	0.12	2	0.08	8	5.9
7		0	0.86	0	0.38	0	0.31	3	0.44	0	0.02	0	0.12	0	0.05	0	0.03	3	2.2
8		0	0.57	0	0.26	1	0.20	0	0.30	0	0.01	0	0.08	0	0.03	0	0.02	1	1.5
Column Total	O	33		24		20		22		1		2		1		2		105	
	E	40.9		18.3		14.6		21.1		0.7		5.9		2.2		1.5			105.2

* O = observed; E = Expected

TABLE 33. PROPORTION OF THE TOTAL NUMBER OF SYLLABLES IN 37 SONG VARIANTS IN EACH OF THE EIGHT TYPES OF SYLLABLES.

Type of syllable	N	Frequency
1	56	0.389
2	25	0.174
3	20	0.139
4	29	0.201
5	1	0.007
6	8	0.056
7	3	0.021
8	2	0.014
Total	144	1.001

TABLE 34. OBSERVED AND EXPECTED FREQUENCIES OF TRIPLETS OF SYLLABLES OF THE ISOLATE MALE.

Triplets	Observed	Expected
1,1,2	9	3.12
1,1,3	1	0.55
1,1,4	3	2.93
1,1,7	1	0.18
1,2,3	9	2.54
1,3,2	1	0.97
1,3,3	1	0.97
1,4,1	8	5.18
1,4,2	3	2.59
1,4,3	1	0.43
1,4,4	1	1.30
1,4,6	1	0.43
1,6,1	1	0.49
1,7,4	1	0.44
4,1,1	6	2.19
4,1,2	5	2.49
4,1,4	1	2.35
4,2,3	4	2.54
4,4,1	1	0.97
4,4,2	1	0.97
4,4,5	1	0.08
4,6,1	1	0.49
6,1,1	4	1.10
6,1,2	1	1.25
6,8,3	1	0.08
7,4,4	1	0.24
Total	68	36.87

TABLE 35. COMPARISON OF CHARACTERISTICS OF SONG OF ONE ISOLATE MALE AND SONGS RECORDED FROM KALBFLEISCH THAT CONSISTED OF ONE NOTE-COMPLEX PHRASE.

	Individual isolate	Wild Kalbfleisch males
Duration of song (secs)	1.28 ± 0.649 (4)[a]	0.74 ± 0.133 (8)
Freq. range of song (kHz)	3.3 ± 1.17 (4)	3.5 ± 1.08 (8)
Max. freq. of song (kHz)	5.5 ± 0.95 (4)	6.0 ± 0.90 (8)
Min. freq. of song (kHz)	2.2 ± 0.38 (4)	2.4 ± 0.36 (8)
Longest syllable in song (secs)	0.58 ± 0.316 (4)	0.20 ± 0.063 (8)
Duration of syllables (secs)	0.32 ± 0.205 (6)	0.15 ± 0.083 (13)
No. notes/syllable	1.3 ± 0.33 (6)	4.4 ± 4.69 (14)
Rate of delivery of syllables (syllables/sec)	2.52 ± 1.031 (4)	3.91 ± 0.641 (8)

[a] Mean ± standard deviation (N)

FIG. 16. Tracings of eight syllables recorded from the isolate male in 1975 and 1976.

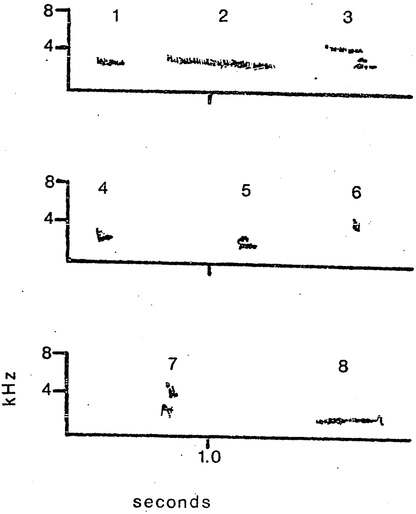
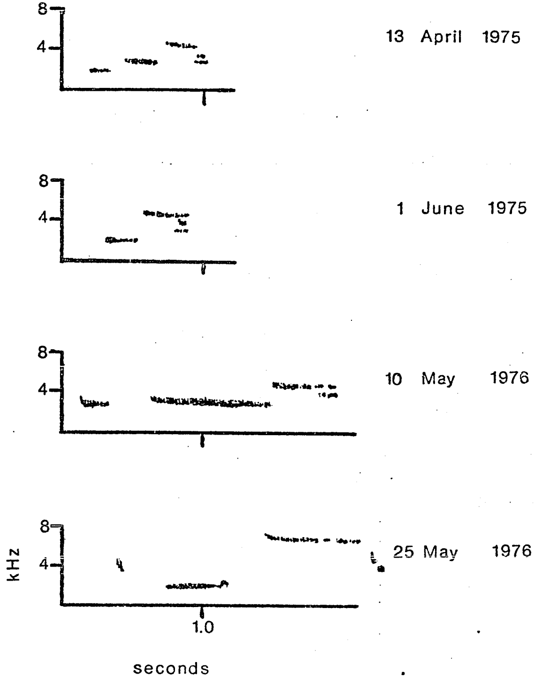

8
4
1
2
3
8
4
4
5
6
8
4
kHz
7
8
1.0
seconds

FIG. 17 . Tracings of sonograms of the modal song of the isolate male recorded on four dates in 1975 and 1976.


8
4
13 April 1975
8
4
1 June 1975
8
4
10 May 1976
8
4
kHz
25 May 1976
1.0
seconds

APPENDIX 1. BIRDS TAPE RECORDED AT KALBFLEISCH, WITH BANDING DATA WHERE KNOWN, GIVING YEAR(S) OF OCCURENCE AND YEAR(S) WHEN TAPE RECORDED.

Individual	Band no.	(color combination)[1]	Date of banding	Status at time[2] of banding	Year(s) at Kalbfleisch	Year(s) recorded
K1	71-185311	(XR-YY)	30 June 1968	AHY-M	1968-1972	1969-1972
K2	71-185547	(BX-BY)	20 Aug. 1968	AHY-M	1968-1972	1969-1972
K3	68-103526	(XR-GG)	16 July 1965	AHY-M	1965-1972	1969-1972
K4	?	(XB-B)	?	?	1969, 1970	1969, 1970
K5	73-147433	(WX-YG)	3 July 1969	AHY-M	1969	1969
K6	?	(-X)	?	?	1969	1969
K7	unbanded		-	-	1969, 1970	1969, 1970
K11	?	(X-)	?	?	1969	1969
K12	?	(X-)	?	?	1969	1969
K13	unbanded		-	-	1969	1969
K14	unbanded		-	-	1970	1970
K16	unbanded		-	-	1970	1970
K17	73-147348	(Y-BX)	10 May 1969	AHY-M	1969-1971	1970, 1971

APPENDIX 1. (continued).

Individual	Band no. (color combination)[1]	Date of banding	Status at time[2] of banding	Year(s) at Kalbfleisch	Year(s) recorded
K18	? (-X)	?	?	1970, 1971	1970, 1971
K19	74-145390 (RR-WX)	27 May 1970	AHY-M	1970, 1971	1970, 1971
K22	73-147576 (XG-YB)	12 Aug. 1969	AHY-M	1969-1973	1970-1973
K23	73-147506 (GG-XR)	1 Aug. 1969	HY-M	1969-1976	1970-1975
K24	unbanded	-	-	1971	1971
K25	? (X-GW)	?	?	1971	1971
K26	75-174206 (GX-WB)	5 July 1972	AHY-M	1972	1972
K27	75-174187 (YX-RR)	17 May 1972	AHY-M	1972	1972
K28	unbanded	-	-	1972	1972
K29	unbanded	-	-	1972	1972
K30	75-174138 (GY-XR)	17 Aug. 1971	HY-M	1971-1973	1972, 1973
K31	75-174334 (XY-YY)	5 July 1974	AHY-M	1972-1977	1972-1975
K32	75-174337 (BY-XR)	6 July 1974	AHY-M	1972-1977	1972-1975

APPENDIX 1. (continued).

Individual	Band no. (color combination)[1]	Date of banding	Status at time[2] of banding	Year(s) at Kalbfleisch	Year(s) recorded
K33	unbanded	-	-	1973	1973
K34	75-174302 (XB-RW)	28 May 1973	AHY-M	1973	1973
K35	unbanded	-	-	1973	1973
K36	unbanded	-	-	1973	1973
K37	unbanded	-		1973, 1974	1973, 1974
K38	75-174336 (XG-RW)	6 July 1974	AHY-M	1974-1976	1974, 1975
K39	75-174308 (GW-XR)	14 June 1973	AHY-M	1973-1975	1974, 1975
K40	75-174339 (BX-BW)	10 July 1974	AHY-M	1974, 1975	1974, 1975
K41	unbanded	-	-	1974	1974
K42	unbanded	-	-	1974, 1975	1974, 1975
K44	unbanded	-	-	1975	1975
K45	75-174351 (XB-BY)	27 June 1975	AHY-M	1975	1975
K46	unbanded	-	-	1975	1975

APPENDIX 1. (continued).

[1] X = U.S. Fish and Wildlife aluminum band; B = blue; G = green; R = red; Y = yellow; W = white.

[2] AHY = after hatching year; HY = hatching year; M = male.

APPENDIX 2. THE NUMBER OF DIFFERENT SONG-TYPES AND SYLLABLES, AND THE SONG-TYPES (INCLUDING THE TAPE FROM WHICH THE "TYPE" SONOGRAM WAS MADE) THAT WERE TAPE RECORDED FROM INDIVIDUALS FROM KALBFLEISCH.

Individual	Number of song-types	Number of syllables	Song-type[1]	Tape no., side, (digital count), collection
K1	4	8	H-2	002B (820), Ewert
			H-13	002B (572), Ewert
			Z-1	002B (346), Ewert
			V,D-56	002A (880), Ewert
K2	5	11	C-40	141A (094), Lanyon
			D-1	140A (388), Lanyon
			F,C-13	140A (444), Lanyon
			S,F-49	140A (363), Lanyon
			V,D-52	140A (520), Lanyon
K3	3	8	H-3	002A (703), Ewert
			V,D-9	002A (477), Ewert
			AAA,V-25-15	002A (567), Ewert
K4	2	5	H-51	140A (284), Lanyon
			V,D-39	140A (304), Lanyon
K5	5	10	H, A,A	140A (098), Lanyon
			H,Y-9	140A (080), Lanyon
			V,D-13	140A (068), Lanyon
			Z,Y-9	140A (151), Lanyon
			Z,FF-59	140A (161), Lanyon
K6	2	5	S,H-59	141A (114), Lanyon
			V,D-58	141A (141), Lanyon

APPENDIX 2. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
K7	2	6	S,E-40	140A (627), Lanyon
			V,D-51	141A (038), Lanyon
K11	1	4	S,Z,D-52	140A (338), Lanyon
K12	1	4	Z,V,D-17	140B (470), Lanyon
K13	2	4	Z-8	140B (439), Lanyon
			Y,Y-25	140B (432), Lanyon
K14	2	5	I,AA-25	148B (192), Lanyon
			I,AA-32-51	148B (195), Lanyon
K16	6	12	Z-2	148A (358), Lanyon
			H,D-1	148A (320), Lanyon
			S,H-51	148A (276), Lanyon
			S,FF-59	148A (246), Lanyon
			V,D-1	148A (314), Lanyon
			V,AA-9	148A (282), Lanyon
K17	2	6	V,D-51	148A (196), Lanyon
			PP,H-8	148A (507), Lanyon
K18	4	11	VV,WW	164B (036), Lanyon
			RR,D-1	148A (239), Lanyon
			Z,V,D-17	164B (048), Lanyon
			SS,TT,D-56	164B (081), Lanyon

APPENDIX 2. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
K19	4	13	C,Z-13	165A (716), Lanyon
			V,D-39	165A (799), Lanyon
			XX,FF-9	149A (039), Lanyon
			U,Z,YY-39	165A (694), Lanyon
K22	4	10	WW-44	010A (130), Ewert
			V,D-15	010B (010), Ewert
			Z,D-9	010A (670), Ewert
			Z,H-23	010A (645), Ewert
K23	2	7	S,H,CCC	018A (096), Ewert
			I,V,D-51	018A (255), Ewert
K24	3	10	V,D-33	164A (683), Lanyon
			DDD,EE,EEE-36	164B (561), Lanyon
			FFF,II,D-28	164A (657), Lanyon
K25	2	6	E-25	165B (301), Lanyon
			Z,V,D-53	165B (316), Lanyon
K26	4	8	S,H-51	005B (166), Ewert
			V,D-40	005B (137), Ewert
			V,D-51	005B (120), Ewert
			GGG,H-39	009A (124), Ewert

APPENDIX 2. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
K27	3	5	H-1	003B (109), Ewert
			H-13	003B (162), Ewert
			V,D-13	003B (236), Ewert
K28	4	10	H-39	004B (796), Ewert
			Z-1	004B (798), Ewert
			V,D-52	004B (726), Ewert
			H,H-51-26	004B (890), Ewert
K29	4	11	C,FF,UU	001B (235), Ewert
			C,FF-25	001B (206), Ewert
			H,D-25	002B (301), Ewert
			Z,V,D-39	004A (062), Ewert
K30	2	5	HHH,HHH,III	010A (327), Ewert
			V,D-51	011A (316), Ewert
K31	5	10	S,Z	018A (131), Ewert
			D-17	018A (127), Ewert
			S,D-39	016A (310), Ewert
			V,D-1	016A (226), Ewert
			V,D-51	017B (174), Ewert
K32	3	8	F-49	017A (326), Ewert
			V,D-51	016B (384), Ewert
			Z,D-29	018A (081), Ewert
K33	2	5	V,D-51	012A (236), Ewert
			Z,V,D-53	011A (044), Ewert

APPENDIX 2. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
K34	2	6	H,C-39	011A (185), Ewert
			L,E-25	010B (411), Ewert
K35	3	6	V,D-1	011A (146), Ewert
			V,D-32	011A (165), Ewert
			H,V,D-22	011A (162), Ewert
K36	3	6	V,D-39	011B (197), Ewert
			V,D,JJJ-5	011B (189), Ewert
			V,D,JJJ-52	011B (230), Ewert
K37	2	4	V,D-40	010B (474), Ewert
			V,D-51	016A (008), Ewert
K38	4	9	E-1	017B (459), Ewert
			Z-39	018A (143), Ewert
			V,D-52	018A (144), Ewert
			Z,H-13	018B (278), Ewert
K39	3	10	Z,HHH,WW-14	017B (372), Ewert
			S,Z,V,D-39	017A (235), Ewert
			S,Z,Y,Y-47	017A (386), Ewert
K40	4	12	S,S,H,CCC	016A (117), Ewert
			Z,D-39	016A (163), Ewert
			I,V,D-51	016A (130), Ewert
			Z,Y,Y-55	016A (156), Ewert
K41	1	4	Z,V,D-1	016A (185), Ewert

APPENDIX 2. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
K42	6	11	V,D-1	018B (236), Ewert
			V,D-50	018B (225), Ewert
			PP,D-39	018A (059), Ewert
			PP,JJ,AAA-41	019B (079), Ewert
			PP,JJ,AAA,V,D-41	016A (626), Ewert
			PP,AAA-41-39	018A (045), Ewert
K44	4	11	V,D-1	017B (295), Ewert
			V,D-34	017B (044), Ewert
			Z,D-29	017B (240), Ewert
			FF,H-29	017B (055), Ewert
K45	5	11	S,WW,CCC	019B (225), Ewert
			I,D-1	019B (239), Ewert
			V,D-1	018A (264), Ewert
			PP,D-11	019B (102), Ewert
			13-D-1	019B (231), Ewert
K46	5	13	S-39	020A (293), Ewert
			Z-39	020B (021), Ewert
			S,E-40	020A (347), Ewert
			V,D-51	017B (208), Ewert
			Z,WW-1	017B (129), Ewert

APPENDIX 2. (continued).

[1] Each letter designates a different syllable of the note-complex phrase; each number designates a different syllable of the trill phrase.

APPENDIX · 3. THE NUMBER OF DIFFERENT SONG-TYPES AND SYLLABLES, AND THE SONG-TYPES (INCLUDING THE TAPE FROM WHICH THE "TYPE" SONOGRAM WAS MADE) THAT WERE TAPE RECORDED FROM INDIVIDUALS FROM TOBAY BEACH.

Individual	Number of song types	Number of syllables	Song-type[1]	Tape no., side, (digital count), collection
T1	2	4	V,FF-50	005A (022), Ewert
			1-FF-50	005A (021), Ewert
T2	2	4	AA-51	005A (087), Ewert
			AA,D-13	005A (104), Ewert
T3	6	11	C,C-45	005A (184), Ewert
			V,FF-6	005A (296), Ewert
			Z,KKK,D-9	005A (271), Ewert
			KKK,D,C-45	005A (188), Ewert
			C,KKK,D,C-45	005A (189), Ewert
			1-FF-50	005A (212), Ewert
T4	1	2	S,S-25	005A (324), Ewert
T5	3	7	LLL-8	005A (402), Ewert
			Z,L-45	005A (427), Ewert
			?,MMM-40	005A (404), Ewert
T6	1	2	Z-28	004A (695), Ewert
T7	3	8	C-39	004A (833), Ewert
			GG,D-51	004A (777), Ewert
			GG-50-I-40	004A (725), Ewert

APPENDIX 3. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
T8	5	10	JJJ-51	004B (102), Ewert
			V,D-25	004B (889), Ewert
			V,D-52	004A (034), Ewert
			PPP,C-45	004A (006), Ewert
			1-51	004A (884), Ewert
T9	3	10	TT,AA-50	004B (092), Ewert
			QQQ,LL-19	004A (982), Ewert
			KK,YY,FF-39	004B (054), Ewert
T10	2	6	RRR,RRR-25	004B (079), Ewert
			PP,UU,G-42	004A (021), Ewert
T11	5	14	H-57	004B (164), Ewert
			V,D-39	004B (145), Ewert
			PPP,C-39	004B (266), Ewert
			9-FF-6	004B (172), Ewert
			25-YY-50	004B (333), Ewert
T12	4	12	S,T-40	004B (220), Ewert
			V,D-32	004B (288), Ewert
			V,Z-52	004B (300), Ewert
			VV,TT,YY-28	005A (444), Ewert
T13	3	9	S,C-39	004B (367), Ewert
			V,D-6	004B (252), Ewert
			MMM,BB-13	004B (374), Ewert

APPENDIX 3. (continued).

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[1] Each letter designates a different syllable of the note-complex phrase; each number designates a different syllable of the trill phrase.

APPENDIX 4. THE NUMBER OF DIFFERENT SONG-TYPES AND SYLLABLES, AND THE SONG-TYPES (INCLUDING THE TAPE FROM WHICH THE "TYPE" SONOGRAM WAS MADE) THAT WERE TAPE RECORDED FROM INDIVIDUALS FROM CONNETQUOT.

Individual	Number of song-types	Number of syllables	Song-type[1]	Tape no., side, (digital count), collection
C1	3	9	P,HH-40	011B (094), Ewert
			V,D-1	011B (022), Ewert
			SSS,Z-51	011B (066), Ewert
C2	4	11	V,D-38	011B (035), Ewert
			SSS,Z-59	011B (111), Ewert
			TTT,D-1	011B (073), Ewert
			MM,S,D-40	011B (120), Ewert
C3	1	3	J,GG-40	011B (051), Ewert
C4	4	11	V,D-51	011B (260), Ewert
			MM,S,D-40	011B (125), Ewert
			WW,S,SSS-47	011B (131), Ewert
			WW,AAA,UU-47	011B (132), Ewert
C6	6	15	Z,UUU	012A (044), Ewert
			E-25	011B (296), Ewert
			H-19	012A (005), Ewert
			V,D-39	012A (023), Ewert
			TTT,VVV-48	012A (033), Ewert
			TTT,S,FF-40	012A (035), Ewert
C7	1	3	H,EE-40	012A (012), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
C8	3	8	Z,UUU,TT,BB	012A (294), Ewert
			V,D-10	012A (311), Ewert
			V,D-49	012A (281), Ewert
C9	1	4	S,GG,D-25	012A (102), Ewert
C11	1	3	V,D-39	012A (118), Ewert
C12	4	10	V,D-13	012A (334), Ewert
			V,H-40	012A (670), Ewert
			C,SS,JJJ-60	012A (690), Ewert
			V,D-1-39	012A (641), Ewert
C13	2	7	C,EE-25	012A (377), Ewert
			G,V,D-13	012A (369), Ewert
C14	2	6	C,EE-25	012A (358), Ewert
			S,E-44	012A (710), Ewert
C15	4	13	Z,S,C,C,UU	012A (807), Ewert
			JJJ,Z-25	012A (781), Ewert
			Z,S,H-25	012A (820), Ewert
			Z,H-51-PP,YY,EE	012A (863), Ewert
C17	3	7	H,Z-62	012B (020), Ewert
			Z,H-51	012B (037), Ewert
			Z,S,FF-1	012A (927), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
C18	1	3	V,D-25	012A (418), Ewert
C19	3	8	V,D-1	012B (192), Ewert
			Z,S,D-40	012A (389), Ewert
			9-1	012A (391), Ewert
C20	1	2	Z-2	012A (433), Ewert
C21	1	3	?,JJJ,Y-3	012A (448), Ewert
C22	3	9	V,D-13	012A (745), Ewert
			V,D-27	012B (334), Ewert
			Z,S,WWW,XXX-48	012A (456), Ewert
C25	2	5	S,H-24	012A (912), Ewert
			U,WW-24	012A (890), Ewert
C26	4	11	H-50	013A (059), Ewert
			U,FF-25	013A (058), Ewert
			V,D-3	012B (354), Ewert
			YYY,EE-53	013A (202), Ewert
C28	6	13	III-39	012B (134), Ewert
			S,H-25	012B (639), Ewert
			V,D-1	012B (100), Ewert
			V,D-51	012B (651), Ewert
			TT,E-1	012B (090), Ewert
			31-22	012B (276), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no, side, (digital count), collection
C29	4	10	V,D-39	012B (662), Ewert
			V,D-49	012B (691), Ewert
			TTT,AA-1	012B (152), Ewert
			ZZZ,FF-40	012B (707), Ewert
C30	1	2	TTT-1	012B (164), Ewert
C31	1	3	V,D-51	012B (202), Ewert
C32	1	3	T,EE-40	012B (219), Ewert
C33	1	2	H-3	012B (230), Ewert
C34	1	2	H-13	012B (250), Ewert
C36	1	3	V,D-51	012B (313), Ewert
C38	2	4	AAAA,H-1	012B (370), Ewert
			AAAA,H-44	012B (368), Ewert
C39	2	6	S,Z-9	012B (384), Ewert
			S,E,EE-40	012B (893), Ewert
C40	4	9	EE-44	012B (430), Ewert
			S,H-24	012B (400), Ewert
			Z,F-3	012B (428), Ewert
			Z,H-50	012B (414), Ewert
C43	2	5	G,Z-25	012B (728), Ewert
			G,WW-50	012B (744), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
C44	1	3	V,D-25	012B (750), Ewert
C46	1	3	V,D-39	013A (513), Ewert
C47	1	3	Z,E-46	012B (801), Ewert
C48	4	9	Z-40	012B (824), Ewert
			V,D-1	012B (851), Ewert
			V,D-38	012B (840), Ewert
			H-18-9	012B (867), Ewert
C49	2	6	G,H-25	013A (537), Ewert
			V,D-51	013A (556), Ewert
C50	4	11	H-25	013A (017), Ewert
			H,H-51	013A (019), Ewert
			DDDD,FF-39	013A (002), Ewert
			S,CCCC,F-6	013A (008), Ewert
C52	1	3	C,WW-28	013A (034), Ewert
C53	4	13	H,P,TT,SS	013A (250), Ewert
			S,S,G-25	013A (248), Ewert
			Z,Q, BBB-39	013A (187), Ewert
			Z-31-51	013A (091), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
C54	5	11	I,Z-1	013A (195), Ewert
			J,E-62	013A (293), Ewert
			R,E-62	013A (116), Ewert
			Z,D-30	013A (304), Ewert
			J-31-50	013A (108), Ewert
C55	2	4	V,D-25	013A (127), Ewert
			V,D-30	013A (162), Ewert
C56	4	9	S,D-39	013A (222), Ewert
			V,D-1	013A (242), Ewert
			V,D-46	013A (223), Ewert
			JJJ,EEE-54	013A (208), Ewert
C57	3	9	S,D-39	013A (781), Ewert
			V,Z-50	013A (287), Ewert
			NN ,FF-40	013A (771), Ewert
C58	3	9	Y-50	013A (879), Ewert
			V,D-51	013A (343), Ewert
			S,FF,G-1	013A (327), Ewert
C59	1	3	V,D-51	013A (350), Ewert
C60	1	3	V,D-46	013A (362), Ewert
C61	4	9	J,V-51	013A (392), Ewert
			S,F-50	013A (414), Ewert
			V,YY-38	013A (412), Ewert
			S-40-51	013A (401), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
C62	4	9	C-25	013A (444), Ewert
			Z-25	013A (563), Ewert
			V,D-50	013A (796), Ewert
			Z-31-NN	013A (456), Ewert
C64	3	7	V,D-1	013A (836), Ewert
			V,D-49	013A (637), Ewert
			C-31-21	013A (812), Ewert
C65	1	4	PP,D,I-37	013A (593), Ewert
C66	4	13	W,D-39	013A (855), Ewert
			Z,H-51	013A (873), Ewert
			TTT,FF-62	013A (612), Ewert
			C,C,DD -25	013A (847), Ewert
C68	3	8	F-39	013A (688), Ewert
			P,Z-45	013A (691), Ewert
			Z,H-3	013A (676), Ewert
C69	1	3	V,D-23	013A (703), Ewert
C70	3	8	S,UU-39	013B (014), Ewert
			R-40-1	013B (062), Ewert
			31-43	013B (532), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
C71	4	10	G-13	013B (019), Ewert
			Z-9	013B (573), Ewert
			V,D-12	013B (072), Ewert
			CCCC,EE-25	013B (579), Ewert
C73	4	10	I,H-38	013B (436), Ewert
			V,D-25	013B (457), Ewert
			V,D-28	013B (458), Ewert
			TT,WW-22	013B (415), Ewert
C74	2	6	H,J-39	013B (092), Ewert
			R,G-61	013B (093), Ewert
C75	5	11	EE-39	013B (116), Ewert
			C, CC -25	013B (587), Ewert
			J,H-7	013B (620), Ewert
			S,F-28	013B (168), Ewert
			S,EE-39	013B (180), Ewert
C76	3	9	S,WW-1	013B (502), Ewert
			V,D-25	013B (134), Ewert
			PP,BBB-22	013B (150), Ewert
C77	5	10	UU,Z	013B (188), Ewert
			G-61	013B (212), Ewert
			J,H-23	013B (667), Ewert
			J,Z-23	013B (680), Ewert
			R,H-24	013B (693), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
C78	4	9	U,H-24	013B (232), Ewert
			U,H-30	013B (356), Ewert
			Z,H-24	013B (357), Ewert
			H,S,SSS-38	013B (334), Ewert
C79	4	12	I,H-23	013B (375), Ewert
			V,D-40	013B (723), Ewert
			Z-9-51	013B (394), Ewert
			V,D-43-25	013B (716), Ewert
C80	3	9	V,D-39	013B (403), Ewert
			Z,C,BBBB-40	013B (307), Ewert
			Z-31-46	013B (316), Ewert
C81	4	10	H-25	014A (427), Ewert
			V,D-39	014A (391), Ewert
			Z,C-40	014A (418), Ewert
			Z,V-9	014A (408), Ewert
C82	4	11	SSS-1	014A (699), Ewert
			S,H-30	013B (862), Ewert
			V,D-39	014A (690), Ewert
			BBBB,G-39	014A (717), Ewert
C83	2	6	V,D-39	013B (877), Ewert
			J,V,D-28	013B (943), Ewert
C84	1	3	V,D-45	014A (453), Ewert
C85	1	4	Z,V,D-51	013B (934), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
C86	5	11	WW-50	014A (782), Ewert
			V,D-38	014A (790), Ewert
			V,AA-1	014A (792), Ewert
			V,FF-40	014A (320), Ewert
			WW,D-25	014A (780), Ewert
C87	2	6	Z,QQ -6	014A (342), Ewert
			EE,WW-50	014A (219), Ewert
C88	2	6	C,D-51	014A (230), Ewert
			V,D-25	014A (242), Ewert
C89	2	4	H-50	014A (256), Ewert
			H,D-37	014A (254), Ewert
C90	2	7	V,D-25	014A (270), Ewert
			S,DD -31-13	014A (307), Ewert
C91	1	2	BB-3	014A (287), Ewert
C92	3	9	Z,E-13	014A (592), Ewert
			Z,V,D-39	014A (586), Ewert
			UU-31-23	014A (479), Ewert
C93	6	19	G-46	014A (497), Ewert
			C,EE-25	014A (605), Ewert
			V,D-1	014A (608), Ewert
			JJJ,H-3	014A (547), Ewert
			S,U,H,D-51	014A (538), Ewert
			S,ZZ-31-50	014A (676), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
C94	2	6	V,D-38 Z,UUU-1	014A (619), Ewert 014A (640), Ewert
C95	2	6	C,H-1 Z,FF-32	014A (660), Ewert 014A (125), Ewert
C96	1	3	V,D-1	014A (821), Ewert
C97	1	4	UU,V,D-25	014A (848), Ewert
C98	2	4	V,D-39 V,D-50	014A (862), Ewert 014A (860), Ewert
C100	3	8	EE-44 V,D-49 N ,E-20	014B (009), Ewert 014B (136), Ewert 014B (026), Ewert
C101	3	9	S,ZZ,CCCC,M,M H-3 JJJ,Z-51	014B (043), Ewert 014B (089), Ewert 014B (096), Ewert
C102	1	3	KKK,D-51	014A (056), Ewert
C103	1	3	V,D-25	014B (106), Ewert
C104	1	2	JJJ-50	014B (116), Ewert
C105	1	3	K ,D-9	014B (158), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
C106	4	11	WW,V,D-1	014B (169), Ewert
			WW,V,D-9	014B (619), Ewert
			Z-31-50	014B (194), Ewert
			Z,C-40-13	014B (314), Ewert
C107	2	5	V,D-46	014B (606), Ewert
			W,D-3	014B (184), Ewert
C108	1	3	C-31-51	014B (212), Ewert
C109	4	11	I,H-62	014B (231), Ewert
			V,D-4	014B (323), Ewert
			C,H,DD -44	014B (346), Ewert
			31-30	014B (353), Ewert
C110	1	3	V,FF-52	014B (254), Ewert
C111	1	3	C,CCCC-25	014B (265), Ewert
C112	2	6	JJJ,D-51	014B (287), Ewert
			Z-9-50	014B (374), Ewert
C114	1	3	S,FF-50	014B (390), Ewert
C115	5	12	C-31	014B (450), Ewert
			S,FF-4	014B (479), Ewert
			NNN,FF-45	014B (440), Ewert
			C,WW,D-59	014B (357), Ewert
			35	014B (421), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
C116	1	3	V,D-13	014B (468), Ewert
C117	1	2	D-40	014B (485), Ewert
C118	2	4	H-1 H-22	014B (505), Ewert 014B (507), Ewert
C119	1	3	V,D-1	014B (519), Ewert
C120	2	6	C,FF-51 V,D-4	014B (563), Ewert 014B (541), Ewert
C121	3	7	D-19 S-39 JJJ,AA-3	014B (593), Ewert 014B (573), Ewert 014B (578), Ewert
C122	1	4	Z,C-40-13	014B (635), Ewert
C123	1	3	V,D-39	014B (654), Ewert
C124	3	7	H-9 Z,S,S,H-5 H-2-B	014B (784), Ewert 014B (757), Ewert 014B (682), Ewert
C125	1	3	S,X-28	014B (700), Ewert
C126	1	3	V,D-39	014B (793), Ewert

APPENDIX 4. (continued).

Individual	Number of song-types	Number of syllables	Song-type	Tape no., side, (digital count), collection
C127	4	10	CCCC-19	014B (906), Ewert
			V,D-40	014B (854), Ewert
			TTT,TTT-13	014B (815), Ewert
			DD ,FF-40	014B (871), Ewert
C128	1	3	C,G-25	014B (837), Ewert
C129	2	3	H-61	014B (925), Ewert
			16-H-61	014B (936), Ewert
C130	1	3	H,GG-6	016A (008), Ewert
C131	3	10	Z,C,EE-25	016A (037), Ewert
			Z,V,D-13	016A (024), Ewert
			H-31-51	016A (040), Ewert

APPENDIX 4. (continued).

[1] Each letter designates a different syllable of the note-complex phrase; each number designates a different syllable of the trill phrase.

APPENDIX 5. DISTRIBUTION OF SYLLABLES OF THE NOTE-COMPLEX PHRASE BY INDIVIDUAL AND BY POPULATION.

Syllable	Population*			Individuals with syllable
	K	T	C	
A	X			K5.
B			X	C124.
C	X	X	X	K2,19,29,34. T3,7,8,11,13. C12,13,14,15,52, 62,64,66,75,80,81,88,93,95,106,108,109,111, 115,120,122,128,131.
D	X	X	X	K1-7,11,12,16-19,22-33,35-42,44,45,46. T2,3,7,8,11,12,13. C1,2,4,6,8,9,11,12,13,18, 19,22,26,28,29,31,36,44,46,48,49,54-60,62,64, 65,66,69,71,73,76,79-86,88,89,90,92-94,96-98, 100,102,103,105-107,109,112,115-117,119-121, 123,126,127,131.
E	X		X	K7,25,34,38,46. C6,14,28,39,47,54,92,100.
F	X		X	K2,32. C40,50,61,68,75.
G		X	X	T10. C13,43,49,53,58,71,74,77,82,93,128.
H	X	X	X	K1,3,4,5,6,16,17,22,23,26,27,28,29,34,35,38,40, 44. T11. C6,7,12,15,17,25,26,28,33,34,38,40, 48,49,50,53,66,68,73,74,75,77,78,79,81,82,89, 93,95,101,109,118,124,129,130,131.
I	X	X	X	K14,23,40,44. T7. C54,65,73,79,109.
J			X	C3,54,61,74,75,77,83.
K			X	C105.
L	X	X		K34. T5.
M			X	C101.
N			X	C100.
P			X	C1,53,68.
Q			X	C53.
R			X	C54,70,74,77.

APPENDIX 5. (continued).

Syllable	Population			Individuals with syllable
	K	T	C	
S	X	X	X	K2,6,7,11,16,23,26,31,39,40,45,46. T4,12,13. C2,4,6,9,14,15,17,19,22,25,28,39,40,50,53,56,57,58,61,70,75,76,78,82,90,93,101,114,115,121,124,125.
T		X	X	T12. C32.
U	X		X	K19. C25,26,78,93.
V	X	X	X	K1-7,12,16,17,18,19,22-33,35-42,44,45,46. T1,3,8,11,12,13. C1,2,4,6,8,11,12,13,18,19,22,26,28,29,31,36,44,46,48,49,55-62,64,69,71,73,76,79-86,88,90,92,93,94,96,97,98,100,103,106,107,109,110,116,119,120,123,126,127,131.
W			X	C66,107.
X			X	C125.
Y	X		X	K5,13,39,40. C21,58.
Z	X	X	X	K1,5,11,12,13,16,18,19,22,25,28,29,31,32,33,38,39,40,41,44,46. T3,5,6,12. C1,2,6,8,15,17,19,20,22,39,40,43,47,48,53,54,57,62,66,68,71,77,78,79,80,81,85,87,92,94,95,101,106,112,122,124,131.
AA	X	X	X	K14,16. T2,9. C29,86,121.
BB		X	X	T13. C8,91.
CC			X	C75.
DD			X	C66,90,109,127.
EE	X		X	K24. C7,13,14,15,26,32,39,40,71,75,87,93,100,131.
FF	X	X	X	K5,16,19,29,44. T1,3,9,11. C6,17,26,29,50,57,58,66,86,95,110,114,115,120,127.
GG		X	X	T7. C3,9,130.
HH			X	C1.
II	X			K24.

APPENDIX 5. (continued).

	Population			
Syllable	K	T	C	Individuals with syllable
JJ	X			K42.
KK		X		T9.
LL		X		T9.
MM			X	C2,4.
NN			X	C57,62.
PP	X	X	X	K17,42,45. T10. C15,65,76.
QQ			X	C87.
RR	X			K18.
SS	X		X	K18. C12,53.
TT	X	X	X	K18. T9,12. C8,28,53,73.
UU	X	X	X	K29. T10. C4,15,70,77,92,97.
VV	X	X		K18. T12.
WW	X		X	K18,22,39,45,46. C4,25,43,52,73,76,86,87,106,115.
XX	X			K19.
YY	X	X	X	K19. T9,11,12. C15,61.
ZZ			X	C93,101.
AAA	X		X	K3,42. C4.
BBB			X	C53,76.
CCC	X			K23,40,45.
DDD	X			K24.
EEE	X		X	K24. C56.
FFF	X			K24.
GGG	X			K26.
HHH	X			K30,39.

APPENDIX 5. (continued).

	Population			
Syllable	K	T	C	Individuals with syllable
III	X		X	K30. C28.
JJJ	X	X	X	K36. T8. C12,15,21,56,93,101,104,112,121.
KKK		X	X	T3. C102.
LLL		X		T5.
MMM		X		T5,13.
NNN			X	C115.
PPP		X		T8,11.
QQQ		X		T9.
RRR		X		T10.
SSS			X	C1,2,4,78,82.
TTT			X	C2,6,29,30,66,127.
UUU			X	C6,8,94.
VVV			X	C6.
WWW			X	C22.
XXX			X	C22.
YYY			X	C26.
ZZZ			X	C29.
AAAA			X	C38
BBBB			X	C80,82.
CCCC			X	C50,71,101,111,127.
DDDD			X	C50.

* K = Kalbfleisch; T = Tobay Beach; C = Connetquot.

APPENDIX 6. DISTRIBUTION OF SYLLABLES OF THE TRILL PHRASE BY INDIVIDUAL AND BY POPULATION.

Syllable	Population*			Individuals with syllable
	K	T	C	
1	X	X	X	K1,2,16,18,27,28,31,35,38,41,42,44,45,46. T1,3,8. C1,2,12,17,19,28,29,30,38,48,54,56, 58,64,70,76,82,86,93,94,95,96,106,118,119.
2	X		X	K1,16. C20,124.
3	X		X	K3. C21,26,33,40,68,91,101,107,121.
4			X	C109,115,120.
5	X		X	K36. C124.
6		X	X	T3,11,13. C50,87,130.
7			X	C75.
8	X	X		K13,17. T5.
9	X	X	X	K3,5,16,19,22. T3,11. C19,39,48,71,81,105, 106,112,124.
10			X	C8.
11	X			K45.
12			X	C71.
13	X	X	X	K1,2,5,19,27,38,45. T2,13. C12,13,22,34,71,90, 92,106,116,122,127,131.
14	X			K39.
15	X			K3,22.
16			X	C129.
17	X			K12,18,31.
18			X	C48.
19		X	X	T9. C6,121,127.
20			X	C100.
21			X	C64.

APPENDIX 6. (continued).

	Population			
Syllable	K	T	C	Individuals with syllable
22	X		X	K35. C28,73,76,118.
23	X		X	K22. C69,77,79,92.
24			X	C25,40,77,78.
25	X	X	X	K3,13,14,25,29,34. T4,8,10,11. C6,9,13,14, 15,18,26,28,43,44,49,50,53,55,62,66,71,73,75, 76,79,81,86,88,90,93,103,111,128,131.
26	X			K28.
27			X	C22.
28	X	X	X	K24. T6,12. C52,73,75,83,125.
29	X			K32,44.
30			X	C54,55,78,82,109.
31			X	C28,53,54,62,64,70,80,90,92,93,106,108,109,115, 131.
32	X	X	X	K14,35. T12. C95.
33	X			K24.
34	X			K44.
35			X	C115.
36	X			K24.
37			X	C65,89.
38			X	C2,48,61,73,78,86,94.
39	X	X	X	K4,19,26,28,29,31,34,36,38,39,40,42,46. T7,9,11,13. C6,11,12,28,29,46,50,53,56,57, 66,68,70,74,75,80,81,82,83,92,98,121,123,126.
40	X	X	X	K2,7,26,37,46. T5,7,12. C1,2,3,4,6,7,12,19, 29,32,39,48,57,61,70,79,80,81,106,117,122,127,86.
41	X			K42.
42		X		T10.

APPENDIX 6. (continued).

	Population			
Syllable	K	T	C	Individuals with syllable
43			X	C70,79.
44	X		X	K22. C14,38,40,100,109.
45		X	X	T3,5,8. C68,84,115.
46			X	C47,56,60,80,93,107.
47	X		X	K39. C4.
48			X	C6,22.
49	X		X	K2,32. C8,29,64,100.
50	X	X	X	K42. T1,3,7,9,11. C26,40,43,54,57,58,61,62, 86,87,89,93,98,104,106,112,114.
51	X	X	X	K4,7,14,16,17,23,26,28,30,31,32,33,37,40,46. T2,7,8. C1,4,15,17,28,31,36,49,50,53,58,59, 61,66,79,85,88,93,97,101,102,108,112,120,131.
52	X	X	X	K2,11,28,36,38. T8,12. C110.
53	X		X	K25,33. C26.
54			X	C56.
55	X			K40.
56	X			K1,18.
57		X		T11.
58	X			K6.
59	X		X	K5,6,16. C2,115.
60			X	C12.
61			X	C74,77,129.
62			X	C17,54,66,109.

* K = Kalbfleisch; T = Tobay Beach; C = Connetquot.

APPENDIX 7. SOURCE AND DESCRIPTION OF TAPES USED IN PLAYBACK EXPERIMENTS.

Tape #	Catalog #	Side	Digital count	Collection	Description of playback tape
1	148	B	368	Lanyon	"Drink-your-tea" song of K2.
2	148	B	368	Lanyon	Note-complex phrase of song on Tape 1.
3	148	B	368	Lanyon	Trill phrase of song on Tape 1.
4	148	B	110	Lanyon	Song of K23 that lacks a trill phrase.
5	001	B	113	Ewert	Song of Guatemala bird.
26	Song #1, Western Bird Songs (Peterson)				Song of Green-tailed Towhee.
27	Song #6, Western Bird Songs (Peterson)				Song of Rufous-sided Towhee from Calif.
28	148	B	368	Lanyon	Song of Tape 1 altered so trill phrase appears before note-complex phrase.
29	148	B	368	Lanyon	First syllable of note-complex phrase on Tape 2.
30	148	B	368	Lanyon	Second syllable of note-complex phrase on Tape 2.
31	uncatalogued			Ewert	Song of isolate male.
32	013	B	092	Ewert	First syllable of song of C74.
33	001	B	113	Ewert	Trill phrase of song on Tape 5.
34	148	B	368	Lanyon	Like Tape 2 but silent interval between syllables increased by factor of 4.6.

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS.

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD[1]	BREEDING STATUS	DATE (TIME)
TAPE 1	TAPE 2				
3	1	midway	C 16	paired	5 July 1977 (08:10)
3	0	2	C 17	?	5 July 1977 (09:00)
2	0	midway	C 18	?	5 July 1977 (09:55)
1	0	2	C 19	paired	6 July 1977 (08:21)
2	0	2	C20	paired	6 July 1977 (09:15)
2	0	2	C21	?	6 July 1977 (10:08)
1	0	2	C22	?	6 July 1977 (11:15)
TAPE 1	TAPE 3				
3	2	3	K50	?	15 June 1977 (09:38)
4	2	?	K51	?	14 June 1977 (10:24)
3	0	midway	K32	paired	16 June 1977 (10:41)
4	0	3	C5	paired	28 June 1977 (15:50)
2	0	3	C6	?	30 June 1977 (09:20)
2	0	3	C7	paired	30 June 1977 (10:10)
2	1	3	C8	?	30 June 1977 (10:57)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 1	TAPE 4				
3	0	1	C69	fledgling	6 July 1976 (15:15)
3	0	4	C70	?	7 July 1976 (10:56)
3	0	4	C71	?	7 July 1976 (14:30)
5	0	4	C72	paired	7 July 1976 (16:03)
5	0	4	C73	?	7 July 1976 (16:55)
3	0	midway	C9	paired	30 June 1977 (15:30)
1	0	1	C10	?	30 June 1977 (16:20)
TAPE 1	TAPE 5				
7	0	?	C5*	nestlings	20 June 1972 (14:40)
4	1	?	C14*	paired	24 June 1972 (10:50)
3	0	?	K20*	eggs	24 June 1972 (08:00)
1	0	5	C131	?	30 July 1973 (09:30)
4	0	midway	C13	paired	2 July 1977 (11:35)
4	0	midway	C14	?	2 July 1977 (15:15)
5	0	midway	C15	paired	2 July 1977 (16:25)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS TAPE 1	 TAPE 26	TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
4	0	?	C20*	paired	25 June 1972 (13:10)
4	1	26	C23	?	10 July 1977 (10:37)
4	0	26	C24	?	10 July 1977 (11:38)
3	0	1	C25	?	10 July 1977 (12:17)
2	0	midway	C26	?	10 July 1977 (15:02)
2	0	1	C27	paired	10 July 1977 (15:48)
2	0	26	C28	?	11 July 1977 (09:50)
TAPE 1	TAPE 28				
3	0	?	C23*	young	27 June 1972 (08:28)
1	1	28	C95	paired	19 July 1973 (10:25)
4	0	1	C113	?	26 July 1976 (09:19)
1	0	28	C114	paired	26 July 1976 (10:10)
2	0	28	C115	?	26 July 1976 (11:03)
1	0	28	C11	?	2 July 1977 (09:49)
2	1	28	C12	paired	2 July 1977 (10:42)
TAPE 1	TAPE 29				
5	0	29	C51*	paired	4 July 1972 (16:00)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 1	TAPE 31				
4	0	31	C37	paired	22 July 1977 (08:57)
3	0	31	C38	?	22 July 1977 (10:37)
1	0	31	C39	paired	22 July 1977 (12:18)
3	0	midway	C40	?	26 July 1977 (10:50)
5	1	midway	C41	paired	26 July 1977 (11:52)
TAPE 2	TAPE 3				
0	1	?	C31*	eggs	29 June 1972 (07:25)
1	4	2	C34*	?	29 June 1972 (12:20)
1	0	?	C37*	paired	1 July 1972 (09:25)
4	0	?	C38*	fledgling	1 July 1972 (12:10)
0	1	3	C39*	paired	2 July 1972 (07:45)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT			
TAPE 2	TAPE 3	BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
0	1	?	C41*	fledgling	2 July 1972 (10:05)
2	0	midway	C42*	?	3 July 1972 (08:20)
0	2	3	C43*	paired	3 July 1972 (09:55)
1	1	?	C44*	paired	3 July 1972 (11:50)
0	3	?	C48*	?	4 July 1972 (10:25)
1	3	3	C49*	paired	4 July 1972 (12:15)
0	1	?	K26*	paired	1 July 1972 (18:45)
2	0	midway	K26*	paired	5 July 1972 (06:50)
1	3	3	C 12	?	20 July 1974 (13:25)
1	0	midway	C 19	?	21 July 1974 (14:20)
2	0	2	C 14	fledgling	16 June 1976 (08:17)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 2	TAPE 4				
1	4	4	H3	paired	7 July 1972 (19:15)
0	3	2	C53	nestlings	21 June 1973 (14:05)
3	6	2	C76	paired	4 July 1973 (10:25)
1	3	2	C79	?	2 July 1973 (09:37)
1	3	2	C81	?	8 July 1973 (11:50)
1	3	2	C82	?	13 July 1973 (11:20)
1	0	2	C85	paired	8 July 1973 (10:25)
1	1	2	C90	?	14 July 1973 (08:35)
0	1	midway	C14	?	20 July 1974 (15:20)
1	0	4	C15	fledglings	16 June 1976 (08:56)
TAPE 2	TAPE 5				
2	1	5	C22	?	18 June 1976 (08:25)
1	2	midway	C23	paired	18 June 1976 (09:10)
0	1	5	C25	?	18 June 1976 (10:40)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 2	TAPE 5				
1	0	midway	C28	nest (4 eggs)	18 June 1976 (15:29)
1	1	5	C45	paired	27 June 1976 (08:57)
4	0	5	C47	paired	27 June 1976 (13:23)
1	1	?	C69	fledgling	6 July 1976 (15:00)
2	0	5	C70	?	7 July 1976 (10:41)
0	2	midway	C71	?	7 July 1976 (14:15)
3	0	5	C72	paired	7 July 1976 (15:48)
2	0	5	C73	?	7 July 1976 (16:40)
TAPE 2	TAPE 28				
2	0	?	C25*	?	27 June 1972 (09:54)
1	0	?	C25a*	paired	27 June 1972 (11:41)
0	2	2	C59	fledgling	12 July 1972 (09:40)
1	1	28	C2	?	11 June 1973 (11:55)
1	2	2	C17	nestlings	14 June 1973 (09:35)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 2	TAPE 28				
0	2	2	C22	?	16 June 1973 (10:10)
2	1	2	C24	paired	18 June 1973 (07:25)
2	4	2	C70	paired	4 July 1973 (12:00)
0	4	midway	C71	paired	4 July 1973 (13:30)
0	3	28	C73	paired	4 July 1973 (08:45)
1	2	2	C75	?	4 July 1973 (15:00)
TAPE 2	TAPE 29				
1	0	2	C45*	paired	4 July 1972 (07:25)
5	0	2	C57	?	14 July 1972 (09:05)
3	1	?	C57	?	14 July 1972 (09:45)
1	1	29	C65	fledglings	15 July 1972 (08:25)
2	0	2	C66	?	25 July 1972 (13:30)
1	0	29	K30*	?	6 July 1972 (13:40)
0	2	29	K31	paired	21 July 1972 (19:05)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 2	TAPE 29				
1	0	2	H1	?	6 July 1972 (10:35)
3	0	2	C4	?	18 July 1974 (13:12)
2	1	midway	C8	?	18 July 1974 (10:20)
1	0	2	C9	?	18 July 1974 (11:15)
2	0	29	C10	?	18 July 1974 (11:55)
TAPE 2	TAPE 30				
3	0	?	C52	paired	7 July 1972 (11:35)
1	0	midway	C54	?	10 July 1972 (09:15)
1	0	midway	C66	?	25 July 1972 (13:45)
2	0	midway	C68	?	25 July 1972 (14:55)
4	0	midway	H4	paired	8 July 1972 (08:10)
0	0	midway	H7	paired	10 July 1972 (06:30)
2	0	30	C29	?	20 June 1973 (08:15)
1	0	30	C12a	paired	13 June 1973 (09:10)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 2	TAPE 31				
2	0	31	C17	?	16 June 1976 (09:56)
4	0	31	C18	?	16 June 1976 (11:06)
3	0	31	C15	paired	2 July 1977 (16:40)
2	0	midway	C23	?	10 July 1977 (10:52)
3	0	2	C24	?	10 July 1977 (11:43)
3	0	31	C25	?	10 July 1977 (12:32)
1	0	midway	C26	?	10 July 1977 (15:17)
TAPE 2	TAPE 32				
2	0	midway	C48	?	30 June 1976 (10:11)
4	0	midway	C64	?	5 July 1976 (11:45)
1	0	2	C65	paired	6 July 1976 (08:36)
2	0	32	C66	paired	6 July 1976 (09:38)
2	0	32	C67	fledgling	6 July 1976 (10:30)
0	0	midway	C9	paired	30 June 1977 (15:45)
0	1	midway	C10	?	30 June 1977 (16:35)
1	0	32	C11	?	2 July 1977 (10:05)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 2	TAPE 34				
1	1	midway	C79	fledgling	13 July 1976 (08:37)
1	0	34	C80	paired	13 July 1976 (09:32)
2	1	2	C81	paired	13 July 1976 (11:43)
3	2	midway	C82	paired	13 July 1976 (12:32)
2	2	midway	C83	paired	13 July 1976 (14:21)
2	1	34	C84	?	13 July 1976 (15:55)
4	1	34	C85	paired	13 July 1976 (16:47)
TAPE 3	TAPE 4				
2	2	?	C33*	paired	29 June 1972 (08:40)
0	3	midway	C33*	paired	29 June 1972 (09:40)
1	0	3	C47	?	4 July 1972 (09:35)
0	2	4	C52	paired	7 July 1972 (11:55)
2	2	midway	H4	paired	8 July 1972 (08:30)
0	2	3	C12a	paired	13 June 1973 (08:50)
0	3	midway	C77	paired	5 July 1973 (07:10)
0	1	3	C80	?	5 July 1973 (11:45)
4	0	midway	C9	?	18 July 1974 (10:55)
1	2	4	C11	?	13 June 1976 (10:02)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT			
TAPE 3	TAPE 5	BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
2	1	5	K31	paired	21 July 1972 (19:15)
5	0	3	C24	paired	18 June 1973 (07:05)
1	3	3	C53	nestlings	24 June 1973 (14:25)
2	3	?	C84	fledgling	9 July 1973 (07:55)
0	1	3	C87	paired	14 July 1973 (10:10)
1	2	5	C95	paired	19 July 1973 (10:45)
3	0	3	C124	?	25 July 1973 (13:10)
2	0	midway	C128	?	26 July 1973 (15:14)
0	4	midway	C8	?	18 July 1974 (10:05)
1	4	midway	C10	?	18 July 1974 (12:15)
2	0	3	C14	?	20 July 1974 (15:40)
3	1	5	N1	paired	9 June 1976 (11:25)
0	3	midway	N2	paired	9 June 1976 (10:40)
3	1	midway	C1	paired	11 June 1976 (10:20)
3	0	3	C2	?	11 June 1976 (11:10)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 3	TAPE 5				
3	2	5	C3	paired	12 June 1976 (08:55)
2	0	midway	C4	paired	12 June 1976 (09:35)
2	0	?	C5	?	12 June 1976 (10:10)
4	3	5	C6	fledgling	12 June 1976 (11:00)
3	1	?	C7	?	12 June 1976 (12:35)
4	1	5	C9	?	13 June 1976 (08:42)
2	0	5	C19	?	16 June 1976 (11:59)
TAPE 3	TAPE 26				
1	0	3	K31	paired	24 May 1973 (16:05)
2	1	26	C4	fledglings	5 June 1973 (09:05)
3	0	26	C32	fledgling	15 July 1977 (09:47)
2	0	26	C33	fledglings	15 July 1977 (10:47)
1	0	26	C34	paired	15 July 1977 (12:34)
1	0	26	C35	nestlings	19 July 1977 (09:15)
2	0	3	C36	?	19 July 1977 (10:22)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 3	TAPE 28				
1	4	3	H3	paired	7 July 1972 (19:35)
2	1	3	H7	paired	10 July 1972 (06:50)
0	2	3	C49	paired	23 June 1973 (09:50)
3	5	3	C76	paired	4 July 1973 (10:45)
0	5	3	C81	?	8 July 1973 (11:30)
0	5	3	C82	?	13 July 1973 (11:00)
0	2	28	C90	?	14 July 1973 (08:15)
1	0	midway	C92	paired	13 July 1973 (06:50)
TAPE 3	TAPE 29				
5	2	3	H6	?	12 July 1972 (15:25)
0	1	3	C67	?	25 July 1972 (15:47)
1	1	29	C68	?	25 July 1972 (14:40)
1	0	29	C70	paired	4 July 1973 (12:20)
4	0	3	C71	paired	4 July 1973 (13:50)
2	1	29	C73	paired	4 July 1973 (09:05)
0	0	29	C75	?	4 July 1973 (15:20)
2	0	29	C87	paired	14 July 1973 (09:50)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 3	TAPE 29				
2	0	3	C93	?	13 July 1973 (08:45)
TAPE 3	TAPE 30				
1	0	midway	K30*	?	6 July 1972 (14:00)
0	4	?	C55a	paired	12 July 1972 (10:20)
4	0	3	C56*	?	10 July 1972 (07:15)
3	0	3	C59	fledgling	15 July 1972 (09:20)
4	0	?	C65	fledglings	22 July 1972 (08:05)
2	0	3	C8	paired	9 June 1973 (09:50)
2	0	?	C85	paired	8 July 1973 (10:05)
TAPE 3.	TAPE 31				
3	0	midway	C42	paired	26 June 1976 (16:20)
4	0	31	C91	paired	14 July 1976 (14:20)
2	0	31	C92	fledgling	14 July 1976 (15:12)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT			
TAPE 3	TAPE 31	BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
4	1	midway	C93	paired	14 July 1976 (16:35)
3	0	3	C94	?	14 July 1976 (17:37)
3	0	31	C12	paired	2 July 1977 (10:57)
2	0	3	C13	paired	2 July 1977 (11:50)
5	1	31	C14	?	2 July 1977 (15:30)
TAPE 3	TAPE 33				
3	0	33	C75	?	8 July 1976 (10:35)
1	0	midway	C76	?	8 July 1976 (11:29)
3	0	33	C77	?	8 July 1976 (14:07)
2	0	midway	C79	fledgling	13 July 1976 (08:22)
1	1	33	C80	paired	13 July 1976 (09:17)
2	1	33	C81	paired	13 July 1976 (11:28)
3	0	33	C82	paired	13 July 1976 (12:17)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 3	TAPE 34				
3	0	34	C86	fledgling	13 July 1976 (18:10)
4	0	34	C87	paired	14 July 1976 (09:00)
2	0	3	C88	paired	14 July 1976 (10:10)
4	0	3	C89	?	14 July 1976 (11:25)
3	0	34	C29	?	11 July 1977 (10:40)
0	1	34	C30	?	11 July 1977 (13:55)
1	1	3	C31	paired	11 July 1977 (14:50)
TAPE 4	TAPE 5				
1	2	?	K26*	?	23 June 1972 (07:55)
1	0	?	K31*	?	23 June 1972 (07:00)
1	0	?	K31*	?	23 June 1972 (07:15)
3	0	?	C26*	fledglings	27 June 1972 (15:29)
0	1	5	C4	fledglings	5 June 1973 (08:45)
0	1	5	C12	paired	13 June 1973 (07:40)
1	0	4	C17	nestlings	14 June 1973 (09:15)
1	0	4	C22	?	16 June 1973 (09:50)
1	1	5	C49	paired	23 June 1973 (09:30)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 4	TAPE 5				
0	1	midway	C93	?	13 July 1973 (08:25)
3	1	4	C4	?	18 July 1974 (12:52)
0	1	5	C12	?	20 July 1974 (13:45)
1	0	?	C19	?	21 July 1974 (14:40)
1	1	5	C18	?	16 June 1976 (11:16)
0	4	4	C20	paired	16 June 1976 (15:37)
1	1	4	C21	paired	16 June 1976 (16:23)
1	0	5	C50	paired	30 June 1976 (11:50)
4	0	5	C52	paired	30 June 1976 (14:35)
0	1	5	C53	?	30 June 1976 (15:25)
2	0	4	C74	?	7 July 1976 (17:43)
1	0	5	C96	?	15 July 1976 (19:05)
TAPE 4	TAPE 26				
3	0	?	K26*	paired	1 July 1972 (19:05)
1	0	?	C41*	fledgling	2 July 1972 (10:25)
1	0	4	C131	?	30 July 1973 (09:50)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 4	TAPE 26				
0	0	midway	C20	paired	6 July 1977 (09:30)
0	0	4	C21	?	6 July 1977 (10:23)
0	0	4	C22	?	6 July 1977 (11:30)
1	0	26	C29	?	11 July 1977 (10:55)
2	0	26	C30	?	11 July 1977 (14:10)
0	1	midway	C31	paired	11 July 1977 (15:05)
TAPE 4	TAPE 27				
7	1	27	K47	not paired	19 June 1976 (10:55)
3	1	27	K48	paired	21 June 1976 (12:18)
3	1	4	K49	paired	19 June 1976 (11:44)
3	0	4	C32	fledgling	15 July 1977 (10:02)
0	0	27	C33	fledglings	15 July 1977 (11:02)
0	0	midway	C34	paired	15 July 1977 (12:49)
0	0	?	C35	nestlings	19 July 1977 (09:30)
2	0	27	C36	?	19 July 1977 (10:37)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS TAPE 4	TAPE 28	TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
4	2	4	H6	?	12 July 1972 (15:45)
3	0	midway	C29	?	20 June 1973 (07:50)
1	0	28	C84	fledgling	9 July 1973 (08:15)
1	1	midway	C86	?	14 July 1973 (10:47)
0	2	28	C124	?	25 July 1973 (12:50)
2	0	4	C127	?	26 July 1973 (16:10)
2	0	midway	C128	?	26 July 1973 (15:35)
TAPE 4	TAPE 31				
1	0	31	K32	fledgling	7 June 1976 (16:10)
1	1	31	N1	paired	9 June 1976 (11:15)
4	0	31	N2	paired	9 June 1976 (10:30)
0	3	31	C1	paired	11 June 1976 (10:10)
3	0	4	C2	?	11 June 1976 (11:00)
1	1	?	C3	paired	12 June 1976 (08:45)
1	0	midway	C4	paired	12 June 1976 (09:25)
1	0	31	C5	?	12 June 1976 (10:20)
0	1	31	C6	fledgling	12 June 1976 (11:10)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT			
TAPE 4	TAPE 31	BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
0	1	31	C9	?	13 June 1976 (08:32)
1	0	31	C10	paired	13 June 1976 (09:10)
5	1	31	C34	paired	25 June 1976 (09:36)
2	0	31	C35	paired	25 June 1976 (10:28)
3	0	31	C38	paired	26 June 1976 (09:33)
TAPE 5	TAPE 26				
2	1	26	C35*	?	29 June 1972 (13:30)
2	1	midway	C37	paired	22 July 1977 (09:12)
3	2	26	C38	?	22 July 1977 (10:52)
1	0	midway	C39	paired	22 July 1977 (12:33)
1	0	midway	C40	?	26 July 1977 (11:05)
2	1	midway	C41	paired	26 July 1977 (12:07)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 5	TAPE 27				
3	0	?	C36*	paired	29 June 1972 (15:13)
3	0	midway	C86	?	14 July 1973 (11:10)
3	0	?	C92	paired	13 July 1973 (07:10)
1	0	5	C16	paired	5 July 1977 (08:25)
1	0	27	C17	?	5 July 1977 (09:15)
0	0	27	C18	?	5 July 1977 (10:10)
0	0	?	C19	paired	6 July 1977 (08:36)
TAPE 5	TAPE 28				
0	1	?	C30*	paired	28 June 1972 (15:42)
0	2	28	C31*	paired	29 June 1972 (06:22)
0	4	?	C34*	?	29 June 1972 (11:14)
1	3	5	C55a	paired	12 July 1972 (10:40)
0	3	28	C8	paired	9 June 1973 (10:15)
2	0	28	C77	paired	5 July 1973 (08:20)
0	4	28	C79	?	5 July 1973 (10:00)
0	2	28	C80	?	5 July 1973 (12:05)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT			
TAPE 5	TAPE 29	BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME).
3	1	29	C30	young	22 June 1976 (08:43)
0	1	29	C31	?	22 June 1976 (09:53)
0	2	29	C32	?	22 June 1976 (10:35)
3	0	29	C57	?	1 July 1976 (15:25)
2	0	midway	C58	fledglings ?	2 July 1976 (08:27)
2	0	midway	C62	?	5 July 1976 (09:56)
1	0	midway	C63	paired	5 July 1976 (10:46)
TAPE 5	TAPE 31				
1	0	5	K32	fledglings	9 June 1976 (06:45)
4	0	5	K32	fledglings	7 June 1976 (16:00)
2	0	31	C11	?	13 June 1976 (09:52)
2	0	5	C14	fledgling	16 June 1976 (08:07)
0	1	31	C5	paired	28 June 1977 (16:05)
0	0	31	C6	?	30 June 1977 (09:35)
1	0	midway	C7	paired	30 June 1977 (10:25)
2	0	31	C8	?	30 June 1977 (11:12)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT			
TAPE 5	TAPE 33	BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
0	0	33	C84	?	13 July 1976 (15:40)
2	1	33	C85	paired	13 July 1976 (16:32)
0	1	33	C86	fledgling	13 July 1976 (17:50)
3	0	33	C87	paired	14 July 1976 (08:45)
2	0	33	C88	paired	14 July 1976 (09:55)
2	0	33	C89	?	14 July 1976 (11:10)
4	0	midway	C90	paired	14 July 1976 (13:07)
TAPE 5	TAPE 34				
1	0	5	C106	?	21 July 1976 (10:43)
1	0	midway	C107	fledgling	21 July 1976 (11:28)
1	0	midway	C108	?	21 July 1976 (12:05)
0	1	34	C109	?	22 July 1976 (12:55)
0	2	34	C110	fledgling	22 July 1976 (14:25)
1	0	5	C111	fledgling	23 July 1976 (10:37)
1	0	34	C112	?	23 July 1976 (11:26)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT			
TAPE 26	TAPE 27	BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
0	0	?	C21*	?	26 June 1972 (14:13)
TAPE 26	TAPE 29				
0	3	29	C38*	fledgling	1 July 1972 (11:02)
TAPE 27	TAPE 30				
1	2	27	C64	?	5 July 1976 (11:30)
1	0	27	C74	?	7 July 1976 (17:28)
0	2	27	C101	?	17 July 1976 (09:30)
1	2	27	C102	paired	17 July 1976 (10:20)
1	0	27	C103	paired	17 July 1976 (10:51)
0	1	30	C104	?	17 July 1976 (11:35)
0	1	30	C105	fledgling	17 July 1976 (12:47)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT			
TAPE 27	TAPE 31	BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
0	1	31	C15	fledglings	16 June 1976 (08:46)
0	0	27	C19	?	16 June 1976 (11:49)
0	0	?	C20	paired	16 June 1976 (15:27)
0	1	midway	C21	paired	16 June 1976 (16:13)
0	3	midway	C22	?	18 June 1976 (08:15)
0	0	midway	C23	paired	18 June 1976 (09:00)
0	0	?	C25	?	18 June 1976 (10:30)
0	1	27	C28	nest (4 eggs)	18 June 1976 (15:19)
TAPE 27	TAPE 32				
0	0	27	C34	paired	25 June 1976 (09:46)
0	1	midway	C35	paired	25 June 1976 (10:18)
0	2	27	C38	paired	26 June 1976 (09:23)
1	0	27	C95	paired	15 July 1976 (18:19)
0	1	32	C97	?	16 July 1976 (09:17)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued)

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 27	TAPE 32				
0	1	midway	C98	paired	16 July 1976 (10:46)
0	0	27	C99	fledgling	16 July 1976 (12:35)
1	0	27	C100	?	16 July 1976 (13:35)
TAPE 29	TAPE 30				
2	0	30	C42*	?	3 July 1972 (07:57)
2	0	30	C43*	paired	3 July 1972 (09:35)
1	2	30	C44*	paired	3 July 1972 (11:30)
0	0	?	C45*	paired	7 July 1972 (07:10)
2	1	29	C47	?	7 July 1972 (09:15)
4	0	29	C49*	paired	4 July 1972 (11:54)
1	1	?	C50*	fledgling	4 July 1972 (14:20)
1	0	29	C12	paired	13 June 1973 (07:20)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 29	TAPE 31				
0	6	midway	K47	not paired	19 June 1976 (10:45)
1	0	31	K48	paired	21 June 1976 (12:00)
2	0	29	K49	paired	19 June 1976 (11:34)
3	0	midway	C59	paired	2 July 1976 (09:20)
0	1	31	C60	paired	2 July 1976 (10:15)
0	0	midway	C61	paired	2 July 1976 (11:05)
1	0	31	C65	paired	6 July 1976 (08:21)
1	0	29	C66	paired	6 July 1976 (09:23)
0	2	31	C67	paired	6 July 1976 (10:15)
TAPE 29	TAPE 32				
1	1	29	C50	paired	30 June 1976 (11:35)
2	1	32	C52	paired	30 June 1976 (14:20)
0	1	midway	C53	?	30 June 1976 (15:10)
3	0	29	C54	?	1 July 1976 (09:17)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued)

NO. ORIENTATIONS TAPE 29	TAPE 32	TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
0	2	32	C55	paired	1 July 1976 (10:13)
2	0	midway	C56	paired	1 July 1976 (11:14)
0	0	32	C75	?	8 July 1976 (10:50)
0	0	32	C76	?	8 July 1976 (11:44)
1	0	29	C77	?	8 July 1976 (14:22)
TAPE 29	TAPE 33				
3	3	midway	C83	paired	13 July 1976 (14:06)
3	0	?	C99	fledgling	16 July 1976 (12:20)
2	0	midway	C101	?	17 July 1976 (09:15)
1	1	33	C102	paired	17 July 1976 (10:05)
1	0	?	C103	paired	17 July 1976 (11:06)
2	1	33	C104	?	17 July 1976 (11:50)
2	2	33	C105	fledgling	17 July 1976 (13:02)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 29	TAPE 34				
1	1	29	C90	paired	14 July 1976 (13:22)
2	3	29	C95	paired	15 July 1976 (18:04)
1	0	29	C96	?	15 July 1976 (18:50)
1	0	29	C97	?	16 July 1976 (09:02)
0	2	midway	C98	paired	16 July 1976 (10:31)
0	2	midway	C100	?	16 July 1976 (13:20)
0	0	midway	K32	paired	16 June 1977 (10:56)
0	0	34	C27	paired	10 July 1977 (16:03)
TAPE 30	TAPE 31				
0	0	30	C30	nestlings	22 June 1976 (08:33)
0	0	30	C31	?	22 June 1976 (09:43)
0	1	30	C32	?	22 June 1976 (10:25)
1	4	midway	C48	?	30 June 1976 (10:26)
0	2	30	C54	?	1 July 1976 (09:32)
0	2	30	C55	paired	1 July 1976 (10:28)
1	1	30	C56	paired	1 July 1976 (11:29)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
TAPE 30	TAPE 32				
0	1	30	C41	?	26 June 1976 (10:52)
1	0	30	C42	paired	26 June 1976 (16:10)
0	1	30	C45	paired	27 June 1976 (08:47)
0	0	30	C47	paired	27 June 1976 (13:13)
0	1	30	C57	?	1 July 1976 (15:10)
0	0	30	C58	fledglings?	2 July 1976 (08:12)
0	0	30	C59	paired	2 July 1976 (09:05)
1	0	midway	C60	paired	2 July 1976 (10:00)
0	1	32	C61	paired	2 July 1976 (10:50)
0	0	32	C62	?	5 July 1976 (09:41)
0	0	30	C63	paired	5 July 1976 (10:31)
TAPE 31	TAPE 32				
2	0	32	C106	?	21 July 1976 (10:28)
0	0	32	C107	fledgling	21 July 1976 (11:13)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

NO. ORIENTATIONS		TAPE CLOSEST TO BIRD AT			
TAPE 31	TAPE 32	BEGINNING OF EXPER.	EXPER. BIRD	BREEDING STATUS	DATE (TIME)
0	0	?	C108	?	22 July 1976 (11:50)
1	0	31	C109	?	22 July 1976 (12:40)
0	0	32	C110	fledgling	22 July 1976 (14:10)
0	0	midway	C111	fledgling	23 July 1976 (10:22)
1	0	32	C112	?	23 July 1976 (11:11)
TAPE 32	TAPE 33				
1	3	32	C113	?	26 July 1976 (09:04)
0	1	midway	C114	paired	26 July 1976 (09:55)
0	1	32	C115	?	26 July 1976 (10:48)
1	0	32	C28	?	11 July 1977 (10:05)
TAPE 33	TAPE 34				
0	1	34	C91	paired	14 July 1976 (14:05)
0	2	33	C92	fledgling	14 July 1976 (14:57)
1	2	34	C93	paired	14 July 1976 (16:20)
1	2	33	C94	?	14 July 1976 (17:22)

APPENDIX 8. DATA FROM THE DUAL-SPEAKER EXPERIMENTS (continued).

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[1] The letter prefix designates the population where the individual was found (C = Connetquot; K = Kalbfleisch; N = Nissequoque; H = Havermeyer estate) and the number following the letter designates the individual of that population.

APPENDIX 9. SEQUENCE OF SONGS OF AN ACOUSTICALLY ISOLATED MALE FROM RECORDINGS MADE IN 1975 AND 1976. NUMBERS DESIGNATE SYLLABLES. SONGS ARE SEPARATED BY SEMICOLONS.

1975

13 April. 1,2,3; 1,2,3; 1; 1,4; 1,2; 1,2,3; 1; 1,1,2; 1,2,3;
1,1,4; 1,1; 2,3; 1; 1,2,3; 1; 1; 1,4; 1,1,4; 1,2,3;
1; 1,2,3.

1 June. 1,4,2; 1,4,1,1,3,2; 1,3,3; 1,1,2,3; 4,1,1,2; 1,4,4,5;
1,2,3; 1,3; 1,3; 1,4,1,2; 1; 1,4,3; 1,3; 1,3; 1,3; 1,3; 1,4;
1,3; 1,3; 1,4; 1,3; 1; 1,3; 1,3; 1; 1; 1,3; 1,3; 1,3;
1,3; 1,3; 1,4; 1,2,3; 1,4,1,1,2,3; 1,3; 1,3; 1,3;
1,4,1,1,4,1,2,3; 1,4; 1; 1,4,1,2,3; 4,1,1,2; 6,1, 1,4,1,1,2;
6,1,1,2; 6,1,1,2,3; 1,4,1,1,2; 1,6,1,1,2,3; 1,4; 1,4,2,3;
1,4,6,1,2,3; 1,3; incomplete song; 1,4,3; 1,3,3; 1,4,6,1,2,3;
1,4; 1,3.

1976

10 May. 1,1,7,4; 1,1,4; 7,4; 7,4,4,1,2; 1,4,2; 4,2; 4; 4,1,4,2,3;
4,2,3; 4,1,2,3; 4,2,3; 4,4,2,3; 4,1,2,3; 4,2,3; 4,2,3;
4,2,3; 4,2,3.

25 May. 6,8,3; 6,8,3; 6,8,3; 6,8,3; 6,8,3; 6,8,3; 6,8,3; 6,8,3;
6,8,3; 6,8; 6,8,3; 6,1; 6,8; 6,8,3; 6,8,3; 6,8,3; 6,8,3.

APPENDIX 10. CHARACTERISTICS OF THE MOST FREQUENT SONG OF THE ISOLATE MALE THAT WAS RECORDED ON EACH OF FOUR DAYS.

	13 April 1975	1 June 1975	10 May 1976	25 May 1976
	1,2,3[a]	1,3	4,2,3	6,8,3
Song duration (secs)	0.84	0.62	1.74	1.93
Freq. range of song (kHz)	2.9	3.1	2.3	5.0
Max. freq. of song (kHz)	5.0	5.0	5.0	6.9
Min. freq. of song (kHz)	2.1	1.9	2.7	1.9
Longest syllable in song (secs)	0.28	0.34	0.87	0.84
Length of syllables (secs)				
1	0.17	0.22	-	-
2	0.25	-	0.87	-
3	0.28	0.34	0.42	0.84
4	-	-	0.20	-
6	-	-	-	0.03
8	-	-	-	0.45
No. notes/syllable				
1	1	1	-	-
2	1	-	1	-
3	3	3	3	3
4	-	-	1	-
6	-	-	-	1
8	-	-	-	1
Rate of delivery of syllables (syllables/sec)	3.57	3.23	1.72	1.55

[a] Syllable sequence

APPENDIX 11. CHARACTERISTICS OF SONGS FROM EIGHT KALBFLEISCH INDIVIDUALS THAT CONSIST OF ONLY ONE NOTE-COMPLEX PHRASE. THE SERIES OF LETTERS LISTED UNDER THE DESIGNATION FOR EACH INDIVIDUAL (K5, etc.) INDICATES THE SEQUENCE OF SYLLABLES IN EACH SONG-TYPE.

	K5 H,A,A	K18 VV,WW	K23 S,H,CCC	K29 C,F,UU	K30 HHH,HHH,III	K31 S,Z	K40 S,S,H,CCC	K45 S,WW,CCC
Song duration (secs)	0.77	0.44	0.77	0.79	0.89	0.70	0.81	0.75
Freq. range of song (kHz)	5.3	4.9	2.9	2.8	3.5	2.4	3.4	2.5
Max. freq. of song (kHz)	7.8	6.6	5.6	5.1	5.5	5.9	6.1	5.1
Min. freq. of song (kHz)	2.5	1.7	2.7	2.3	2.0	2.5	2.7	2.6
Longest syllable in song (secs)	0.20	0.21	0.23	0.18	0.06	0.26	0.25	0.22
Length of syllables (secs)								
First	0.14	0.03	0.04	0.14	0.06	0.03	0.02	0.03
Second	0.20	0.21	0.23	0.18	0.06	0.26	0.02	0.22
Third	0.20	-	0.23	0.07	0.06	-	0.25	0.16
Fourth	-	-	-	-	-	-	0.25	-
No. notes/syllable								
First	3	2	2	2	3	2	2	1
Second	3	4	3	20	3	2	2	5
Third	3	-	5	2	6	-	2	3
Fourth	-	-	-	-	-	-	8	-
Rate of delivery of syllables (syllables/sec)	3.88	4.54	3.90	3.80	3.37	2.86	4.94	4.00

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