PATTERNS OF SINGING IN A POPULATION OF THE PLAIN TITMOUSE

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In recent years students of bird song have concerned themselves with the system of communication involved in this conspicuous behavior. For example, provision for individual recognition has been inferred from analysis of the seemingly monotonous songs of the Chipping Sparrow (*Spizella passerina*) by Borror (1959) and Marler and Isaac (1960), and such recognition has been demonstrated in the differential responses of Ovenbirds (*Seiurus aurocapillus*) to broadcasts of songs of neighboring and distant males (Weeden and Falls 1959). In contrast, the suppression of individual variation appears evident in the songs of the White-crowned Sparrow, *Zonotrichia leucophrys* (Marler and Tamura 1962), and the Cardinal, *Richmondena cardinalis* (Lemon 1965). In the last two species and in the Chaffinch (*Fringilla coelebs*) the existence of local "dialects" has been shown. The Plain Titmouse (*Parus inornatus*) exhibits a system similar to that of the Cardinal, several song-types being shared by members of the population. However, an impression of great variability (Dawson 1923:604) results from regional variation in dialects. This paper will explore some facets of the song system in the population of Plain Titmice occupying the Hastings Natural History Reservation, two miles east of Jamesburg, Monterey Co., California.

METHODS

During the breeding season of 1959 songs were identified by audition, augmented by spectrographic analysis of tape recordings made at this locality in 1955 (by William R. Fish), on 1 April 1959 and from 8 through 12 March 1965. The audition method was generally satisfactory, although some arbitrary grouping of song-types was necessary. The observations in 1959 were incidental to a study of the territoriality of 15 color-banded males occupying contiguous areas (Dixon, MS). The tape recordings from 1955 and 1959 were made on a Magnecord tape recorder, and those from 1965 on a Nagra III BH with an Altec 633 microphone mounted in a 24-inch parabolic reflector. Sound spectrographs were made on a Kay Electric Company Sona-Graph, using the wide band setting and FL 1 filter (time/frequency display).

RESULTS

Most songs of the Plain Titmouse are composed of syllables or note-complexes (of Mulligan's 1963 terminology) that are repeated several times, usually with a definite meter. Some syllables consist of a single note repeated at intervals shorter than the duration of the note (fig. 1A); others may recur in a rapid sequence and constitute a trill (figs. 1E and 4A). More complex units of repetition, better designated as note-complexes, are formed of an introductory note or vibrato of a frequency above 4 kc/sec followed by one or more notes of different structure. The latter may be single (fig. 2C) or coupled (figs. 1C and 2A), or may consist of two note types (fig. 4D). Single-note syllables range from 0.035 sec (fig. 4A) to 0.21 sec (fig. 1A) in duration, whereas some note-complexes extend for 0.34 sec (fig. 4C).

The introductory note often is sibilant, the result of the wide frequency range and duration of the vibrato, and the subsequent notes usually have melodic properties as indicated by overtones (figs. 2A and 5A). A given introductory note is used in conjunction with few principal notes such that the number of themes is limited.

Note-complexes may be repeated from one to six times in a burst or "bout" of singing. Rarely is more than one note-type or syllable emitted in one bout. The exceptions known to me involve trilled songs in which a preliminary trill is followed by another consisting of syllables of another type (fig. 4A). Another pattern is a song burst begun with repetition of a note-complex with an immediate shift to a trilled sequence of a single note-type.

A characteristic utterance, usually not repeated in a bout, consists of several similar, high-pitched notes, followed by two closely spaced, emphatic sounds. The latter (fig. 3A) have a dominant frequency below 4 kc/sec, with overtones and some elements of noise.

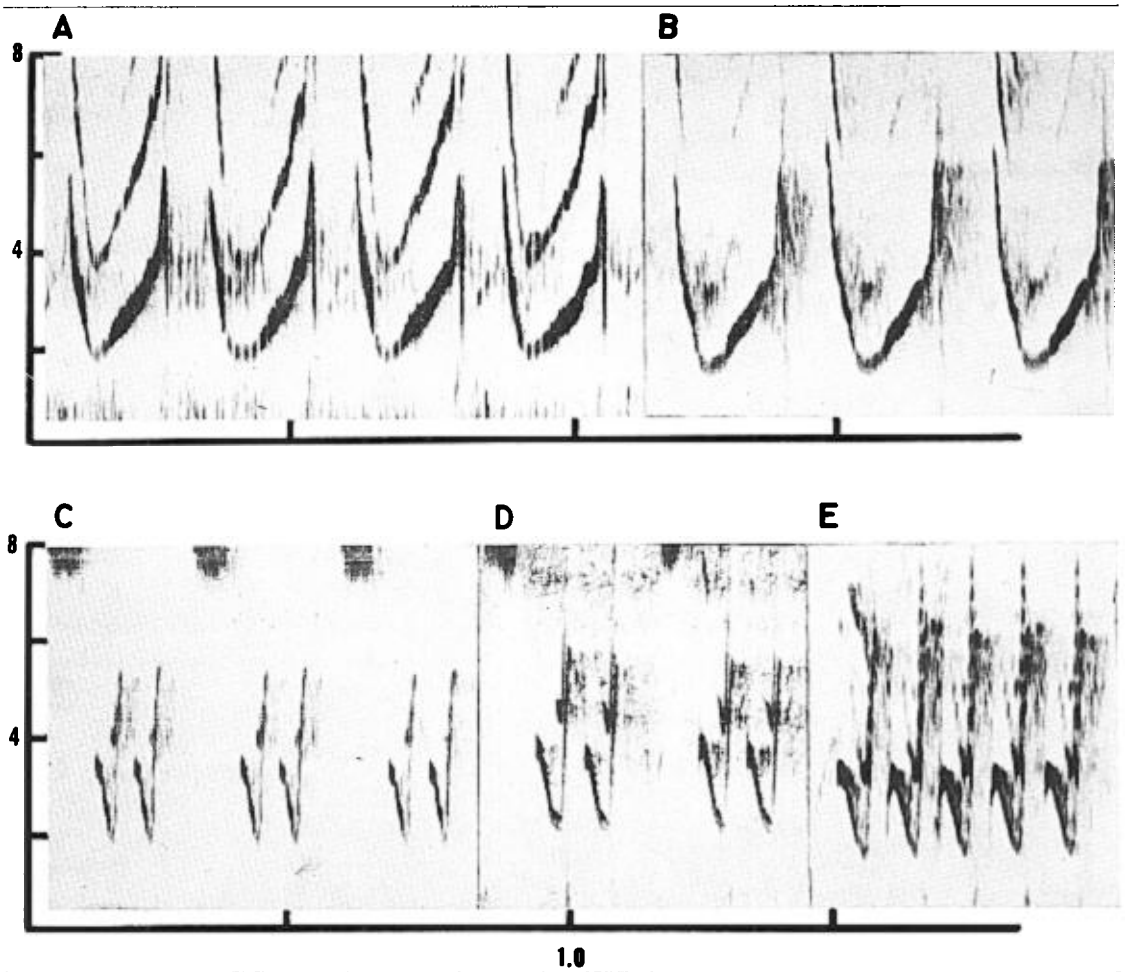

FIGURE 1. Sound spectrographs of songs of the Plain Titmouse recorded at Hastings Reservation in different years. A and B, recorded in 1955 and 1959, respectively; syllables transliterated as "churwee"; C and D, recorded in 1959 and 1965, respectively, rendered as "chulip-chulip"; E, a trill with introductory vibrato absent and frequency of principal notes slightly lower than in C and D. Vertical axis, kc/sec; horizontal axis, time in sec.

This call appears to have been derived with slight modification of the motor patterns that produce the "tsicka dee dee" call (compare fig. 3A and 3C). The latter vocalization, used by females as well as by males, apparently is a homolog of the "name" call of the Black-capped Chickadee (*Parus atricapillus*). Such utterances are delivered by one member of the pair during the breeding season, usually in a context indicating announcement of occupancy. Frequently the rather variable vocalizations included in this category are delivered in response to the more characteristic song motifs of neighbors. These vocalizations do not impress me as carrying as far as many of the note-complexes discussed above. However, they are distinctive for the species. They are more prevalent in the latter part of the morning, and appear to reflect lower motivation than other territorial utterances. In these respects their utilization appears to parallel that of the "tink" note of the Great Tit (*Parus major*) as discussed by Gompertz (1961:385, 389). However, because of their context, manner of delivery, seasonal occurrence, and prevalent use by males, these vocalizations are included here among the songs of the Plain Titmouse.

Contexts of singing. Song usually is uttered in an advertising or announcement context in which the singer takes a high but somewhat screened perch. Thus singing and foraging may be somewhat separated, but the singer is not especially vulnerable to aerial predators. Singing may occur during actual boundary skirmishes, but these were not observed often at the Hastings Reservation, possibly because of the relative openness of the vegetation (see

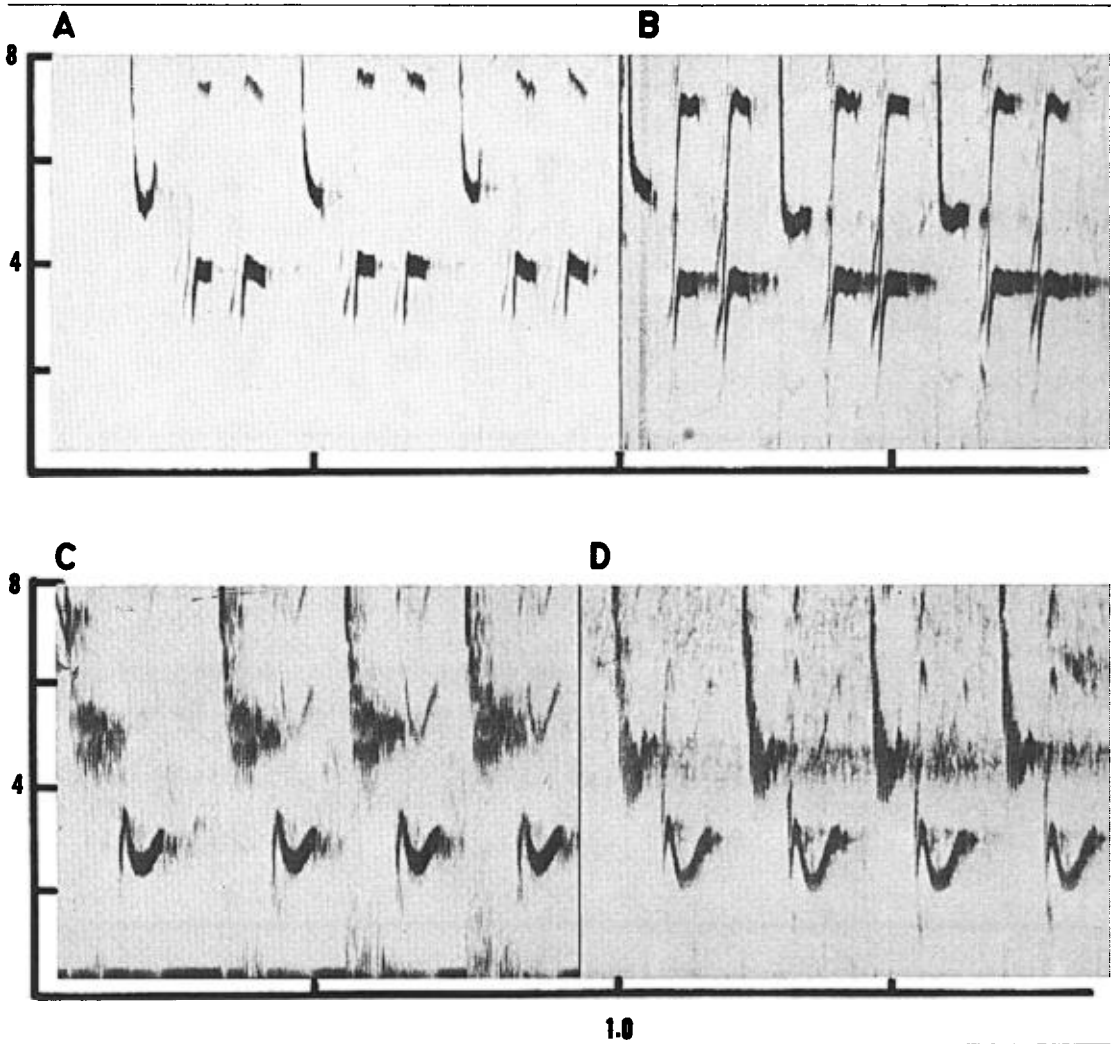

FIGURE 2. Comparisons of songs of the Plain Titmouse: A, recorded in 1955, B, in 1965, transliterated as "speedeet speedeet"; C and D, from 1959 and 1965, respectively, syllables noted as "sturick sturick." The second phrase appears to be stressed in both song-types, and the coupled notes of A are not separable by the human ear.

White 1966:232–233, photographs). However, titmice occasionally encountered neighbors that were trapped in the course of banding operations. The attack on the entrapped bird in such instances afforded an opportunity to determine relationships of singing to fighting. From early October to early January the vocalizations uttered by the attacker impressed me as identical to song themes, but were uttered softly. After mid-January, such vocalizations were delivered with full volume, coinciding with the appearance of singing and song exchanges in the population. Eight recognizable themes were used as "fighting notes" and their incidence did not depart from that heard in more general contexts. Themes included are shown in figures 1C, 1E, 2A, 4A, 4C, and 4D.

Occasionally a male sang after its release from a trap. One male, trapped three times in one week in January 1959, sang different themes when released each time (figs. 4C, 2C, and 5A). Only males were known to sing under such conditions, and such singing may have been elicited by absence of the mate.

Number of motifs in the population. In the interval from 8–12 March 1965 I tape-recorded the songs exchanged by titmice in an area encompassing perhaps one dozen contiguous territories. Particular attention was devoted to the singing of four males. Subsequent spectrographic analysis led me to identify 17 song themes in this population. The three males whose vocabularies appeared most thoroughly documented, uttered 11, 10, and 9 motifs, re-

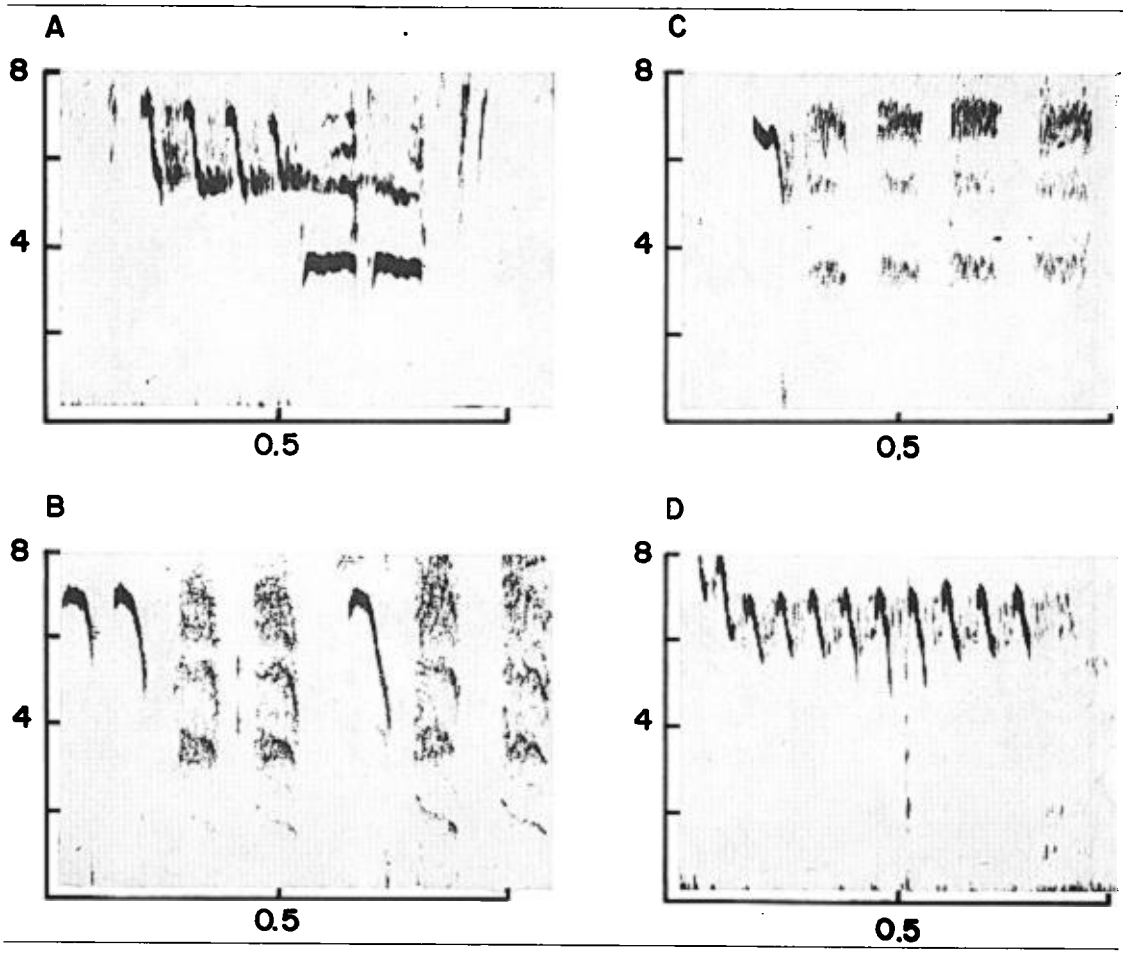

FIGURE 3. A, the "call derivative" song of the Plain Titmouse (see text). B, calls uttered by the titmouse as an Acorn Woodpecker foraged near the presumed nestsite. C, the "tsicka dee dee" call, comparable to the "name" call of the Black-capped Chickadee. D, trill of notes comparable to those in the introductory phrase of A.

spectively. These three males in the aggregate delivered 14 of the 17 themes recognized. Five motifs were shared by all three males, six by two males, and three were heard from a single bird.

Absence of a motif (or of its constituent notes) is difficult to prove. However, the tendency toward answering a male in his initial theme in countersinging (see beyond) would strengthen the supposition that failure to utter a note-complex indicates its absence from the individual's repertoire. In 1959 I did not detect the note-complex shown in figure 1C in the vocalizations of a male whose territory I traversed almost daily. The same theme was "absent" for the utterances of an unmated, first-year male in an adjacent territory.

Frequency of occurrence of song themes. In the interval from 22 February through 30 May 1959, 480 songs were noted under circumstances in which color-banded participants were identified. Five motifs recognized by audition comprised 72 per cent of the total. None of these "major" themes was dominant, the frequencies ranging from 13 to 16 per cent. Most of the other motifs were heard infrequently and some doubtless fell into disuse. The commonly heard motifs are represented by figures 1A, 2A, 4A, 4C, and 5. This situation stands in contrast to that reported from the Berkeley area 10 years earlier (Dixon 1949:115), in which two song-types (approximating 4C, 4D) were prevalent.

One of the intensively studied males which appeared to be unmated sang six different themes in 17 min while countersinging in midmorning on 10 March 1965. The same male emitted five song motifs in his first 14 min of singing on the following morning, and six in 23 min an hour later. During the last two

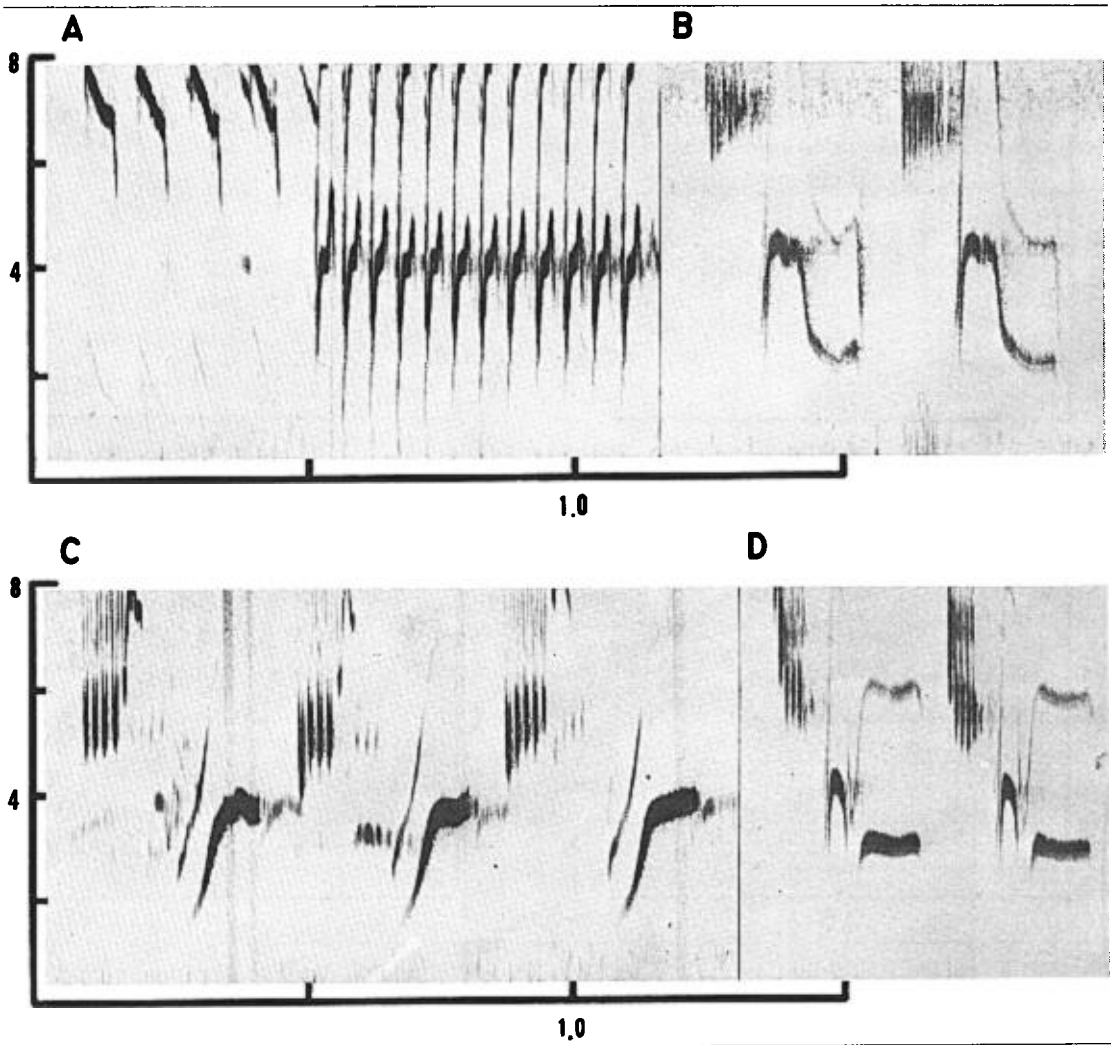

FIGURE 4. A, the two-syllable trill sequence of the Plain Titmouse (compare to 3D). B, C, and D, songs in which the subsequent phrase consists of more than one note type. Syllables are transliterated as follows: B, "speeyurk," C, "sweet," D, "seetur." Motif D was recorded at Berkeley, California, in March 1961.

intervals this male totalled eight song themes in 37 min of singing, and, in the three intervals on two days, exposed the 11 motifs identified in his repertoire.

Seasonal changes in occurrence. Trilled songs and the motif shown in figure 1C declined in frequency after late March 1959, whereas the "churwee" song (fig. 1A) became more prevalent as the season progressed. It is my impression that the first two themes are not as audible at a distance as are some others. Further, they may be elicited more frequently by visual contact, which may diminish as the activity of pairs is restricted by attention to nest building and related activities.

Persistence of song themes. Sound spectrographs representing songs recorded at Hastings Reservation in 1955, 1959, and 1965, show that some note-complexes and songs recurred in this locality for many years. Usually such motifs were emitted by several individuals, and were frequently heard. In addition to the motifs shown in figures 1A–B, 2A–B, and 1C–D, the latter trill in 4A and theme 4C were tape-recorded in two seasons 10 years apart. Other note-complexes were heard on only a few occasions, and in 1959 most were heard only in February and March. Additional themes, rare or not detected at Hastings Reservation, were conspicuous at Berkeley, 100 miles away, in 1961 (Dixon, MS).

Countersinging of males. Titmice often answer a rival in the latter's motif, or shift to the note-complex inaugurated by the neighbor. In 62 of 120 instances in 1959, in which I was certain that I heard the first response elicited

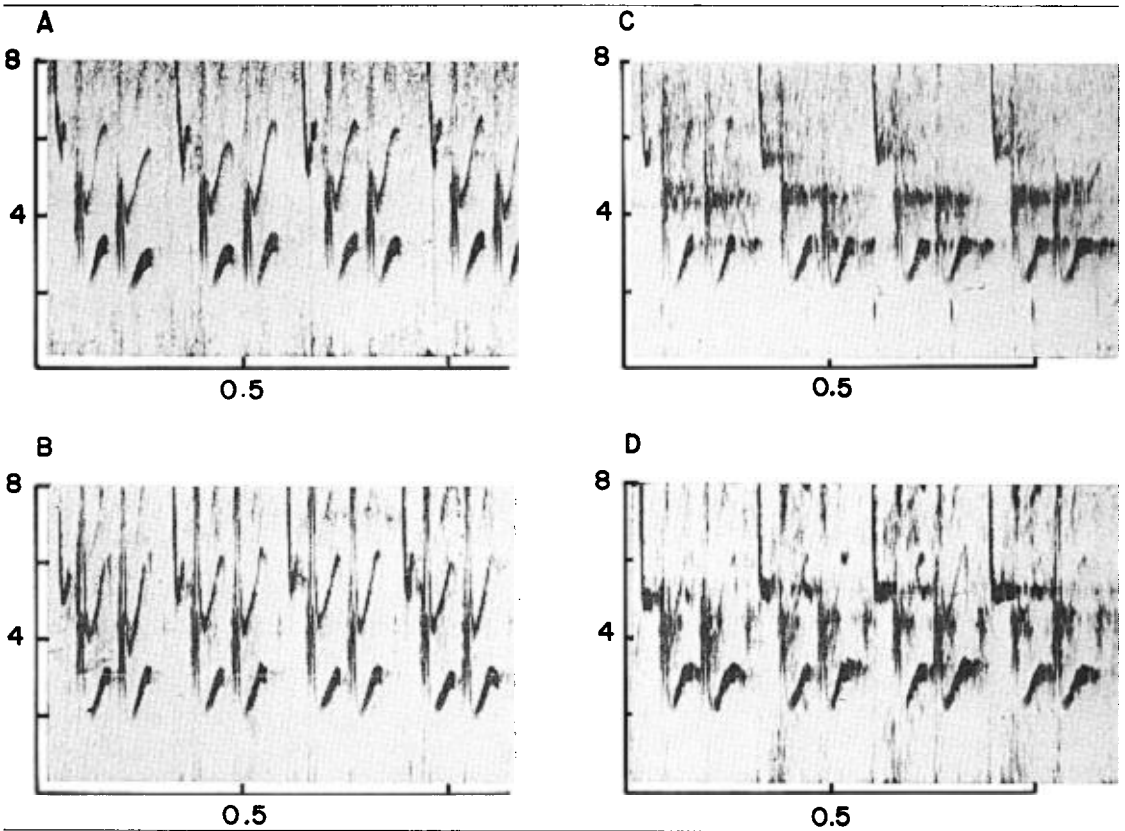

FIGURE 5. Songs of three Plain Titmice occupying contiguous territories in March 1965. Songs are represented as repetitions of syllable "stewlert." B and C, recorded from the same individual. D, delivered in response to C.

by a neighbor's singing, the latter's song theme was matched. The precision of matching is indicated by comparison of figures 5C and 5D, uttered in countersinging by two individuals in March 1965.

As a rule, a male will change themes after eight or ten bursts. On several occasions this change occurred much more rapidly, three or four motifs being delivered in one minute of singing in an advertising context. The sequences were uttered so rapidly that the individual might not have detected an answer had it been forthcoming. Even in its normal pattern of singing, the Plain Titmouse changes themes more rapidly than does the Cardinal, in which Lemon (1965:559) found that at least a one hour's listening was necessary to determine the extent of an individual's repertoire.

The tendency toward countersinging and the sharing of motifs by many males of a population result in a pattern of local dialects. The persistence of themes certainly derives from these factors, and from the relatively low turnover among adults in some populations of this species (Dixon 1956).

DISCUSSION

Local dialects have been described in a number of passerine species, some of which differ markedly in the number of song-types per individual. The White-crowned Sparrow (Marler and Tamura 1962) has only a single motif, the Chaffinch two to six (Nottebohm 1967), and at the other extreme, thrushes have an almost infinite variety (see Isaac and Marler 1963). The Plain Titmouse resembles the Cardinal most closely in size of repertoire. Lemon (1965) found that a population of 25 individuals (ca. 10 territories per year) produced a total of 28 themes, only 10 of which were used commonly in the five years of his study.

The sharing of many song-types results in conformity to a populational pattern, as Lemon has observed. This conformity in the Plain Titmouse is attested by the essential identity of motifs recorded in different years (figs. 1 and 2), and by the matching of note-complexes during countersinging (fig. 5). A question arises as to why this matching should be attempted.

Many of the songs exchanged by Plain Titmice are more than assertions of occupancy of a territory. As shown by the attacks on trapped titmice, many, perhaps most, song-types are "fighting notes." They function as threats, as indicators of a tendency to attack. Delivered at full volume, they constitute a distant threat, a substitute for physical combat (Thorpe 1961:15). The occurrence of countersinging near boundaries suggests a process of conditioning of the threat to a particular site, reiterating a boundary relationship that will be neglected subsequently while nestlings are being fed.

Although the ontogeny of songs has not been studied in *P. inornatus,* the structural and contextual similarity of some song-types in this species to the fighting notes used in boundary skirmishes by Black-capped Chickadees (Dixon and Stefanski, MS) suggests the derivation of titmouse songs from such close-quarters threat calls rather than the reverse. If this inference is correct, Andrew's (1961:549) reservation concerning the aggressive motivation of song is not supported in the Plain Titmouse.

Why should a variety of stereotyped songs (distant threats) be shared by the males of a population of the Plain Titmouse? The employment of the "call derivative" song (fig. 3A) suggests a selective advantage to an increase in variety. For the Great Tit, in which matching of themes also occurs, Gompertz (1961:393) supported the anti-monotony principal of Hartshorne (1956), an effect of equal importance to the recipient. In addition to the effects of auditory feedback on the singer, shifts of song-type may stimulate the rival to prolong the song exchange. Conceivably other neighbors may be provoked to commence singing also. Such singing from accustomed perches or positions may aid males in keeping track of their neighbors, as Marshall (1964: 354) suggested for towhees of the *Pipilo fuscus* group. Intruders may be recognized readily, and the status quo maintained.

In the Chaffinch, Hinde (1958) demonstrated that song motifs are not of equal importance to the individual, each male having a "preferred" type. In the Plain Titmouse, the individual may be more responsive to one of the shared motifs than to another, the possible result of prior experience. If a titmouse answers a neighbor in the theme being sung, the strongest challenge may be flung, reinforcing the initiator's stimulus. The initiator, by a subsequent change of motif, may strike one of greater valence to the respondent. This postulate receives some support from observation of rapid shifts in song-types observed while trapped titmice are being attacked, and in the frequent shifting of song themes (without waiting for a reply) witnessed on a few occasions. If the bird in proximity is assailed with a threat of particular valence he should flee more readily, with less chance that physical combat will be required.

SUMMARY

The songs of *Parus inornatus* were studied by audition in one population in central coastal California in the breeding season of 1959, and by analysis of tape recordings made in 1955 and 1965. The songs consist of repetitions of syllables of different complexity. Seventeen spectrographically distinct song-types were distinguished in a group of some 12 males. Individuals averaged 10 motifs, many shared with their neighbors. The stereotypy of individual repertoires is shown by the virtual identity of themes recorded from countersinging males, and by the constancy of these note-complexes over a span of years. The result is a local "dialect" of shared song-types.

The delivery of some of these song themes by free-living individuals while fighting trapped titmice suggests derivation from "fighting notes," and function as a distant threat. The production of a number of themes during a short interval of countersinging may stimulate continued vocal exchange. In this way males may obtain information on their neighbors' positions, and reiterate threats at established boundaries.

ACKNOWLEDGMENTS

I am grateful to the late Alden H. Miller for his encouragement of these studies, and to John Davis, Betty S. Davis, Martha W. Dixon, William R. Fish, Donald Isaac, Peter Marler, and John O. Sullivan for assistance in various ways. The field work in 1958–59 was conducted as a part of the program of studies at the Hastings Reservation generously supported by the late Mrs. Russell P. Hastings and Mr. Hastings. Subsequent studies were supported by National Science Foundation grants G-12915 and GB-2343.

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