

COMMUNICATION WITH REPERTOIRES OF SONG THEMES IN TUFTED TITMICE

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Abstract. This study examined the possibility that song themes of tufted titmice (*Parus bicolor*) might communicate information about the singer to territorial neighbours. The 8-12 themes sung by each individual in our population were divided into three classes based on acoustic structure and frequency of use. Class-I themes (the most frequently used) occurred disproportionately often early in the day, early in the breeding season, and in the central portion of the singer's territory, while class-III themes (the least frequent) showed the opposite trends. Playbacks revealed differences in responses of territorial neighbours to the three classes of themes. When the subject failed to match the playback, it sang class-III themes disproportionately. Also, class-II themes were sung in response to playbacks of class-I themes, but not the converse. Class-II themes also tended to be used by females separated from their mates. These results, together with observations of the use of themes in natural encounters at boundaries, suggest that class-I themes serve primarily for long-range advertisement, class-II themes of males indicate a tendency to escalate an encounter, and class-III themes indicate a low probability of aggression or a tendency to terminate an encounter.

Introduction

Individuals of many species of passerine birds have songs of two or more distinct patterns, called themes or song types. Much recent research has focused on how these repertoires of themes serve to enhance territorial defence or the attraction and stimulation of mates (Krebs & Kroodsma 1980; McGregor et al. 1981).

The hypotheses for the advantages of repertoires fall into two distinct categories. On the one hand, the behaviour of receivers like territorial rivals and prospective mates might depend on the overall size or diversity of a singer's repertoire. For example, diverse repertoires might reduce habituation, misrepresent territorial density, confuse territorial neighbours, attract or stimulate mates, or indicate the singers' capabilities for defending their territories (Hartshorne 1956; Howard 1974; Krebs 1976, 1977a, b; Kroodsma 1976; Krebs et al. 1978; Yasukawa 1978, 1981; Smith and Reid 1979; Catchpole 1980; Yasukawa et al. 1980; Morton 1983). For each of these effects, receivers would have to respond to the overall properties of repertoires. On the other hand, receivers might react differently to themes or sets of themes within a repertoire. We might expect such behaviour particularly if themes encode information about the singer's situation or behavioural state.

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It is important to emphasize that the various effects of repertoires are not mutually exclusive. Each deserves investigation in its own right. This study of tufted titmouse (*Parus bicolor*) focuses especially on the last of the above hypotheses about repertoires: encoding of information by different sets of themes. Male tufted titmice sing 8-12 themes, which can be distinguished by ear in the field (Schroeder & Wiley, 1983). Pairs are resident on their territories for most of the year.

Several previous studies have indicated that a singer's use of themes varies with its location and social situation. Warblers in the genera *Dendroica* and *Setophaga* provide a particularly illuminating case. Early reports suggested that species often have two classes of themes, one used predominantly in territorial encounters with other males (unaccented-ending songs), the other used in interactions with females and near the centre of the territory (accented-ending songs) (Morse 1966, 1967, 1970; Ficken & Ficken 1970). In other passerines also, songs in the presence of females differ from those in encounters with males (Smith 1959; Nicolai 1964; Thielcke & Thielcke 1970; Baptista 1978; Payne 1979; Sossinka & Bohner 1980).

More detailed study of singing by *Dendroica* warblers has suggested that accented- and unaccented-ending songs are associated with the male's location in his territory, the latter used mostly in peripheral areas, the former mostly

during undisturbed singing in central areas (Lein 1972, 1978). In chestnut-sided warblers (*Dendroica pensylvanica*) a third category of songs is almost completely restricted to actual territorial encounters (Lein 1978). Yellow-throated vireos (*Vireo flavifrons*) provide another example in which use of themes differs with location in the territory (Smith et al. 1978). This association of themes with locations within the territory suggests that themes might encode information about the singer's agonistic tendencies.

The lack of more evidence for association of song themes with the behavioural states and external circumstances of singing birds might result in part from the difficulty of collecting suitable data, particularly the difficulty of categorizing social situations and internal states. In place of direct demonstrations of associations between themes and social situations, variations in use of themes at different times or locations can provide some indirect evidence. Diurnal and seasonal changes in the use of themes could result from changes in the frequencies of different internal states or situations of singers. In different parts of a territory, such as the vicinity of boundaries, the nest, or frequently used foraging and singing sites, a male experiences different distributions of social situations and thus might select different distributions of themes.

Even when themes are known to be associated with different circumstances or states of the singer, however, it remains to be demonstrated that conspecifics respond to them differently. In the absence of such demonstrations, we have no evidence that any information encoded in different themes is used by conspecific receivers. Our study explored possibilities for the association of themes with the singer's behavioural state and circumstances. In addition, we employed playbacks of tape-recorded song to investigate responses to different themes.

Methods

Field Methods

The temporal and spatial distribution of song themes and their associations with different social contexts were studied by means of timed samples of singing by five male tufted titmice on contiguous territories, two (C and C/R) studied from January to July 1976, one (O) from January to February, one (B/R) from January to April, and one (R) from April to July. Males O and B/R disappeared in the course of the

study, and male R expanded his territory into the study area.

The study area consisted of nearly mature hardwood forest (Wiley 1977). A grid of stakes 25 m apart over an area of 18 ha permitted mapping of the subjects' locations throughout their territories, which averaged 200–300 m in diameter. Territorial males in this population sang 9–10 themes each and shared all or most of their repertoires with their neighbours (Schroeder & Wiley, 1983). With a little practice, each theme could be recognized by ear in the field.

To document the use of themes during undisturbed activities, we undertook two kinds of observational sampling: timed observations of singing and systematic tape-recording.

During timed observations of singing, the focal bird's location and theme, if any, as well as the locations of females and neighbouring males, if known, were recorded every 30 s. One male served as the focal animal for 3 h each morning, beginning half an hour before sunrise, and observations on successive days rotated among the subjects. Two complete cycles of timed samples of each male were completed each month. In addition, each of the males was tape-recorded for 3 h on two mornings each month. Notes dictated during these periods provided further information on the use of themes.

Playbacks of tape-recorded songs provided an opportunity to study responses to different themes. For playbacks, an Amplivox S-610 amplifier-speaker placed 2–2.5 m above ground and covered with an olive-coloured piece of burlap was driven by a Uher tape recorder from 15 m away. Volume, standardized for all playbacks, approximated that of normal songs of titmice, as judged by ear. The amplifier-speaker was placed inside the subject's territory within 25 m of the boundary. These experiments were conducted between 0900 and 1200 hours, from mid-May to July on males C, C/R and R. Unless otherwise noted, playbacks lasted 4 min at a rate of 12 songs/min, normal for this species (Schroeder & Wiley, 1983). Playbacks always presented themes in the subjects' repertoire.

We use the terms note, for a sound producing a continuous trace on a sound spectrogram, and syllable, for a repeated unit consisting of one or more notes.

Classes of Themes

To simplify the problem of evaluating associations between themes and social situations

or responses, we grouped the themes of our population into three categories, based on two criteria: frequency of use and acoustic structure.

Our classification resulted from extensive recording and observation in the field in 1975. It might not be the best one for differentiating the situations or responses of titmice, since we did not try alternative ones. If titmice use a different classification, it would weaken any associations of our classes of themes with situations and responses. Consequently, any conclusions about these associations are bound to be conservative.

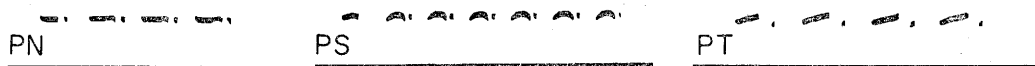
The first category of themes (class I) contains the most frequently used themes in the population, both in numbers of bouts and in minutes of song (see below). All had syllables that consisted of a long note followed by a short note on the same or a lower pitch (Fig. 1). These themes are the ones often transliterated as 'peter, peter, peter' in field guides. The themes in this group, PN, PS and PT, were shared by all males in the study area and were also present in the repertoires of neighbours.

The second group (class II) included themes with a pronounced change of frequency within

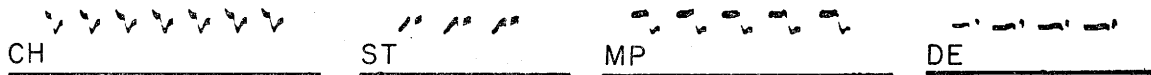
syllables (frequency range/duration > 0.6 kHz/s), or with the second short note of each syllable higher than the first long note (Fig. 1), features that separate these themes from those in class I. Syllables of these themes had durations similar to or shorter than those of class-I themes. Class-II songs were sung frequently only if they were in the repertoires of neighbours or if they were used to match a theme missing from the male's repertoire. Class-II songs include CH, ST, MP and DE. Only CH was shared by all and ST by most of the population (Schroeder & Wiley, 1983).

The remaining songs (class III), were used infrequently in comparison with those in classes I and II (see below). They also differed in having long (> 0.2 s) notes in syllables (themes PK, RB, BR, WP, SP), a short note preceding the long note in a syllable (themes PK, BR, KD), or syllables of a single note (theme PL) (Fig. 1). Themes SP and WP resembled each other; SP occurred in the repertoires of all birds except B/R, who used WP. Male B/R's theme BR resembled theme RB of other males but reversed the order of notes.

CLASS I



CLASS II



CLASS III

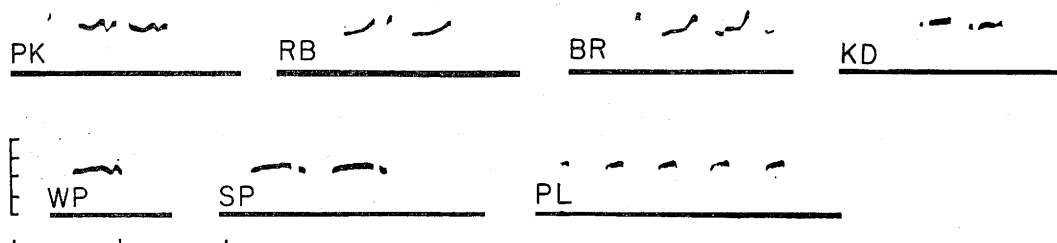


Fig. 1. Three classes of themes recognized in this study. See text for the criteria for inclusion of themes in each class. All themes vary somewhat in the number of syllables included. For a discussion of variation in these themes see Schroeder & Wiley (in press). Vertical scale, 0–4.0 kHz in 1-kHz intervals; horizontal scale, 1.0 s in 0.5-s intervals.

All five males under study had at least two of each class of themes in their repertoires. All five shared the same three class-I themes. Of class-II themes, all shared theme CH and all but male R had theme ST. Males B/R and R had theme MP and only male R had theme DE. Each male had three or four class III themes, but only theme KD was shared by all (see Schroeder & Wiley, 1983).

Results

Diurnal Patterns

A striking pattern in the population under study was the use of theme PN (class I) as the first song of the day. This theme occurred first in 30 of 48 timed samples. All five males showed this trend clearly (50–67% of days of timed samples for males C, C/R, B/R, R; 83% of days for male O). Theme PN accounted for 14–22% of songs at other times, excluding those matching a neighbour's song (57% for male O). All remaining first songs were theme PS or PT (also class I), but in several instances when these were used first there had been no song early in the morning.

In timed samples, class-I themes were used more often early in the day than later by all birds in the study (Fig. 2). They dominated the first hour of song, when they constituted at least 75% of songs. During the second and third hours, class-I themes decreased in both relative and absolute frequencies, although they were

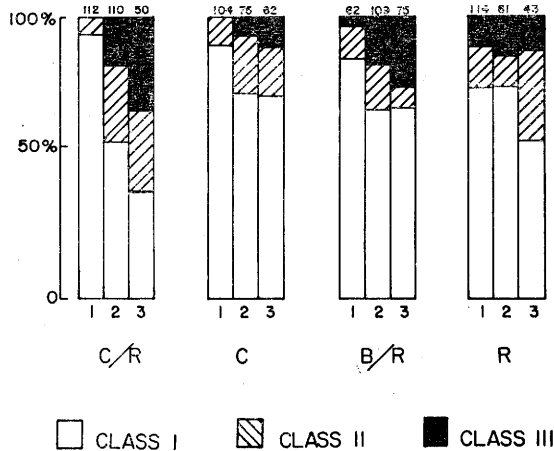


Fig. 2. Classes of song themes in the 3 h after first light. Comparing the proportions of class-I themes in hours 1 and 3, $t=2.92$, $df=3$, $P<0.1$, two-tailed, with arcsine transformation of proportions. For other comparisons, $P>0.1$. Number at the top of each column indicates minutes of singing observed.

still more frequent than songs of classes II and III. There were corresponding increases in class-II and III song in the second and third hours of the day.

Seasonal Patterns

A seasonal pattern paralleled the diurnal pattern. Class-III song was absent from timed samples in four of five birds in January and February. In late June and July, males C/R and C (the only two observed throughout the study) sang class-III songs proportionately more than earlier (Fig. 3).

The season of most prolonged singing was not the period of greatest variety (Fig. 4). Time spent singing reached a maximum in late April and early May. In the eight 3-h samples from this period, the focal animal never used more than six themes on a particular day and averaged 5.0. During June–July, the mean number of themes per day was 7.6 ($t=2.31$, $df=14$, $P<0.05$, two-tailed).

In addition, recurrence intervals for bouts of the same theme increased late in the breeding season. In the June–July sampling period, long recurrence intervals (>6) occurred more often than in earlier periods (Table I). Individual samples from the April–May sampling period, during the most persistent singing, showed a striking lack of variety in song. For instance, on 27 April, when C sang for 80.5 min in the first 3 h, two themes (PN and PT) accounted for 75% of his song.



Fig. 3. Use of themes of class III early (January–May, except only April–May for male R) and late (June–July) in the breeding season. Number at the top of each column indicates total records at 30-s intervals.

Spatial Patterns

More singing occurred in the centre of a territory, in relation to the area included, than in the periphery (Fig. 5). We defined the periphery as the circumferential band composed of the outermost two 25-m² quadrats around the area in which singing occurred (a band roughly 50 m wide, in other words). Within the territory, some spots were used as singing stations much more than others. The areas near feeders were favourite singing locations, especially if they were not near boundaries. Other favoured

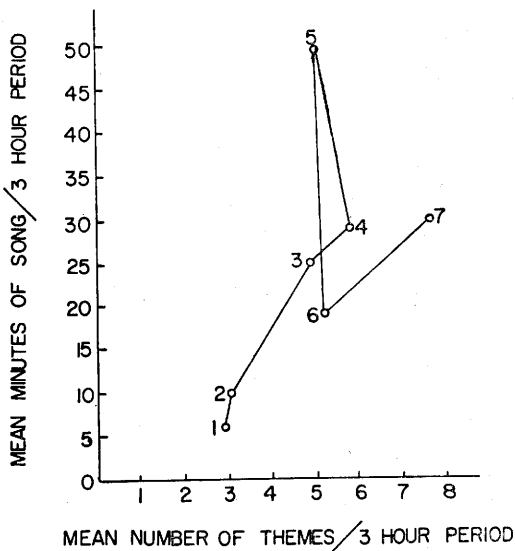


Fig. 4. Relationship between the amount of song and the number of themes for monthly sampling periods (1-7) between January and July. Samples with no song, which usually occurred during inclement weather, are excluded.

Table I. Seasonal Change in Distribution of Recurrence Intervals*

Sampling periods†	Recurrence intervals		
	2	3-6	7-19
1-4 (Jan-early April)	16	26	9
5 (late April-early May)	33	28	4
6 (late May-early June)	8	10	2
7 (late June-July)	22	17	16‡

*Number of changes before a theme repeats (minimum value: 2).

†Periods 1-4 included males C, C/R, B/R and O; periods 5-7 included males C, C/R, and R. Statistical comparison across these groups is not appropriate.

‡Period 7 differs from periods 5 and 6: $\chi^2=12.4$, $P<0.01$. No other comparisons differ statistically with $P<0.05$.

locations often had tall trees adjacent to breaks in the canopy. The heavily-used singing areas of neighbours rarely abutted.

Class-III themes were less concentrated in the centre of the territory than were themes of classes I and II for three birds, although the spatial separation of theme classes was not marked (Fig. 5). After male R annexed a large piece of B/R's territory in April, he sang frequently on the newly acquired area. His class-I themes were not as concentrated in central areas as those of the other males.

Transitions Between Themes and Bout Lengths

Analysis of transitions between bouts of themes did not reveal any sequential associations of themes or classes of themes, probably because neighbours often affected the choice of songs during concurrent singing (see Schroeder & Wiley, 1983). Class-I themes, however,

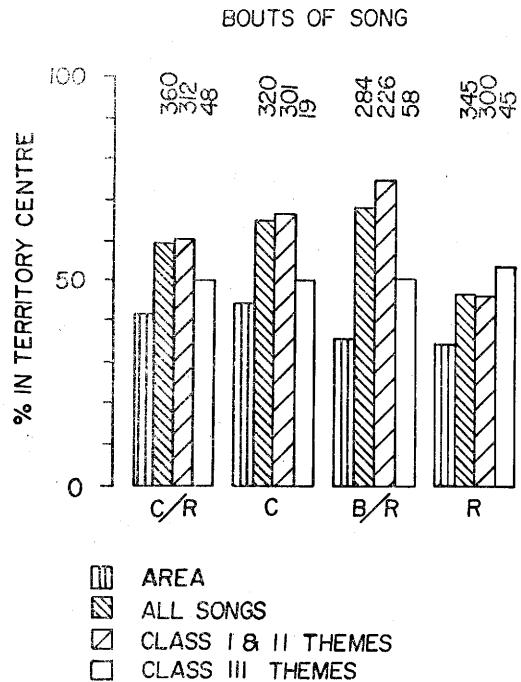


Fig. 5. Spatial distribution of song bouts within territories. The periphery of a territory is a circumferential band composed of the two outermost 25-m quadrats in which singing occurred. Male R expanded his territory and changed his singing positions just before the observations of his behaviour began (see text). Comparing classes I and II with class III, excluding male R, $t=3.97$, $df=2$, $P<0.1$, two-tailed, with arcsine transformation of proportions.

were more likely than other classes of themes to be preceded by at least 5 min of silence by the subject (Fig. 6). The mean length of bouts of class-I themes was greater than that of classes II and III for all birds.

Use of Themes in Responses to Playback

Titmice tended to match playbacks of tape-recorded themes (Schroeder & Wiley, 1983). On occasion, though, a subject still in the vicinity of the speaker failed to match, even though it had the theme in its repertoire, or switched from a matching theme to another theme during or immediately after the playback. On these occasions, class-III themes were sung more frequently, and class-I themes less frequently, than expected (Table II).

Calculation of expected values for song classes in this analysis required adjustments for the season and time of day of the playback. Data from the control periods prior to broadcast of playbacks were combined with data from timed samples of the appropriate season and hour. Since each subject sang its themes with different frequencies, the expected frequencies for each class of theme in the absence of matching the playback also had to be adjusted for the frequency of the playback theme. For each instance of failure to match the playback theme, the expected probabilities of response with each class of themes are respectively $(c-a)/(1-a)$, $d/(1-a)$, and $e/(1-a)$, where a = the probability of singing the playback theme, c = the probability of singing another theme in the same class as the playback, and d and e = the probabilities of singing a theme in each of the remaining two

classes. The expected frequency for each class of theme then equals the sum of the probabilities for that class for all instances of failure to match.

When the subject engaged in sustained countersinging with the playback but did not match the theme, class-II themes occurred more frequently than expected in response to playback of class-I songs. The converse was not true (Table III). Class-II themes were also sung at a faster rate than the playback more often than were class-I themes (Table IV), regardless of whether the response was matching or not. This difference is not a result of differences in the duration of themes. On the other hand, the class of song in the playback did not affect overall response rate ($\chi^2=1.10$, $N=35$, NS).

In nine of 20 experiments at the peak of the singing season, titmice terminated their response to playback by singing the PN theme (class I). Singing of PN usually began at favourite sites in territories and not near the speaker.

Use of Themes in Natural Encounters

Interpretation of the timed observations and the responses to playback is clarified by con-

Table II. Responses when the Playback Theme was not Matched by the Subject

Bird	Song class			χ^2	P
	I	II	III		
C/R	5(14.0)*	11(8.9)	11(4.1)	17.8	<0.01
C	2(11.2)	6(6.3)	16(6.4)	21.8	<0.01
R	8(15.3)	8(5.3)	10(5.4)	8.8	<0.05

*Expected values (in parentheses) equal the total responses times the proportion of song bouts of that class of themes (excluding the theme used for playback) in normative data for the subject for the hour of the day of the playbacks. In all cases, the subjects' repertoires included the playback theme.

Table III. Classes of Themes in Sustained Countersinging (At Least 1 min) During Playback Experiments*

Playback theme class	Response theme class	
	I	II
I	18(12.9)†	7(12.1)
II	0(5.1)	10(4.9)‡

*Class-III themes were used three times in sustained countersinging with class-I playback but were not included in the analysis.

†Expected values in parentheses.

‡ $\chi^2=12.8$ (corrected for continuity), $P<0.001$.

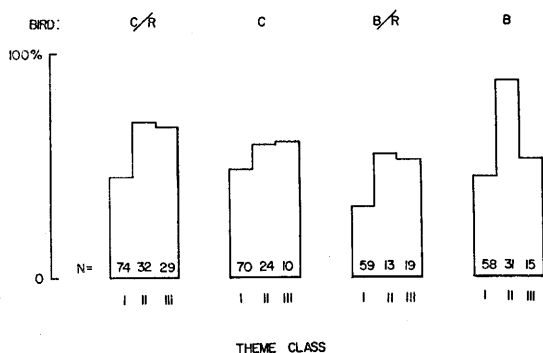


Fig. 6. Frequency with which each theme class was preceded by song within 5 min. Comparing classes I and II, $t=3.61$, $df=3$, $P<0.05$; comparing classes I and III, $t=4.40$, $df=3$, $P<0.05$ (two-tailed tests with arcsine transformation of proportions).

Table IV. Rate of Response for Two Classes of Themes in Sustained Countersinging (At Least 1 min) During Playback Experiments

Response theme class		Rate of response*	
		Normal	Rapid
I		13(8.7)†	5(9.3)
	II	4(8.3)	13(8.7)‡

*Rapid rate: at least 50% greater than the playback rate. Normal rate: similar to playback rate. Class-III responses are not included in the analysis.

†Expected values in parentheses.

‡ $\chi^2=6.46$ (corrected for continuity), $P<0.05$.

sidering the uses of themes in encounters at boundaries. The following paragraphs describe some typical encounters.

On 7 April the titmice B/R, R, and an unmarked neighbour met near their boundaries. Initially, B/R sang theme ST, R sang theme CH and the neighbour sang theme PC, all class-II themes. Later, R switched to PT, a class-I theme, and the unmarked neighbour moved away singing an unfamiliar theme. Meanwhile, B/R sang a series of class-III songs and some muted songs of other classes. Class-II song here appeared to indicate a willingness to escalate and class-III a low probability of fighting.

On the same day, singing of themes KD and CH attracted attention to a pair of intruders, apparently mates, in male C/R's territory. Calls were also frequent. Then the stranger sang a class-II theme. The two pairs then engaged in chases interspersed with short bursts of several themes. The intruding male moved away singing PK, a class-III theme. C/R sang a class-II theme while escorting the intruding pair from the territory. He later returned to the site of the encounter and sang class-II themes, facing the route of the intruder's departure. Finally, C/R sang SP, a class-III theme, his last song before returning to normal foraging activities. Class II again indicated apparent readiness to escalate and class III a low probability of fighting.

Four days later, a pair of intruders sang in the same area. Male C/R called and chased them. His mate G/O sang short bursts of CH, a class-II theme, in a different part of the territory. Male C/R eventually responded with theme CH and his mate joined him, calling. Then the pair of intruders moved away, calling. Here class-II again indicated an increased challenge, but also served for communication between members of a pair.

On 25 February, males C/R and O and their mates were seen in the same tree near their common boundary. They called and gradually began to move apart. When separated, male O sang ST briefly and male C/R sang CH, both class-II themes. Later, male C/R sang PK, a class-III theme, more than 100 m away.

These incidents demonstrate some general features of encounters. Intense challenges involve some singing of class-II themes. Some encounters include rapid switching of themes. Encounters are likely to end with singing of class-III themes. Frequently, class-III themes began as one or both birds moved away from the site of the exchange. In other cases, one switched to class III while the other continued with class I or II. When the birds are in visual contact, calling is the most frequent vocalization, but class-II or III themes are sometimes used.

Class-III themes or calls were often used by birds moving about near boundaries. They were not sung from high perches at full volume. They were also used in the midst of the family flock, including instances in which two flocks moved apart after approaching at a boundary.

Singing Behaviour and Pair Formation

Pairs in this study were formed well before territorial singing reached a peak in early May and remained together throughout the year. Males O and C obtained new mates in February. Male R's mate disappeared in January, and he had acquired a new one by April. Male C/R and his mate G/O were observed together in all seasons. They successfully fledged young in both 1975 and 1976. Male R and his mate B/G, after nesting successfully in 1975, were seen on their territory until B/G disappeared.

Mated females often used class-II themes when separated from their partners. Female G/O frequently used the class-II theme CH in this situation. For instance, once when her mate C/R was trapped, G/O sang theme CH frequently before he was released. In a few cases, she and her mate countersang themes PS and CH near to each other. Female C/O sang the class-II theme ST on several occasions when separated from her mate.

Discussion

Advantages of Repertoires

In addition to the possibility that song themes might convey information to listeners, our study permits evaluation of several other hypotheses for the evolution of repertoires based on the

advantages of a larger number or diversity of themes. Since no two of these hypotheses are mutually incompatible, it is appropriate to judge each separately.

Of these hypotheses, the attraction of mates seems unlikely to account for repertoires in tufted titmice. Pairs usually persist for the lifetime of the individuals, and new pairs often form during winter or early spring before singing reaches its peak. Repertoires might still affect the reproductive development of mates, particularly since singing reaches its peak in April and May, when nesting is beginning. We cannot assess the possibility that repertoires might indicate the capabilities of males for territorial defence.

Misrepresentation of density by the use of repertoires, the 'Beau Geste' hypothesis, applies especially to birds like tufted titmice which live in habitats where they are not readily visible (Krebs 1977b). To enhance the ruse, singers should change position between bouts of different themes. Deception should be most pronounced during the season of territory establishment.

For tufted titmice, the patchy distribution of singing sites is consistent with a ploy to simulate high density. However, titmice frequently sing while moving from one place to another, behaviour that would not mimic high density. Also against the hypothesis is the sharing of frequently-used songs among neighbours. Only six themes were used frequently over a 25-ha area. Furthermore, the variety of songs was greater after the period of territorial establishment, which is puzzling if the variety in repertoires aids territorial defence. During the peak of the singing season only about half of the repertoire was used on any given morning. Characteristics of singing by tufted titmice thus suggest that a Beau Geste effect cannot provide a complete explanation of repertoires in this species.

Information Conveyed by Sets of Themes

Communication between territorial neighbours. Our principal aim in this study was to assess the possibility that a singing bird's use of themes might convey information about his state or situation to other titmice. The receivers in this case include established territorial neighbours more often than newcomers. Of course, interactions with neighbours as well as those with intruders serve to establish a male's territorial boundaries and the size of its territory. Neigh-

bours, particularly in a non-migratory species like the tufted titmouse, have the opportunity to become acquainted with each other over appreciable periods of time. As a consequence, their relationships are more likely to include reciprocally-advantageous interactions than are the relationships of residents and strange intruders (Axelrod & Hamilton 1981). It is thus not unreasonable to expect some exchange of information in the course of mutual agreement on boundaries.

Classification of themes. To make a study of this sort practical, we had to lump themes into classes and to focus on a few features of the singers' situations. Both of these steps make it difficult to detect much detail in associations of themes with particular situations. Furthermore we do not know whether the specific features of situations or classes of signals selected are the most relevant ones for titmice.

Our selection of classes of themes developed in the course of field work before the normative and experimental studies reported here began. It is possible that other classifications of themes, situations or responses would have yielded even clearer associations. If titmice classify themes in a way different to ours, any associations that we could detect would be weakened.

Temporal and spatial patterns in theme choice.

The class-I themes PN, PS and PT together made up 75% of the song heard in the first hour. These themes were shared by all males in the study and also by their neighbours. Not all widely-shared themes were frequently used, however. The use of class-I themes especially during early morning suggests they are important in long-range advertisement. Territorial males might need to advertise their continued presence as the first order of business each day. Meteorological conditions, in addition, make this time the best for long-range advertisement (Henwood & Fabrick 1979; Wiley & Richards 1983).

Theme PN apparently had a special role in long-range territorial advertisement. Its frequent use as the first song of the day constituted a predictable 'signing-on' by the territorial males in our population. Theme PN was never used by females in our population. Besides its use as a first song, this theme was often heard from the centre of the territory following response to intruders or playbacks.

The importance of class-I themes in long-range territorial advertisement is also suggested

by their prevalence early in the season. Class-III themes, in contrast, were most frequent during the post-nesting period. The absence of class-III songs in many samples until after the peak of the singing season suggests that class-III themes do not serve primarily for territorial advertisement and do not serve to reduce habituation during territorial establishment.

Although Krebs et al. (1978) found no seasonal differences in the use of themes by great tits (*Parus major*), the periods they compared were all during territorial establishment. Social contexts might well vary more between pre-nesting, nesting and post-nesting periods than within any one period. In tufted titmice the selection of themes changed most in the post-nesting period.

Use of class-I and II themes was concentrated at favourite singing sites in the centre of the territory. In contrast, class-III songs occurred nearly as frequently in the periphery as in the centre of the territory and were usually sung from low perches. The spatial distribution of class-III themes reinforces evidence from seasonal patterns that class-III themes are not primarily used for territorial advertisement.

Although Krebs et al. (1978) reported no difference in the use of themes between the northern and southern halves of territories of great tits, social situations seem more likely to differ between the periphery and centre than between the northern and southern parts of a territory.

Theme choice and social contexts. The use of class-I themes in response to playbacks and in natural contexts is consistent with a primary role in territorial advertisement. Class-II themes, on the other hand, although used in some of the same contexts as class-I themes, appeared to indicate readiness to escalate an interaction.

There were four principal differences in the use of these two classes of themes by males. (1) Class-I themes were more likely to be preceded by silence than were other themes. Such spontaneity is a characteristic feature of vocalizations for territorial advertisement (Marler 1968). Class-II themes were preceded by song more frequently and were thus more likely to be part of an ongoing interaction than class-I themes. (2) Class-I themes did not occur in response to playbacks of class-II themes when there was a failure to match in sustained countersinging. Class-II themes, however, occurred in response to playback of class-I themes. (3) Class-II themes were also more likely to be

sung at high rates in response to playback experiments than were class-I themes. (4) Class-II themes were used particularly when repelling intruders and in intense boundary encounters. Males were often closer together during class-II song than during class-I song. Thus the use of class-II themes by males suggests that they were associated with more intense aggressive responses than were class-I themes.

Females used class-II themes more frequently than class-I themes. Class-II songs from females sometimes elicited song or approach by mates after separation. Apparently, in this situation class-II themes increased the probability of approach by mates.

Class-III themes, though not as frequently used as the others, appeared significantly more than expected in response to playback when the subject failed to match, usually only after the playback had first been answered by class-I or II songs. These themes were used by titmice when leading family flocks away from boundaries where they had approached each other. Class-III themes were always given from relatively low perches, no higher than the lower canopy, when flocks were in motion and after an interaction, before a return to activity such as foraging. Class-III themes thus indicated a low probability of imminent aggression. They became proportionately more frequent during movement away from playbacks and during withdrawal from a boundary after a close approach to a neighbouring flock.

Conclusions

The results of this study illustrate two patterns in the associations of avian vocalizations with contexts. First, song themes are associated with different locations within a male's territory and with different agonistic tendencies. The tufted titmouse, chestnut-sided warbler and yellow-throated vireo (Lein 1978; Smith et al. 1978) all make different choices of themes in central and peripheral locations in the male's territory. The first two also select themes differently in close-range interactions and undisturbed singing. Both choose themes differently during escalation and withdrawal from encounters. The association of themes with different agonistic tendencies could explain their associations with different locations in a territory.

Second, some vocalizations occur in remarkably disparate situations. A clear case is the disproportionate use of class-II themes both by males escalating an interaction with intruders or

at boundaries and by mates before approaching each other. In such cases, the initial spatial relationships and the identities of participants are important variables in determining responses to vocalizations (Wiley 1976). As Smith (1969, 1977) emphasizes, the use of contextual information by the recipient extends the possibilities for communication. Although ethologists have often sought a common motivational basis for displays with similar structure in different situations, it is just as appropriate in such cases to seek common requirements for communication. For instance, the need for ease of location and recognition could make similar signals suitable in very different circumstances.

We can conclude that the repertoires of themes used by tufted titmice, like those of some vireos and warblers, do encode information about the singing bird, in the sense that a listener can make some predictions about a bird on the basis of the theme it sings. Furthermore, the playbacks of tape-recorded themes show that titmice adjust their responses to the themes they hear. Although we cannot claim to have established that our classifications of themes, situations or responses have advantages over any others, it is clear that titmice recognize some differences among at least some of the themes that we placed in different categories. In short, we have evidence that repertoires of themes, in addition to any other effects they might have, serve in part for transmitting information between territorial titmice.

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REFERENCES

- Axelrod, R. & Hamilton, W. D. 1981. The evolution of cooperation. *Science, N.Y.*, **211**, 1390-1396.
- Baptista, L. F. 1978. Territorial, courtship and duet songs of the Cuban grassquit (*Tiaris canora*). *J. Ornithol.*, **119**, 91-101.
- Catchpole, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour*, **74**, 149-166.
- Ficken, M. S. & Ficken, R. W. 1970. Responses of four warbler species to playback of their two song types. *Auk*, **87**, 296-304.
- Hartshorne, C. 1956. The monotony threshold in singing birds. *Auk*, **73**, 176-192.
- Henwood, K. & Fabrick, A. 1979. A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. *Am. Nat.*, **114**, 260-274.
- Howard, R. D. 1974. The influence of sexual selection and interspecific competition on mockingbird song. *Evolution*, **28**, 428-438.
- Krebs, J. R. 1976. Habituation and song repertoires in the great tit. *Behav. Ecol. Sociobiol.*, **1**, 215-227.
- Krebs, J. R. 1977a. Song and territory in the great tit. In: *Evolutionary Ecology* (Ed. by B. Stonehouse & C. M. Perrins), pp. 46-62. New York: Macmillan.
- Krebs, J. R. 1977b. The significance of song repertoires: the Beau Geste hypothesis. *Anim. Behav.*, **25**, 475-478.
- Krebs, J. R., Ashcroft, R. & Webber, M. I. 1978. Song repertoires and territory defence. *Nature, Lond.*, **271**, 539-542.
- Krebs, J. R. & Kroodsma, D. E. 1980. Repertoires and geographic variation in bird song. *Adv. Stud. Behav.*, **11**, 143-177.
- Kroodsma, D. E. 1976. Reproductive development in a female song bird: differential stimulation by quality of male song. *Science, N.Y.*, **192**, 574-575.
- Lein, M. R. 1972. Territorial and courtship songs of birds. *Nature, Lond.*, **237**, 48-49.
- Lein, M. R. 1978. Song variation in a population of chestnut-sided warblers (*Dendroica pensylvanica*): its nature and suggested significance. *Can. J. Zool.*, **56**, 1266-1283.
- Marler, P. 1968. Aggregation and dispersal: two functions in primate communication. In: *Primates: Studies in Adaptation and Variability* (Ed. by P. C. Jay), pp. 420-438. New York: Holt, Rinehart & Winston.
- McGregor, P. K., Krebs, J. R. & Perrins, C. M. 1981. Song repertoires and lifetime reproductive success in the great tit (*Parus major*). *Am. Nat.*, **118**, 149-159.
- Morse, D. 1966. The context of songs of the yellow warbler. *Wilson Bull.*, **78**, 444-455.
- Morse, D. 1967. The contexts of songs in black-throated green and Blackburnian warblers. *Wilson Bull.*, **79**, 64-74.
- Morse, D. 1970. Territorial and courtship songs of birds. *Nature, Lond.*, **226**, 659-661.
- Morton, E. S. 1983. Grading, discreteness, redundancy and motivational-structural rules. In: *Acoustic Communication in Birds*. Vol. 1. *Production, Perception and Design Features of Sounds*. (Ed. by D. E. Kroodsma & E. H. Miller), pp. 183-212. New York: Academic Press.
- Nicolai, J. 1964. Der Brutparasitismus der Viduinae als ethologisches Problem: Prägungsphänomene als Faktoren der Rassen- und Artbildung. *Z. Tierpsychol.*, **21**, 129-204.
- Payne, R. B. 1979. Song structure, behaviour, and sequence of song types in a population of village indigobirds, *Vidua chalybeata*. *Anim. Behav.*, **27**, 997-1013.
- Schroeder, D. J. & Wiley, R. H. 1983. Communication with shared song themes in tufted titmice. *Auk*, **100**, 414-424.
- Smith, D. G. & Reid, F. A. 1979. Roles of the song repertoire in red-winged blackbirds. *Behav. Ecol. Sociobiol.*, **5**, 279-290.
- Smith, R. L. 1959. The songs of the grasshopper sparrow. *Wilson Bull.*, **71**, 141-152.

- Smith, W. J. 1969. Messages of vertebrate communication. *Science, N.Y.*, **165**, 145-150.
- Smith, W. J. 1977. *The Behavior of Communicating*. Cambridge, Mass.: Harvard University Press.
- Smith, W. J., Pawlukiewicz, J. & Smith, S. T. 1978. Kinds of activities correlated with singing patterns in the yellow-throated vireo. *Anim. Behav.*, **26**, 862-884.
- Sossinka, R. & Bohner, J. 1980. Song types in the zebra finch *Poephila guttata castanotis*. *Z. Tierpsychol.*, **53**, 123-132.
- Thielcke, G. & Thielcke, H. 1970. Die sozialen Funktionen verschiedener Gesangsformen des Sonnenvogels (*Leiothrix lutea*). *Z. Tierpsychol.*, **27**, 177-185.
- Wiley, R. H. 1976. Communication and spatial relationships in a colony of common grackles. *Anim. Behav.*, **24**, 570-584.
- Wiley, R. H. 1977. Census 33. *Am. Birds*, **31**, 41.
- Wiley, R. H. & Richards, D. G. 1983. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: *Acoustic Communication in Birds*. Vol. 1. *Production, Perception and Design Features of Sounds*. (Ed. by D. E. Kroodsma & E. H. Miller), pp. 131-181. New York: Academic Press.
- Yasukawa, K. 1978. Aggressive tendencies and levels of a graded display: factor analysis of response to song playback in the redwinged blackbird (*Agelaius phoeniceus*). *Behav. Biol.*, **23**, 446-459.
- Yasukawa, K. 1981. Song repertoires in the red-winged blackbird (*Agelaius phoeniceus*): a test of the Beau Geste hypothesis. *Anim. Behav.*, **29**, 114-125.
- Yasukawa, K., Blank, J. L. & Patterson, C. B. 1980. Song repertoires and sexual selection in the redwinged blackbird (*Agelaius phoeniceus*). *Behav. Ecol. Sociobiol.*, **7**, 233-238.

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