COMMUNICATION WITH SHARED SONG THEMES IN TUFTED TITMICE

DONNA J. SCHROEDER[1] AND R. HAVEN WILEY

Curriculum in Ecology and Department of Biology, University of North Carolina,
Chapel Hill, North Carolina 27514 USA

ABSTRACT.—Individual Tufted Titmice (*Parus bicolor*) sing 8–12 song themes. Most or all themes in an individual's repertoire are shared with neighbors, although slight but consistent differences often separate neighbors' performances of a particular theme. Birds first begin to sing recognizable themes while still juveniles on their parents' territory. Established territorial residents can modify their themes slightly from year to year to achieve a closer similarity to neighbors' themes. Neighbors matched themes during concurrent singing more often than would be expected at random. Furthermore, titmouse tended to begin singing in response to a neighbor, particularly if it could match the theme. Playbacks of recorded song also evoked matched singing in response. Playbacks of strangers' songs, recorded 3 km away, evoked a less intense response than did playbacks of neighbor's songs, but an attempt to demonstrate individual recognition of a neighbor's shared themes failed. Evidently, the advantages of coordinated singing by opponents with shared themes outweigh any advantages of individual recognition of neighbors with distinctive songs. *Received 12 April 1982, accepted 15 October 1982.*

IN many species of birds, neighboring individuals sing nearly identical themes (song types). In some species, individuals share different sets of themes with each neighbor. In others, neighboring individuals share all themes in their repertoires. The effects of such sharing on communication and, consequently, the evolutionary advantages of shared themes have remained elusive (see Krebs and Kroodsma 1980).

Shared themes could facilitate recognition of conspecifics from the locally resident population. Cardinals (*Cardinalis cardinalis*) (Lemon 1967) and White-crowned Sparrows (*Zonotrichia leucophrys*) (Milligan and Verner 1971) respond more intensely to playbacks of themes from the local population than to themes of different populations. Shared themes might, on the other hand, increase the difficulty of individual recognition by neighbors. Individual recognition could be achieved more effectively if each individual sang a single, unique theme. Shared themes do not eliminate the possibility of individual recognition, however, because the fine structure and timing of songs might still differ sufficiently to allow identification of neighbors and mates.

When individuals sing more than one theme, possibilities for matching themes in countersinging suggest additional effects of shared themes. Singing a matched theme in some cases seems to represent a stronger response to a neighbor than singing an unmatched theme (Dixon 1969). Cardinals, for instance, match more often in countersinging when, by other measures, the intensity of interaction is greater (Lemon 1968a). Matching might also enhance the repulsion of singing intruders (Krebs et al. 1978).

Whether a neighbor or an intruder is the intended recipient, matching serves at least to indicate which individual has the singer's attention (Armstrong 1973) and might enhance the listener's ability to judge the singer's position (Krebs et al. 1981). If matching is important in effective communication with neighbors, themes that can be matched by neighbors might elicit countersinging more frequently than themes that cannot be matched, and the mean duration of bouts of matched countersinging might be greater than that of bouts of unmatched countersinging.

These possible consequences of sharing and matching themes are not mutually exclusive. Each requires evaluation in its own right. Tufted Titmice (*Parus bicolor*) are good subjects for
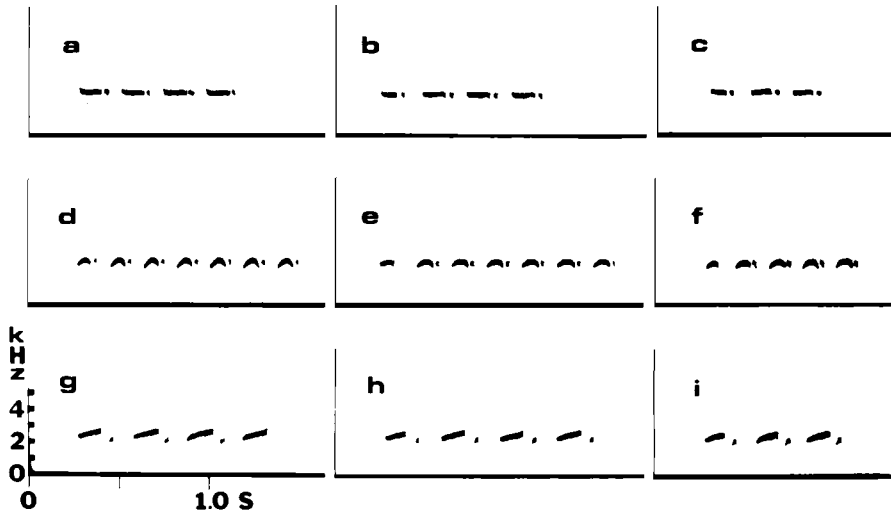
Fig. 1.   Sound spectrograms of themes at site 1: PN (a–c), PS (d–f), and PT (g–i). Birds recorded from left to right for each theme: R, C/R, and C.

such studies. They sing a moderate number of themes. Themes are frequently shared with neighbors, and countersinging neighbors often match themes. In order to investigate sharing and matching of themes in communication by titmice, we examined the structure and delivery of song, the amount of sharing in a local population, and the use of shared themes by neighbors, as revealed by normative studies and experimental playbacks of tape-recorded songs.

METHODS

Study site.—The main study area (site 1), located 4 km southeast of Chapel Hill, North Carolina, includes 40 ha of nearly mature forest. Dominant canopy trees are oaks (*Quercus stellata* and *Q. alba*) and hickory (*Carya* spp.) (see Wiley 1977). Sixteen hectares of the research site are gridded with stakes spaced at 25 m. For this study, 21 feeders were distributed throughout the plot. The resident titmice were marked individually with colored bands and small leg streamers. A second area (site 2), 3 km northwest of site 1 in a residential area, provided a location for recording non-neighboring titmice.

Recording and identification of themes.—The vocalizations of resident titmice were recorded with a Uher 4000 Report L tape recorder at 19 cm/s and a Sennheiser MKH 815 directional microphone. Sound spectrograms of the repertoire of each male were prepared with a Kay 7029A Sound Spectrograph (80–8,000 Hz frequency range, resolution 300 Hz). For the

analyses, examples of each theme were selected from different bouts on the same day or from different days. Study of the spectrograms and practice in the field eventually allowed identification of themes by ear.

Normative studies.—To document normal use of themes, we obtained timed samples of singing by five resident males on contiguous territories from January to early July 1976. In each month two timed samples were obtained for each focal animal. Each morning one focal male was followed for 3 h, beginning at first light, 30 min before sunrise. The disappearance of two focal males, O and B/R, in February and April, respectively, made it necessary to add a neighboring titmouse, R, to the study in April. Males C and C/R were present throughout the study.

For timed samples, the following information was recorded every 30 s on a signal from an interval timer: location of the focal bird; theme sung, if any; proximity of its mate, if known; identity of the nearest singing male, if known; and theme of the nearest singing male. If the bird was not in view but was singing, its location was estimated within 50 m. Agonistic interactions were noted whenever they occurred.

In addition to the timed samples two mornings were spent tape-recording each male in each month from March through June. During these periods, notes were dictated on the locations and behavior of the focal bird.

Experimental playbacks of song.—Tapes for playback were prepared with a constant peak volume on a Tandberg Series 15 tape recorder. All of the experimental tapes had 12 song/min, the modal value for
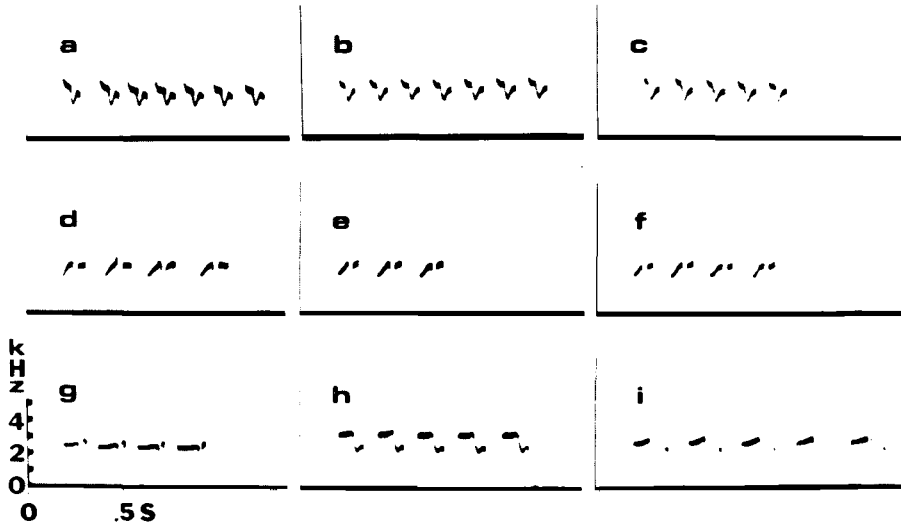
Fig. 2. Sound spectrograms of themes at site 1: CH (a–c), ST (d–f), DE (g), MP (h), and CP (i). Birds recorded: R (a, g–i), C/R (b, e), C (c, f), and B/R (d).

song rates in the population at site 1. Each playback consisted of a 4-min bout of song, roughly normal for Tufted Titmice.

For playbacks we employed an Amplivox S-610 amplifier-speaker placed 2–2.5 m above ground and covered with a piece of olive-colored burlap for camouflage. The amplifier was fed by a Uher tape recorder operated 15 m away. The volume, at a standard setting for each playback, approximated a normal titmouse at full volume. All experiments were conducted between 0900 and 1200 and between 25 May and 3 August. Unless otherwise noted, the speaker was placed less than 25 m inside the subject's territorial boundary.

From 10 min before until at least 10 min after each playback, all themes sung by the subject or his neighbors were noted, and the distances of the birds from the speaker were estimated. If birds were active in the vicinity of the speaker at the end of the playback, observations continued until the responding birds were 25 m away and either had stopped singing or were responding to neighbors away from the amplifier location. When there was no detectable response to the playback, observations continued until 10 min after playback. When the subject's rate of singing had decreased for at least 1 min, a second theme was sometimes played.

One series of playbacks presented themes common to all members of the population (themes PN, PS, PT, and CH; see below). Each of these themes made up at least 10% of the singing of each resident male. In case there were slight individual differences in the themes, these playbacks presented themes of neigh-

boring birds played near the appropriate boundaries. These experiments consisted of 6–8 presentations to each of three subjects (males C, C/R, and R) ($n = 23$).

Five themes, recorded in response to playbacks at site 2, were presented to males C, C/R, and R. Playbacks of neighbors' and strangers' themes were presented as matched pairs ($n = 23$) in randomized order on different days within the same week for each subject. In addition, playbacks of a neighbor's theme near the correct boundary and near the opposite boundary of the subject's territory were presented as matched pairs ($n = 11$) in randomized order on the same day or succeeding days for each subject.

RESULTS

Structure and variability of song.—Songs of Tufted Titmice ordinarily consist of repetitions of similar whistled syllables, each composed of one or two notes (Figs. 1–3). No three-note syllables occurred in the repertoires at site 1. Songs fall into distinct patterns, called themes, on the basis of the acoustic structure of the syllables.

The first syllable in a song is the shortest, and the first interval between syllables is usually the longest, so that syllables start at regular intervals. Songs with short syllables commonly also have short intervals between syllables. In songs with two-note syllables, the first and last

Fig. 3.   Sound spectrograms of themes at site 1: PK (a–d), RB (e–g), BR (h), PL (i), KD (j–l), WP (m), and SP (n–p). Birds recorded: B/R (a, g, h, k, m), C/R (b, e, l, n), C (c, f, p), B/O (d), R (i, j) and O (o).

syllables are sometimes truncated by omitting the second note. Such deletions rarely occur in the middle of a song.

Syllable number varies from one to nine in the songs recorded at site 1. Themes with syllables of shorter duration usually have more syllables than themes with syllables of longer duration, but there is variation in syllable number for any given theme.

In addition to this variation in the number of syllables, there is some variation in the timing of syllables and intervals in the performance of a theme by any one individual. Some themes were more variable than others. For instance, the duration of the last interval of male R's theme PN varied from 0.07 to 0.08 s, while the equivalent interval for theme PL varied from 0.05 to 0.12 s.

Sharing of themes by neighbors and mates.— Males in the study sang 9 or 10 themes each (Table 1). Six themes were shared by all of the birds in the study. Four of these themes (PN, PS, PT, and CH), used frequently by all members of the population, accounted for at least 75% of each individual's songs. Three neighbors, C/R, C, and O, shared all themes in their repertoires. R had some unique themes, and B/R had distinctive variants of themes present

in his neighbors' repertoires. For instance, B/R's theme WP resembled SP and his theme BR resembled RB.

All near neighbors of the site 1 population also shared the frequently used themes, PN, PS, PT and CH, and the less frequent KD. Less frequently used themes, except PL and CP in male R's repertoire, were heard from at least

TABLE 1.   Repertoires of titmice at site 1.

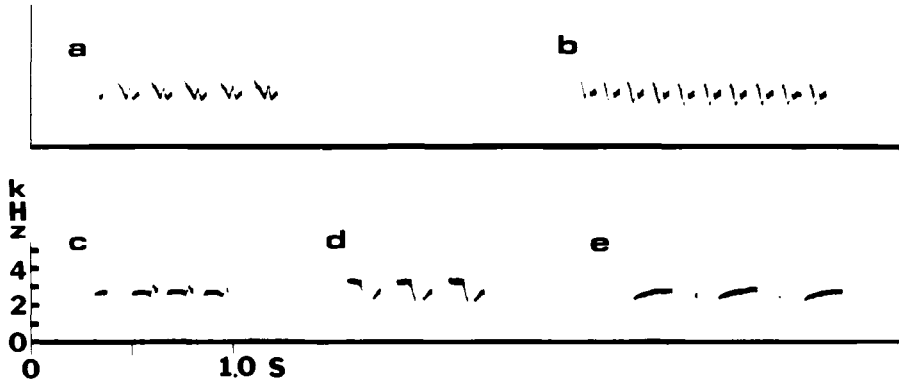| Theme	Bird				
	C/R	C	O	B/R	R
PN	+	+	+	+	+
PS	+	+	+	+	+
PT	+	+	+	+	+
CH	+	+	+	+	+
ST	+	+	+	+	
MP				+	+
DE					+
CP					+
KD	+	+	+	+	+
SP	+	+	+		+
WP[a]				+	
RB	+	+	+		
BR[a]				+	
PK	+	+	+	+	
PL					+

[a] Variant of the preceding theme.

Fig. 4. Themes from site 2 used for playback experiments with strangers' songs.

some neighbors of the site 1 birds. Five themes recorded from a population 3 km away (site 2) were unlike those of themes from site 1 (Fig. 4), although three sounded rather similar to site 1 songs.

Female titmice sang much less than males. Their song bouts were frequently short and usually not sung in proximity to the male. Although we could not determine the females' repertoires completely, most females used themes in the repertoires of their mates. G/O, mate of male C/R, had at least three themes, PS, PT, and CH, the latter used most frequently. Male C's mate, C/O, sang at least ST and PS, although at a higher pitch than those of C. We never noted a female singing PN, though it was the most frequently used song in the repertoires of most males. After his mate disappeared in January 1976, male R nested successfully with a new mate who sang a monotonous three-syllable song that did not match any theme in R's repertoire. This bird sang far more frequently than any other female.

Individual variation in shared themes.—Individuals often differed slightly but consistently in the performance of shared themes. Differences included the frequency, duration (Fig. 5) and number of syllables (Fig. 6), and the duration of intervals between syllables. In addition, deletions of some parts of the introductory or terminal syllables for particular themes were characteristic of certain birds.

The shared songs of B/R were especially distinctive. He was the only male new to the site 1 population in 1976. Many of his songs were irregular in pitch, which gave the songs a quavering quality, much like the songs of young birds in their first summer. This quavering was particularly evident when he sang WP (Fig. 3m), his variant of the SP theme. He rarely used more than one syllable for performances of this song, while neighbors typically used two in SP. B/R also reversed the syllable parts used in one of the less common themes, singing BR instead of the neighborhood's traditional RB (Fig. 3).

R had several distinctive renditions of shared themes, but the distinguishing characteristics were subtler than in the songs of B/R. R sang theme CH with a particularly long first interval, easily detected in the field. He ordinarily used more than two syllables in his performances of the KD theme, while neighbors sang one or two syllables. R's version of the PS theme contained six syllables more frequently than did the song of neighbors. Also, his first syllable for this theme had two parts, and neighbors had only one note, or a second note too low in volume to register on the sound spectrograph. R also dropped the terminal note of the PT theme more often than other birds.

C customarily sang the PN theme with exactly three syllables while neighbors were variable. C was also more consistent than were others in singing PT with three syllables and KD with exactly two.

C/R and O had fewer distinctive characteristics in the delivery of their shared themes. They had the most boundary in common with other population members. For the frequently used themes, PN, PT, PS, and CH, the mean syllable number of C/R fell between the mean syllable numbers of his northern neighbor, R, and his southern neighbor, C.
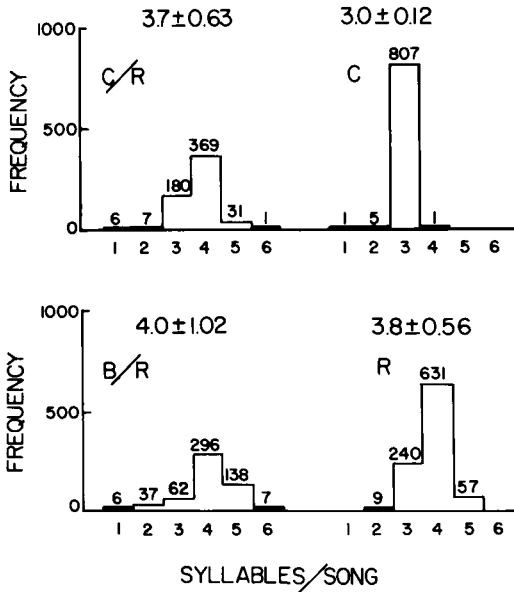
Fig. 5. Distributions of syllables/song in four males' versions of the PN theme. Above each distribution is the mean ± SD. In pairwise comparisons, the distributions differ from each other significantly (χ^2 tests, $P < 0.001$), except those for males C/R and R.
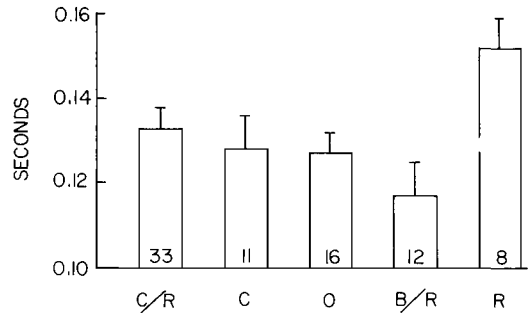

Fig. 6. Durations of the first syllables of theme PN in the repertoires of five males. Bars represent means; vertical lines, SD; and numbers inside bars, n. In pairwise comparisons, the means differ from each other significantly (t-tests, $P < 0.01$), except the means for males C/R and C and those for males C and O.

Singing rates.—Singing rates varied widely, from sporadic single songs to rates of 35/min. There were no significant differences between birds in rate of singing. Birds frequently sang rapidly during countersinging. Lower rates occurred during foraging. High rates were most frequent from March through May.

Rate tended to fluctuate during bouts. In one 20-min bout, male C's rate of singing theme PN varied from 22/min to 4/min. Seldom did a focal animal sing at a constant rate for more than 2 min.

Song acquisition.—Learning of themes begins in the first summer. Themes of parents and neighbors are recognizable in the repertoires of young titmice within 4 weeks of fledging. One tape in June 1976 had 10 recognizable themes of the site 1 population from fledglings in the same flock.

The songs of fledglings are much less constant in pitch and in the duration of intervals and syllables than are songs of adults. The young seem to have particular difficulty copying longer syllables requiring sustained pitch,

like the syllables of SP. Young birds also produce some whistling that is difficult to classify.

Syllable durations in an individual's song can change slightly, even after establishment of a territory, to yield a better match with neighbors. Theme PS of male C provides evidence of this change. In 1975, the first syllable of this song had a mean duration of 0.067 s, while in 1976 the mean was 0.088 s. The latter falls between the durations of the equivalent syllables for males R and C/R. The 1975 measurements did not overlap with those of 1976 ($t = 4.89$, $P < 0.001$). C/R showed no significant change in the equivalent syllable. Only one other of 13 comparisons showed a significant change. The first syllable of C/R's theme CH had a mean duration of 0.093 s in 1975 and 0.083 s in 1976 ($t = 4.32, P < 0.01$). The latter is similar to that of male C, 0.083 s.

Vocal behavior at boundaries and responses to playback.—On close approach at boundaries, males switch from whistled song to calls. At these times females are often present and calling. In one typical encounter, male R and a neighbor, while singing, approached each other from more than 100 m apart. Each was accompanied by his mate. When they were about 10 m apart, song stopped and calling began. They approached to about 4 m facing each other. The females perched within 25 cm of their mates. All participants were calling. After male R made one flight to within a few cm of the neighbor, the two pairs began backing slowly

TABLE 2. Tendency to match during concurrent song.

Bird	Percentage of time matching		Minutes of concurrent song in the sample
	Observed	Expected[a]	
C/R	54	22	132.5
C	78	33	47.5
O	68	41	20.0
B/R	68	23	61.0
R	53	22	21.5
Mean (SD)	64.2 (10.6)**[b]	28.2 (8.5)	

[a] Expected values: $\Sigma f_i n_i c$, where f_i = the proportion of time the focal animal sang theme i, n_i = the proportion of time any of the focal animal's neighbors sang theme i, and c = the minutes of concurrent singing by focal animal and neighbors. Data for determining f_i and n_i excluded time spent in concurrent song.
[b] **t = 9.42, df = 4, $P < 0.005$ (with arc-sine transformation of proportions).

TABLE 3. Tendency to match bouts of concurrent song.

Bird	Percentage of bouts matching		Onsets of concurrent song
	Observed	Expected[a]	
C/R	67	19	63
C	65	21	40
O	71	33	14
B/R	61	21	36
R	50	18	8
Mean (SD)	62.8 (8.5)**[b]	22.4 (6.1)	

[a] Expected values: $\Sigma f_i n_i b$, where f_i = the proportion of the focal animal's bouts (song onsets) that were theme i, n_i = the proportion of time any of the focal animal's neighbors sang theme i, and b = the total number of song onsets in which there was concurrent song.
[b] **t = 15.22, df = 4, $P < 0.005$ (with arc-sine transformation of proportions).

away from each other, still calling. At approximately 20 m, they began to sing again and continued to move apart. In one boundary dispute and in one instance of intrusion, both especially intense encounters, rapid switching of themes accompanied calling.

Playbacks elicited three kinds of response. In 56% of the tests that evoked some response, behavior was similar to that in boundary encounters. The responding bird sang while approaching the amplifier to within 25 m. His mate was frequently present. Ordinarily, once they had approached within 25 m, singing birds moved closer to the amplifier, but in one instance a bird moved away from the playback toward the center of an adjacent territory.

After approaching to within 1–8 m of the amplifier, the responding male often vibrated its wings rapidly as it crouched with body horizontal and crest flattened. This display, which resembled the display used in courtship feeding and nest approach, was also used by resident males before chasing intruders. It was typically accompanied by a high-pitched twitter, but in some instances the male sang during its performance. Aggressive calls and alarm notes were also frequent in responses to playback. The male often sang and flew over the speaker while the female gave scolding calls.

In 13% of the tests receiving some response, singing occurred without approach to within 25 m. In one typical instance a bird at some distance switched to match the playback after 45 s. The bird moved closer but did not come within a 25-m radius of the amplifier.

In the remaining 31% of the tests to which there was some response the resident male approached within sight of the amplifier (about 5–8 m) without singing. After arrival, calls, countersinging, and wing quivering began. In four instances no countersinging occurred, and in three instances singing started only after playback stopped.

After playbacks in which birds approached closely, the subjects stayed in the area for a varible amount of time. They were rarely within a 15-m radius of the amplifier for more than 5 min and often sang as they moved away from the site. In a few instances they moved away and then returned again to sing and call in the area near the speaker.

Coordination and matching of song.—Songs of two countersinging birds seldom overlapped. Avoidance of overlap was most striking in playbacks. Overlap sometimes occurred at the beginning of a response, but when the responding titmouse had sung for a few seconds it either alternated with the playback or sang two songs between the playback songs. In at least one instance of 2:1 response to theme CH, the responder's songs were much shorter than most songs of this theme.

Titmice frequently matched the theme sung by a neighbor. On 11 occasions in the timed samples, three birds sang the same theme concurrently. When matching was not possible,

TABLE 4. The effect of singing by neighbors on the probability of singing by the focal animal (March–May).

Bird	Percentage of time focal animal sang concurrently with neighbors		Minutes in sample
	Observed	Expected	
C/R	8.4	5.8	1,080
C	3.6	2.2	1,080
O	1.7	0.8	360
B/R	5.0	4.4	900
R	1.7	1.3	360
Mean (SD)	4.1 (2.8)*[a]	2.9 (2.1)	

[a] $*t = 4.456$, df = 4, $P < 0.01$ (with arc-sine transformation of proportions).

TABLE 5. Tendencies to sing when neighbors sing matchable and unmatchable song.[a]

Bird	Percentage of time singing		Minutes of neighbors singing in sample
	Neighbors singing matchable songs	Neighbors singing unmatchable songs	
C/R	24	4	489.5
C	24	1	214
O	8	0	304
R	18	4	539
Mean (SD)	18.5 (7.5)**[b]	2.3 (2.1)	

[a] B/R, excluded from this analysis, could match all themes sung by neighbors.
[b] $**t = 8.46$, df = 3, $P < 0.01$ (with arc-sine transformation of proportions).

birds were likely to use the closest approximation in their repertoires. Thus, male R's themes MP or CP elicited themes PT or SP from neighbors. This tendency to match differed significantly from random and held for all birds in the study for both the percentage of time (Table 2) and of bouts (Table 3).

Successive matches are usually separated by silences. The most dramatic examples of matching, when neighbors singing the same theme matched immediately after one had switched to a different theme, occurred only five times in the timed samples. In a more typical example of matching, male C/R sang theme PT for 0.5 min before R matched. They countersang for 1.5 min before falling silent. R began theme PN 1.5 min later. After 2 min, C/R matched briefly before falling silent again. Thus, they had matched two different themes within 6 min.

Singing by a titmouse increased the probability of singing by his neighbors (Table 4). Timed samples showed that this effect was especially true for themes that could be matched (Table 5). Most bouts of one theme were preceded and followed by a period of silence. Thus, the reduced singing in response to themes that could not be matched was due to a failure of titmice to start singing in response to themes not in their repertoires rather than to a cessation of song following a neighbor's switch to an unmatchable theme. When one of two countersinging neighbors switched to an unshared song theme, a rare occurrence, the other continued singing without matching.

Playback experiments confirmed that song selection is not random (Table 6). In response

to 4 min of one theme, the subject usually matched the playback if it had the same theme in its repertoire. Subjects sometimes sang more than one theme in response to playback. Typical patterns included singing a few songs of one theme before switching to a matching theme or singing a matching theme for most of the playback period but switching to another before playback ceased. In about half the tests, though, the subjects sang only one theme during the playback.

When the playback theme could not be matched, the most similar theme in the individual's repertoire was ordinarily used. For instance, playback of C/R's theme ST was "matched" by theme DE from male R. This "match" was noticed in the field several times, as well as during experiments. Theme SK from site 2 elicited theme SP with syllables of similar duration from site 1 (Figs. 4e and 3n–p). Theme CV of site 2 was "matched" with CH from site 1 (Figs. 4a and 2a–c), two themes alike in having short syllables and large intrasyllable pitch changes.

Some preliminary playbacks of a series of 2-min segments of song also demonstrated the birds' tendency to match. Ordinarily only the theme playing during the bird's first response was matched. When the playback subsequently switched themes, the subject continued its initial theme. In just two instances did a switch to match occur. Bouts of song are normally longer than 2 min.

The subject's neighbors, if they responded to playback, also tended to match. In four instances when there was a discrepancy in theme,

TABLE 6. Matching in response to playbacks.

| Bird | Match[a] | | No match | | χ^{2c} | P |
	Observed	Expected[b]	Observed	Expected		
C/R	18	3.59	4	18.41	64.3	<0.001
C	17	3.34	5	18.66	61.2	<0.001
R	16	3.51	6	18.49	48.7	<0.001

[a] If a subject sang more than one theme during playback, matching was considered to have occurred when the majority of the subject's songs were the same theme as the playback. Playbacks that could not be matched or that received no response were excluded.

[b] Expected values for matching: $\Sigma\, b_i p_i$, where b_i = the proportion of bouts of theme i from normative data on the focal animal's repertoire and p_i = the number of playbacks of theme i.

[c] Corrected for continuity.

the neighbor matched the resident and not the playback.

For all birds, the mean length of bouts that were matched was greater than bouts that were not matched in both normative and experimental situations. Much of this difference, however, was due to some exceptionally long matched bouts.

Although themes that could be matched elicited more song from neighbors than did themes that could not be matched, similarity of repertoires was not consistently related to the amount of countersinging. For instance, male C/R countersang less with C, who shared all his themes, than with R, who did not. Every pair of males shared six themes, an adequate selection with which to stimulate a neighbor's response.

Responses to neighbors' and strangers' themes.— Paired comparisons between responses to strangers' songs from site 2 and neighbor's songs indicated that titmice responded to strangers more slowly and less reliably than to neighbors. In 23 experiments, only 10 responses of the three kinds described above were obtained from strangers' themes, while 21 responses were obtained from neighbors' (χ^2 = 12.0, n = 46, P < 0.01).

There were no significant differences in the 11 matched pairs of playbacks of neighbor's themes at correct and wrong boundaries. In seven of the pairs the response at the wrong boundary was greater.

DISCUSSION

Acquisition of shared themes.—Neighboring Tufted Titmice share most of the themes in their repertoires. How this sharing develops is not clear. Our evidence suggests that learning of themes begins before dispersal from the family flock. Males might nevertheless change their themes after dispersal, in order to match neighbors. Regardless of how shared themes develop initially, the perfecting of shared themes continues after a male has established a territory. Male B/R was probably a first-year male, as he first took a territory in 1976. B/R's song was more regular than the song of juveniles, but he definitely had the same difficulty with notes requiring sustained pitch. Slight changes in themes also occur later in life. In two instances, small changes in an individual's song between years increased the match with neighbors' themes, a phenomenon well documented for New Zealand Saddlebacks (*Creadion carunculatus*) (Jenkins 1977).

Vocalizations in the interactions of neighbors.— For Tufted Titmice, song is an important feature of the interactions of neighbors at a distance. Their practice of alternating songs, so that they ordinarily do not overlap, is a clear indication that singing neighbors pay attention to each other. Response to playback demonstrated this behavior especially clearly. Responding birds sometimes even inserted two songs between playback songs without overlap.

Tufted Titmice thus avoid acoustical interference while countersinging with neighbors. White-throated Sparrows (*Zonotrichia albicollis*) and European Blackbirds (*Turdus merula*) also avoid intraspecific acoustic interference (Wasserman 1977, Todt 1981). Avoidance of interference could be important for species whose songs are audible for long distances. Other species, however, including Black-Crested Titmice (*Parus atricristatus*), apparently do not synchronize their songs in response to playbacks (Lemon 1968b).

In contrast to the use of song in interactions of neighbors at a distance, calling was char-

acteristic of close-range encounters. Rapid switching of song themes occurred twice in particularly intense encounters. Rapid switching of themes also occurs in Cardinals (Lemon 1968a) and Plain Titmice (*Parus inornatus*) (Dixon 1969) in intense exchanges with conspecific males. Most of our playback experiments failed to evoke such rapid switching, perhaps because of the lack of visual stimulus usually present in intense encounters. The episode in which four birds responded to playback with eight themes suggests that seeing the opponent is important in stimulating rapid switching.

Individual recognition.—Shared themes presumably make individual recognition of territorial neighbors more difficult. Nevertheless, they do not eliminate all possibilities for individual recognition. Theme choices might be characteristic for an individual, or the shared themes of each bird might differ sufficiently to permit recognition. Our examination of the shared themes of Tufted Titmice indicates that there are differences that could allow discrimination between birds. Presumably, titmice would be more adept than humans at recognition of the individually identifying characteristics of shared themes. Playbacks of neighbors' themes on correct and incorrect boundaries, however, failed to demonstrate individual recognition of territorial neighbors. Established neighbors, of course, could be identified in almost all circumstances by their locations alone, as titmice very rarely sing outside their territories.

Shared themes in communication between neighbors.—Our results provide several indications that sharing and matching of themes have a role in communication between neighboring males. This evidence includes the prevalence and exactness of theme sharing, the strong tendency to match, and the effect of matching in increasing song.

Tufted Titmice, like Plain Titmice (Dixon 1969), share a high proportion of their themes with neighbors, and they are more likely to countersing when matching is possible. In this respect, titmice resemble Chaffinches (*Fringilla coelebs*) (Hinde 1958), Hill Mynahs (*Gracula religiosa*) (Bertram 1970), and Cardinals (Lemon 1968a). Titmice also use shared themes more frequently than themes that are not shared, a tendency found also in Rock Wrens (*Salpinctes*

obsoletus) (Kroodsma 1975), Rufous-collared Sparrows (*Zonotrichia capensis*) (Nottebohm 1969), and Hill Mynahs (Bertram 1970). Nevertheless, sharing and matching have no simple effect on countersinging. The amount of sharing, for instance, did not correlate with the frequency of countersinging between neighbors. In addition, matching does not vary in parallel with singing rates. Cardinals match less during successive playbacks, although song rate remains constant. In Cardinals the proportion of bouts that are matched increases with the intensity of the interaction (Lemon 1968a).

Species in which individuals have multiple shared themes, like Tufted Titmice, tend to be permanent residents with slow turnover and therefore longer association with neighbors (Lemon 1968a). Sharing and matching, which permits coordination of songs among territorial neighbors, is likely to be advantageous, particularly for neighbors with long associations. The characteristic pattern of short matched bouts separated by pauses suggests that multiple shared themes could, for instance, allow neighbors to judge each other's positions (Krebs et al. 1981). For Tufted Titmice, the advantages of communication among neighbors by matching of shared themes evidently outweigh any advantages of recognition by individually distinctive themes.

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The **Hawk Mountain Sanctuary Association** is accepting applications for its fifth annual award for raptor research. To apply for the $500 award, students should submit a description of their research program, a curriculum vita, and two letters of recommendation by **30 September 1983**, to **James J. Brett, Curator, Hawk Mountain Sanctuary, Route 2, Kempton, Pennsylvania 19529.** The Association's Board of Directors will make a final decision late in 1983. Only students enrolled in a degree-granting institution are eligible. Both undergraduate and graduate students are invited to apply. The award will be granted on the basis of a project's potential to improve understanding of raptor biology and its ultimate relevance to conservation of North American raptor populations.

The **North American Bluebird Society** provides grants in aid for ornithological research directed toward cavity-nesting species of North America with emphasis on the genus *Sialia*. Presently three annual grants totalling $3,000 are available consisting of varying amounts; generally stipends of $1,000 are awarded:

Student Research Grant—available to full-time college or university students for a suitable research project focused on a North American cavity-nesting species; **Bluebird Research Grant**—available to student, professional or individual researchers for a suitable research project focused on any of the three species of bluebird from the genus *Sialia*; and **General Research Grant**—available to student, professional, and individual researchers for a suitable research project focused on a North American cavity-nesting species. Further guidelines and application forms are available from **Theodore W. Gutzke, Research Committee Chairman, P.O. Box 66, Upham, North Dakota 58789.** Completed applications must be received by **31 January 1984**; decisions will be announced by 15 March 1984.

The **6ᵗʰ International Workshop on the Ecology of Shorebirds,** under the auspices of the International Waterfowl Research Bureau, will be held at University College, Cardiff, on **12–16 September 1983.** The emphasis will be upon studies of wading birds during the breeding season and the program will include speakers from Britain, Canada, Holland, Israel, Norway, South Africa, and the U.S.A. Other aspects of shorebird ecology will also be included. Further details and booking forms may be obtained from **Dr. P. N. Ferns, Zoology Department, University College, Cardiff, CF1 1XL, U.K.,** or **Dr. J. D. Goss-Custard, Furzebrook Research Station, Wareham, Dorset, BH2O 5AS, U.K.**