

# RECOGNITION OF NEIGHBORS BY ASSOCIATIVE LEARNING IN RUFOUS-SIDED TOWHEES

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**ABSTRACT.**—Previous demonstrations of neighbor vs. non-neighbor discrimination in territorial male passerines have not permitted separation of habituation from associative learning as the basis of the response differences. A few male Rufous-sided Towhees (*Pipilo erythrophthalmus*) sing unusual songs resembling those of Carolina Wrens (*Thryothorus ludovicianus*), yet are able to defend territories. Tape recordings of the unusual songs were played back to the neighbors of an imitator and to non-neighboring birds. The neighbors responded strongly and the non-neighbors responded very weakly. This stronger response by neighbors to an unusual song demonstrates the importance of associative learning in individual recognition. *Received 23 June 1978, accepted 23 April 1979.*

EXPERIMENTS with playbacks of tape recordings have demonstrated discrimination between the songs of neighbors and non-neighbors by a number of species of passerine birds (Weeden and Falls 1959, Emlen 1971, Goldman 1973, Brooks and Falls 1975, Falls and Brooks 1975, Kroodsma 1976, Wiley and Wiley 1977, Wunderle 1978). Two studies (Wiley and Wiley 1977, Falls and Brooks 1975) demonstrate that territorial birds can also associate the songs of each neighbor with the location in which that neighbor usually sings. In all cases, the evidence for recognition consists of a less intense response of territorial birds to the songs of neighbors in the usual location in comparison to songs of non-neighbors. Such differences could arise from habituation to familiar sounds, and thus they fail to establish that associative learning contributes to individual recognition by neighboring territorial birds (Wiley and Wiley 1977, Beer 1970).

Songs by male passerine birds usually serve to attract mates and to defend territories, and thus incorporate species-specific characteristics (Marler 1957). Occasionally, however, individuals of species not normally considered mimics are heard singing the song of another species. Natural mistakes in song learning have been reported for a number of passerines (see Tasker 1955, Lanyon 1957, Baptista 1972, James 1976, Eberhardt and Baptista 1977), including Rufous-sided Towhees (*Pipilo erythrophthalmus*) (Borror 1961, 1977). In many cases the imitators are both taxonomically and ecologically unlike the models (James 1976, Baptista 1972, Borror 1977). These songs may be disadvantageous to the bird that sings them for territorial defense, yet their distinctiveness also makes them potentially useful for individual recognition. Occasional Rufous-sided Towhees singing imitations of songs of Carolina Wrens (*Thryothorus ludovicianus*) are capable of defending territories and attracting mates. In this paper I present evidence that neighboring conspecifics learn to associate these imitations, to which towhees would normally give little response, with a conspecific rival male. The conspecifics on adjacent territories expand their recognition repertoires to include the atypical songs of their neighbor.

In these experiments the evidence for individual recognition consists of a *stronger*

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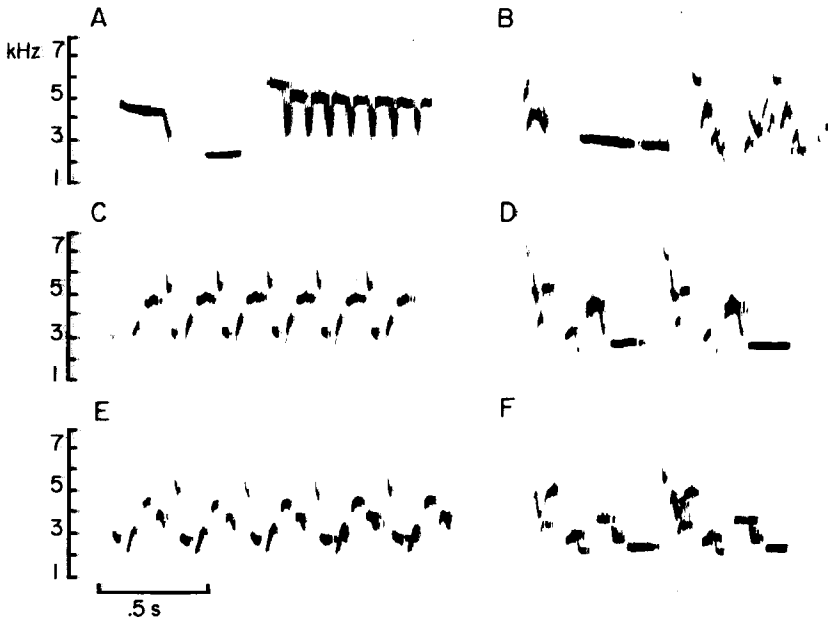


Fig. 1. Spectrograms of songs by Rufous-sided Towhees and Carolina Wrens: A, example of a normal towhee song; B, mixed theme from Bird 3; C and D, examples of wren imitations by towhees; E and F, examples of songs recorded from Carolina Wrens.

response to an unusual song by conspecifics previously exposed to that song than by conspecifics not familiar with the song. This result rules out habituation as a mechanism and requires associative learning. I use the term associative learning to include the possibility of either classical or operant conditioning; discrimination between the two requires a study of the learning process itself (see Manning 1972, Chapt. 8).

#### METHODS

*Study areas.*—Recording and playback were conducted in the North Carolina Botanical Garden (NCBG), the University of North Carolina campus, and residential areas, all in Chapel Hill, North Carolina. In the research area of the NCBG, the dominant canopy trees are post oak (*Quercus stellata*), white oak (*Q. alba*), and hickories (*Carya spp.*). For a more detailed description of the vegetation and avifauna on two plots near the study areas see Wiley (1977) and Hall and Wiley (1978a, b).

*Song description.*—Of approximately 50 male towhees tape recorded during 1976 and 1977, three had portions of their song that closely resembled the song of the Carolina Wren; the birds were separated by the distances of about 10 km. The song of a towhee typically consists of an introduction of 1–4 simple syllables followed by a trill (Fig. 1A); most individuals have repertoires of 3–8 different songs. There is a great deal of individual variation in towhee song and an absence of local dialects in populations in the eastern United States (Ewert 1978, Richards 1978, see Kroodsma 1971, concerning possible dialects in western populations). There is some geographical variation over distances of hundreds of kilometers (Borror 1975), but this variation is not a significant factor in the study area compared to the large variation among individuals.

Bird 1, recorded in late May 1976, had a repertoire of 8 themes, 7 of which contained repetitions of 1 or more syllables typical of Carolina Wrens (Fig. 1); 1 was a typical but faint towhee song. Bird 2, recorded in late June 1976, used two wren syllables, sometimes alone, and sometimes as the introduction to a normal towhee trill. These recording dates were in the middle of the breeding season or later. I recorded and observed Bird 3 during the entire breeding season, from mid-March 1977 through mid-July, when singing ceased. Bird 3's repertoire consisted of 3 themes: 1 normal towhee song, 1 song

composed only of wren syllables, and a mixed song containing 2–3 towhee introductory syllables followed by wren syllables (Fig. 1B). The bird used the mixed theme about 75% of the time. It often countersang with neighboring territorial males, who responded to the mixed theme with normal songs.

All three towhees with wren imitations had apparently normal territorial behavior and defended territories. Bird 3 successfully held a territory throughout the entire breeding season. The mates of Birds 1 and 3 were often present and calling during recording sessions. I observed no female with Bird 2 during the short (about 1 h) recording period. All three birds responded strongly to playback of normal towhee song by singing and flying over the speaker, the usual response to playback of towhees. As Birds 1 and 2 were located in heavily populated areas where long-term study was difficult, I used Bird 3 and its neighbors for the following experiments.

*Playback experiments.*—Experiments with playbacks of tape recordings were designed to determine if the wren imitations would elicit the same aggressive response from a territorial male towhee that a normal song would. I recorded towhee songs on a Nagra 4.2 tape recorder at 19 cm/s, using a Sennheiser MKH 815T directional microphone. I recorded songs for playback on repeating tape loops and produced 5-min playback tapes. Test songs were played from a Uher 4200 Report Stereo IC tape recorder through a Realistic tweeter horn (40-1228) speaker. I placed the speaker about 2 m high in a tree in the center of the subject's territory to elicit maximum response (Falls and Brooks 1975). The frequency response of the speaker was flat ( $\pm 3$  dB) from 1 to 8 kHz.

Each session consisted of a control (normal towhee song) and an experimental (wren imitation) playback, with the order of presentation balanced over each experimental series. I divided each playback period into three segments, a 5-min preplay to quantify a baseline for the subject's behavior, a 5-min playback with 12 songs/min, and a 5-min postplay period. This sequence was immediately repeated for the other playback tape. Each session consisted, therefore, of only 10 total min of playback. A decrease in response with successive presentations of test recordings often occurs in birds (Verner and Milligan 1971, Petrinovich and Peeke 1973). To minimize habituation, sessions with an individual towhee were therefore separated by at least a day.

I noted the following behaviors into a Sony cassette recorder for later transcription: latency to first vocalization, latency to initial approach flight, number of calls, number of songs, and number of flights in the vicinity of the speaker. Songs included any part of a song, such as an isolated introductory note or trill. A flight was any aerial change of position between trees, bushes, or the ground. A change of position within the same tree was not counted as a flight.

I used the level of aggressive response to the playback by the subject as a measure of song recognition. The amount of flying during the preplay period was negligible; flights near the speaker were the most reliable measure of response to the playback and were indicative of a high level of aggression. An increase in the rates of calling and singing was a common but less intense response to playback. To make use of the information contained in all three measures of aggression, I calculated a composite response score based on the relative strength of response indicated by calls, songs, and flights during previous experiments (see Richards 1978). A call received a score of 1, a song a score of 2, and a flight a score of 8. The total response score in each experiment was the sum of these weighted measures during the playback period minus the sum during the preplay to control for baseline response levels. Latencies to the first vocalization and the approach flight were measured to the nearest 15 s. The maximum latency assigned was 600 s (10 min), the end of the postplay period.

I performed two series of experiments, the first to determine the general level of response by towhees to playback of the wren imitations and the second to compare the responses of the neighbors and non-neighbors of an imitator to playback of the most often heard imitation. In Experiment 1, I played back recordings of my sample of imitations to towhees with territories that were not adjacent to an imitator (termed distant birds). I used each of the 10 different imitations twice during the experimental series and compared the responses to a control song recorded from a non-neighboring member of the population. Each of the 10 subjects was therefore exposed to 2 of the 10 possible imitations and to the control song.

Despite the generally weak responses from distant birds to playback of these imitations (see Results), the daily countersinging of the neighbors of Bird 3 suggested that these neighbors had learned to recognize the wren imitations as conspecific song. In experiment 2, I played back the mixed theme (Fig. 1B), used most often in countersinging by Bird 3, to the four towhees with adjacent territories (termed neighbors). Previous experiments (Richards 1978) had shown that North Carolina towhees give little response to introductory syllables without a trill. The control was a normal towhee song from a distant member of the population. I used each subject in two sessions, on different days, with the order of presentation of the songs reversed. I used the same procedure with four distant birds at least 750 m from the territory of Bird 3.

TABLE 1. Comparison of the overall responses of neighbors (N) and distant birds (D) to playbacks of tape recordings of the mixed theme of Bird 3 (imitation, Fig. 1B) and the control song (Fig. 1A). Response scores explained in text.

| Subjects | Test  | Mean response score | P (one-tailed)     | n    |
|----------|---|---------------------|--------------------|------|
| N        | Response to imitation minus response to control | -12                 | 0.01 <sup>a</sup>  | 8, 8 |
| D        |   | -104                |                    |      |
| N        | Response to imitation                           | 86                  | ns <sup>b</sup>    | 8    |
|          | Response to control                             | 97                  |                    |      |
| D        | Response to imitation                           | 28                  | 0.005 <sup>b</sup> | 8    |
|          | Response to control                             | 133                 |                    |      |

<sup>a</sup> Mann-Whitney *U* Test (Siegel 1956).

<sup>b</sup> Wilcoxon Matched-pairs, Signed-ranks Test (Siegel 1956).

## RESULTS

*Experiment 1.*—The pooled responses by distant birds to the 10 imitations were significantly less than those to the control (Imitation mean score = 32; Control mean score = 108;  $P < 0.01$  (two-tailed);  $n = 20$ ; Wilcoxon Matched-pairs, Signed-ranks test; Siegel 1956). In response to both the imitations and control, the birds vocalized and approached with similar latencies (Table 2). Following the initial reaction, however, the response to the imitations was low, suggesting a tendency to react to unfamiliar songs with vocalization and approach but little or no recognition of these songs as towhee songs at close proximity.

*Experiment 2.*—Table 1 shows that the aggressive responses of the neighbors to the mixed imitation of Bird 3 were significantly higher than those of the distant birds. As expected, the responses of the neighbors to the imitation and control songs did not differ significantly, whereas the responses of the distant birds to the imitations were significantly lower than those to the control song. The latencies to vocalization and approach were variable and overlapped considerably, as in Experiment 1 (Table 2).

## DISCUSSION

Except in the early spring, before territorial boundaries are established, singing towhees rarely occur within another individual's territory. Song is primarily used in the morning, when countersinging with neighbors occurs at a distance; an approach

TABLE 2. Mean latencies and standard deviations of first vocalization and approach for: (Experiment 1) distant birds to playbacks of tape recordings of the pooled wren imitations and the control song, and (Experiment 2) neighbors and distant birds to playbacks of tape recordings of the mixed theme of Bird 3 (imitation) and the control song, time in s.

| Experiment | Subjects | Presentation (n) | Vocalization latency | Approach latency |
|------------|----------|------------------|----------------------|------------------|
| 1          | Distant  | Control (20)     | 30 ± 15              | 90 ± 135         |
|            |          | Imitation (20)   | 30 ± 30              | 255 ± 270        |
| 2          | Neighbor | Control (8)      | 60 ± 75              | 195 ± 255        |
|            |          | Imitation (8)    | 45 ± 30              | 270 ± 285        |
|            | Distant  | Control (8)      | 15 ± 00              | 180 ± 255        |
|            |          | Imitation (8)    | 30 ± 15              | 285 ± 270        |

to investigate the source of the song is uncommon. The normal songs of towhees are varied and complex (Borrer 1959, 1975; Ewert 1978; Richards 1978), and the degradation during transmission through the environment would make the received song even more variable (Wiley and Richards 1978). The rapid initial approach to birds singing unfamiliar songs would allow the bird to confirm species identity by sight. If a bird had a neighbor that sang an unusual song, it would save time and energy by learning from early boundary encounters to associate the song with that conspecific male. Long-distance countersinging could then proceed without a need for close investigation of the singer. Hearing the same song from a playback near the center of its territory, each neighbor responded to the wren imitation as it did to a normal song. It is unlikely that the individual recognition in these experiments is a demonstration of an extremely localized dialect; though they were able to recognize the imitation, the neighbors did not incorporate it into their songs. Borrer (1975) and Ewert (1978) have demonstrated the absence of dialects in eastern towhees.

Occasionally birds may learn to react to the song of competing species on adjacent territories (for example, Thielcke 1972, Falls and Szijj 1959). In these cases, the recognition results in the defense of the territory against other species as well as against conspecifics. In this study, however, Carolina Wrens held territories overlapping those of the imitators, and no interspecific defense was observed.

Observational studies (for example, Verner 1976) have suggested that neighbors can learn to individually recognize conspecifics by associative learning. Previous measures of individual recognition in territorial male birds, however, have been of the reduced intensities of response to neighbors' songs, allowing habituation as an explanation. The present study experimentally demonstrates stronger responses by neighbors than by distant birds and thus confirms the role of associative learning in individual recognition.

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