DIFFERENTIAL RESPONSE OF TERRITORIAL YELLOWTHROATS TO THE SONGS OF NEIGHBORS AND NON-NEIGHBORS

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ABSTRACT.—Songs of neighbor and non-neighboring individual Yellowthroats were presented to territorial male Yellowthroats in two different locations within the territory. Territorial males showed a significantly higher aggressive response to the songs of strangers than neighbors when the speaker was placed near the respective neighbor's boundary. Presentation of the two songs in the center of a territory resulted in a high aggressive response to both songs, with no discernable difference in response. Evidence is also presented that suggests that females are capable of recognizing their mates by song alone. *Received 13 October 1976, accepted 28 December 1976.*

THE importance of individual recognition in the efficiency and success of colonial bird species has been emphasized by Thorpe (1961) and Beer (1970) as well as others. Even within noncolonial species, individual recognition has been demonstrated and probably is helpful in pair bond maintenance as well as in the efficient maintenance of the territory. Birds that sing antiphonally, e.g. the *Laniarius* shrikes (Grimes 1966, Hooker and Hooker 1969), recognize their mates by song alone. Certain cardueline finches learn their mate's call by imitation (Mundinger 1970). The ability to discriminate between the songs of neighboring males and those of non-neighbors was demonstrated in the Ovenbird, *Seiurus aurocapillus* (Weeden and Falls 1959), Great Tit, *Parus major* (Gompertz 1961, Krebs 1971), White-throated Sparrow, *Zonotrichia albicollis* (Falls 1969), Indigo Bunting, *Passerina cyanea* (Emlen 1971), Field Sparrow, *Spizella pusilla* (Goldman 1973) and the Song Sparrow, *Melospiza melodia* (Kroodsma 1976) by the use of song playback.

Yellowthroats (*Geothlypis trichas*) are a widespread species commonly found breeding in early seral stages of succession throughout North America. Their territories are in brushy areas and males are rarely in visual contact with neighboring males or with their own mates. It seems unlikely that visual cues are helpful in supplying much contextual information to the song which might expand the number of potential meanings of messages transmitted (cf. Smith 1965). Although visual cues might be important at close range, vocal cues are probably particularly critical in the transmission of information pertaining to an individual's sex, species, motivational state, and the singer's own identity.

The advertisement song of the Yellowthroat is commonly paraphrased as "wich-i-ty wich-i-ty wich-i-ty." Each male sings only one primary song that does not change (Wunderle, unpublished data). Song variation within the individual's repertoire is slight while the variation between the songs of different individuals is great (Borror 1967). The variation within note structure and number of notes per phrase probably provides ample information for individual recognition. The objective of this study was to determine if male Yellowthroats can discriminate between the songs of neighbors and strangers, and to examine the role of song source position within a territory.

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METHODS

During June of 1972 and 1973, playback experiments were run on male Yellowthroats at the Kalbfleisch Field Research Station of the American Museum of Natural History, in Dix Hills, Long Island, New York. In both years territories were mapped by observing singing males and delineating territorial boundaries by use of playback. Each experiment was run approximately 1 week after the territory was mapped. During all playback presentations an Electravoice speaker was placed upright on the ground and was attached to a 7.6-m cable connected to an amplifier and a Uher 4000 Report-L tape recorder. No models or mounts of male birds were used. In the summer of 1972, the speaker was placed in the center of known territories and eight individuals, seven of which were color-banded, were tested. In the summer of 1973 the same speaker was placed at the edge of known territories, where the territory abutted with that of a neighbor. Seven color-banded and one unbanded individual were tested in that configuration.

To test a bird's ability to discriminate between the songs of neighbors and strangers, recordings were made of adjoining neighbors and two individuals located approximately 19.3 km away. It is likely that the test individuals had no previous experience with the two songs of the more distant males. Three-min tapes were made of neighbors and non-neighboring Yellowthroats with songs spaced at 15-s intervals, an interval characteristic of an undisturbed singing bout. All birds were recorded with a Uher 4000 Report-L tape recorder at 19 cm per s using a 61-cm parabolic reflecter with a Uher microphone.

The two songs of the distant males differed from the songs of neighbors in both note morphology and number of notes per repeated phrase. Kalbfleisch males sang songs with three-note repeated phrases, while the songs of the two strangers were made of four-note repeated phrases.

Songs of a neighboring or a non-neighboring male were presented to individuals in random order, with a 15-min interval between the playing of each tape. Prior to each tape presentation, an 8-min period was used to observe and record the behavior of the undisturbed male. Then during the 3-min tape presentation and the following 5 min all behavior was again recorded. The 8-min control period was used as a baseline with which the combined responses obtained from the tape presentation period and the following response observation period were compared. The difference between the control period and the tape period with its associated observation period was calculated for the number of occurrences of each specific behavior as listed in the behavioral index (Table 1). It was this difference (tape response period and following 5 min minus the control count period) that was used to calculate the behavioral index.

Observations of numerous territorial interactions of male Yellowthroats permitted me to calibrate a behavioral scale as used by Emlen (1971). The most reliable technique for measuring response level seemed to be a hybrid index (Sibley 1954) as adapted for behavioral purposes by Emlen (1971). I concluded that the most reliable indication of a highly excited male is the appearance of numerous types of vocalizations, flights over the speaker, and approaches to the speaker. Normally, a strange male singing near the boundary of a territorial resident male would stimulate an increase in singing by the territorial male. Following the increased singing rate, the territorial male would chatter several times before actually approaching and chasing the intruder. The chatter vocalization is made up of a series of rapidly uttered notes having a rattling-chattering quality which was heard only during territorial encounters. If the intruder did not immediately leave the territory, the territorial male might again sing, or more likely, chatter before attacking and chasing again. Several single high-pitched notes (designated as "chit" notes) were often given between singing, chattering and chasing. The behavioral response index (Table 1) lists those behavioral responses that were recorded during playback experiments.

A comparison of the behavioral response index score of the neighbor's song with the stranger's song was made with the Wilcoxon Matched-Pairs Sign-Rank test (Siegel 1956). A two-tailed test was used because the experimental results were not predictable in advance. The Mann-Whitney U-test was used to compare specific behavioral changes between the two songs.

RESULTS

A comparison of the response to the song of a neighbor and of a non-neighbor when the speaker is placed along the respective neighbor's shared boundary (Fig. 1) indicates a significant difference ($P < .01$) in response. Males show a higher response to the song of strangers than to the song of neighbors when the speaker is placed along the mutual boundary. A comparison of the individual response behaviors, i.e. increase in primary song, increase in chit notes, chatters, flights over the speaker, and number of speaker approaches shows a significant difference ($P < .05$). Table 2

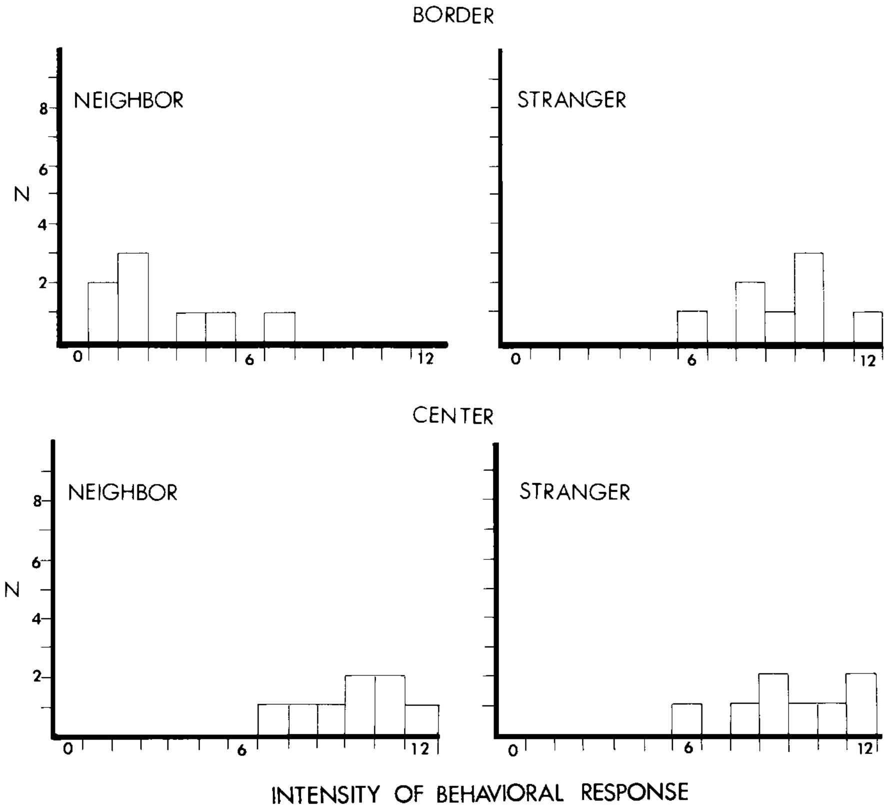

Fig. 1. Responses of male Yellowthroats to the songs of neighbors and strangers when the speaker was placed near the mutual boundary (above) and when the speaker was placed in the center of the territory (below). N = number of birds tested.

displays the average number of responses for each particular behavior elicited by the two different songs. When the speaker was placed in the middle of the territory, however, the resident male responded equally and with high intensity to songs of both neighbors and strangers (Fig. 1, Table 2).

Discussion

These results suggest that male Yellowthroats discriminate between the songs of neighbors and non-neighbors when the speaker is placed near the neighbor's boundary, but presentation of the two different songs in the center of a territory elicited a highly aggressive response to both. Thus male Yellowthroats are capable of discriminating between songs, yet a response indicating such discrimination is dependent upon the location of the singer.

The differential agonistic responses of territorial males elicited by familiar and unfamiliar songs presented along the neighboring male's territorial boundary suggest that the male has habituated to both his neighbor's song and physical location. The occurrence of only one song per male and the existence of many different song types within a Yellowthroat population probably enhance individual recognition. Any change in either the neighbor's song or singing location disrupts the status quo to

TABLE 1. Behavioral response index used to quantify a male's response to playback. Six categories of behavioral activity were used for comparing both the control count period (8 min) with the playback plus response observation periods (8 min total). A score of 0, 1, or 2 for each category indicated no change, slight increase, and large increase, respectively, during playback and following 5 min compared to the control count observation periods. N = number of occurrences of the specific behavior per experiment

Singing rate (songs per 8 min)
0 = No change or decrease
1 = Rate increase $2 \leq N \leq 6$
2 = Rate increase $N \geq 7$

Chit notes (*chit* notes per 8 min)
0 = No change or decrease
1 = Increase $1 \leq N \leq 3$
2 = Increase $N > 3$

Chattering (chatters per 8 min)
0 = No change or decrease
1 = Increase $1 \leq N \leq 2$
2 = Increase $N > 3$

Flights over the speaker (in 8 min)
0 = No change or decrease
1 = Increase $1 \leq N \leq 2$
2 = Increase $N > 2$

Approach distance
0 = None
1 = $3 \text{ m} \geq N \geq 1.5 \text{ m}$
2 = $N < 1.5 \text{ m}$

Number of approaches within 3 m
0 = None
1 = $1 \leq N \leq 3$
2 = $N > 3$

Maximum Possible Score = 12

which the male has habituated. Weeden and Falls (1959) suggested that habituation to the songs of established neighbors results in a considerable saving of energy for the territorial male by reducing the number of "needless" boundary conflicts. Habituation appears to be an important mechanism for maintaining low levels of aggression between neighboring conspecifics (Petrinovich and Peeke 1973).

Where time and energy might be conserved by not responding to a neighbor's song in a familiar location, the occurrence of the neighbor's song in an unexpected site demands an immediate response by the territorial male. The song of an intruder within the center of a territory represents an immediate threat to the territory of the resident male, regardless of the singer's identity.

The song of an unfamiliar male elicited a highly aggressive response, regardless of location. Such an unfamiliar song might represent the song of nonterritorial males, possibly members of a floating population that are constantly attempting to carve out a new territory, often from pre-existing ones (Wunderle, unpublished data). An aggressive response to such unfamiliar males is clearly adaptive.

TABLE 2. A summary of the individual response parameters elicited by playback of the songs of neighboring and non-neighboring males. Eight different males were tested at each speaker location

	Average Number of Various Response Parameters				
	Primary Song	Chit Notes	Chatter	Flights	Approaches[a]
Speaker near the mutual border					
Prior to playback	2.4	0.1	0	0	0
Playback, Non-neighbor song	8.1	2.9	4.5	2.1	0.4
Prior to playback	3.6	0.8	8	8	8
Playback, Neighbor song	1.6	1.0	0.9	.13	2.5
Speaker in center of territory					
Prior to playback	2.1	0	0	0	0
Playback, Non-neighbor song	8.2	3.1	5.1	4.0	4.1
Prior to playback	1.8	0.1	0	0	0
Playback, Neighbor song	8.0	2.9	5.7	4.3	3.9

[a] Refers to the number of approaches to within a 1.5-m radius of speaker

The experimental evidence presented for the Ovenbird (Weeden and Falls 1959), Indigo Bunting (Emlen 1971), and Great Tit (Gompertz 1961, Krebs 1971), in which the speaker was placed in only one location in a territory, does not necessarily indicate that a male can recognize a particular individual by voice alone. As pointed out by Beer (1970: 39), these types of experiments indicate only that a territorial male is capable of differentiating between classes of familiar and unfamiliar songs. Individual recognition by voice cannot be assumed under these circumstances because the bird is responding in a differential fashion to familiar and unfamiliar songs. Playback experiments comparing the response to songs of neighbors and non-neighbors done in only one location in a territory should be designated only as neighbor/non-neighbor discrimination experiments and not as tests of individual recognition. For the efficient maintenance of territoriality it is not necessary to assume that males are capable of individual recognition, but that they can discriminate between the songs of neighbors and strangers (Beer, op. cit.). A male's ability to associate familiar songs with a given location would permit the most efficient territorial defense.

Brooks and Falls (1975) demonstrated that male White-throated Sparrows could differentiate between the songs of neighbors and strangers. In addition, Falls and Brooks (1975) showed that a particular male responded differentially to the song of a given neighbor depending upon the location in which the speaker was placed within the territory. A song of a neighbor played along the mutual boundary elicited a weak response, whereas the rendition of the same song on the opposite boundary elicited a strong response from the territorial male. They essentially demonstrated that a territorial male could differentiate between the songs of neighbors A and B. Such methods, taking location differences of the speaker into consideration (contextual differences), offer strong evidence for individual recognition.

Failure to demonstrate neighbor and non-neighbor discrimination of song could be due to speaker location. Belcher and Thompson (1969) working with Indigo Buntings and Harris and Lemon (1976) working with Song Sparrows found that territorial males did not respond differently to the songs of neighbors and strangers. However, Emlen (1971) with Indigo Buntings and Kroodsma (1976) with Song Sparrows both found that males showed a stronger response to the songs of strangers than neighbors. Such discrepancies could result from differences in speaker location as well as the time in the breeding season when the experiments were run.

If songs are variable among males, and if males can recognize these differences, it seems likely that females could recognize their mates by song alone. During playback of Yellowthroat songs to territorial males, some females were occasionally heard giving the chatter call while their mate gave the normal aggressive response. From these observations it was not possible to determine if the female was responding aggressively to the stranger's song or if she was stimulated by her mate's aggressive response. However, during some preliminary playback experiments a resident color-banded male left his territory. Prior to his leaving he was actively singing and foraging with his mate. Upon his departure, playback of his own song to his visibly present mate elicited no response from her. However, playback of two other songs from unfamiliar males elicited several chatter calls, suggesting recognition of her mate by song alone.

To further test the possibility that females are capable of recognizing their mates by song alone, three different color-banded males were netted and removed from their territories. An hour after their removal, the song of an unfamiliar male and their own song were played in their respective territories. In two of the territories, females responded to the unfamiliar song with several (two and three) chatter calls and remained silent during the playback of their own male's song. The third female remained silent throughout and was not observed; possibly she was incubating at the time. Petrinovich et al. (1976) have demonstrated that a female's aggressive response to playback depends upon whether she has eggs, nestlings, or fledglings. The females that did respond were believed to be in the process of nest building or egg-laying. Such preliminary experiments suggest that females are capable of recognizing their mates by song alone.

Female Yellowthroats do not necessarily mate with the same male each year. I found that females may pair with a neighbor the next year, or may exchange mates in the course of a summer. The number of potential mates that a females might have during a lifetime suggests that she must have a flexible learning scheme if she is to recognize all of her mates individually by song.

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Increased use of computers to store and process data about birds has precipitated a number of problems. One such problem is that of identifying the species (or higher taxonomic unit) under consideration. Many local ornithological organizations have solved this problem by identifying each species in their area with a unique code number (AOU number, for example). The proliferation of local systems could be avoided by development of an internationally recognized coding system for all bird species. The advantages of a standard system include international compatibility of records and facilitation of exchange of data and literature between countries.

Any new system must be taxonomically based, flexible enough to accommodate new species and taxonomic revisions, and be expandable for those interested in subspecific classification. For purposes of discussion, the following system is proposed. A world-wide numerical system will be based on Morony, Bock and Farrand (Reference List of the Birds of the World, 1975, AMNH) with 6-digit numbers identifying each species: the first two digits key order, the third digit family, the fourth digit genus, and the final two digits the species. Thus, each genus has numbers reserved in advance for up to 99 species, and searches of data can be made rapidly and efficiently by computer for any taxonomic level. Individuals wanting subspecific identifications can simply add one or two digits to the 6-digit base.

As an example:

- 270000 Cuculiformes
  - 271000 Musophagidae
    - 271100 Corythaeola
      - 271101 *C. cristata*
    - 271200 Crinifer (2 spp.—201–202)
    - 271300 Corythaixoides (3 spp.—301–303)
    - 271400 Musophaga (2 spp.—401–402)
    - 271500 Tauraco (11 spp.—501–511)
  - 272000–279000 Cuculidae
- 280000 Strigiformes
- 290000 Caprimulgiformes

A conversion table from old numbers (AOU, etc.) to new numbers should be developed for study of zoological material, bird banding, and other references to old numbers. Interested persons are invited to send comments about this proposal to **James R. Karr, Department of Ecology, Ethology, and Evolution, University of Illinois, Champaign, Illinois 61820, U.S.A.**

A special discussion group at the International Ornithological Congress in Berlin will discuss this and other proposals and all comments received by **15 May 1978**. A final recommendation will then be developed and circulated to the international ornithological community for comment and eventual adoption.