DIFFERENTIAL RESPONSES OF MALE OVENBIRDS TO RECORDED SONGS OF NEIGHBORING AND MORE DISTANT INDIVIDUALS

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General observations indicate that song plays an important part in the establishment and maintenance of territory by many species of birds. The role of song in territorial behavior may be investigated experimentally by playing tape-recorded songs in the field. In the present study recorded songs were used to elicit aggressive responses from male Ovenbirds *(Seiurus aurocapillus)* occupying territories. Experiments were designed to study particularly reactions of birds to songs of neighboring and more distant individuals of their own species.

These studies were carried out at the Wildlife Research Station of the Ontario Department of Lands and Forests in Algonquin Park during the summers of 1955 and 1956. A description of the study area and a detailed account of the nature and extent of Ovenbird territories is presented elsewhere (Stenger and Falls, 1959).

Behavior Observed in Natural Encounters Between Male Ovenbirds

In this paper reactions of male Ovenbirds to tape-recorded songs are interpreted in the light of behavior observed when territory-holders encountered intruding males. In such natural encounters chasing and vocalizing were noted frequently, threat display (similar to that described by Freeman, 1950) less often, and physical contact very rarely. Encounters were prolonged and vigorous when boundaries of territories were being established before the arrival of the females but decreased rapidly in duration and intensity as the breeding cycle progressed. During the nestling period and after the young left the nests a few call notes from a territory-holder were sufficient to drive an intruder away.

All the experiments were carried out after the females arrived and most of them after incubation had begun, *i.e.,* after the vigorous encounters between males associated with the establishment of territory were over.

Since vocalizing played an important part in natural encounters as well as in reactions of birds to tape-recorded songs, various sounds given by male Ovenbirds are listed below:

Song. The most frequent song and the one usually heard in encounters is one in which a phrase suggesting the word "teacher" is repeated about ten times at regular intervals, the whole song lasting about three seconds. Songs of individual

birds differ in pitch, speed, and details of the phrases but each individual's song is constant. Thus, an experienced person can separate most individuals by their distinctive songs. Only the males sing. Recordings of "teacher" songs of several birds were used in the experiments.

Warbling. Warbling sounds with or without "teacher" phrases interspersed were heard on a number of occasions, usually at the end of an encounter. These sounds were given from a stationary position but resembled the so-called "flight song" (Bent, 1953).

Call notes. Three types of chipping sounds given by males can be readily distinguished.

A sharp, high-pitched note is elicited by the sudden appearance of another Ovenbird or when a bird is disturbed by humans.

A lower-pitched "chuck", usually given four or five times at intervals of a second or more, often occurs at the end of an encounter.

Rapid call notes, similar in pitch to the "chuck" notes but repeated at intervals of less than one second, are given during encounters with other birds or when birds are disturbed by humans.

EXPERIMENTAL STUDIES

In this study recorded "teacher" songs were played through loudspeakers located within the territories of several Ovenbirds. Reactions of these birds were studied with special reference to differences in responses elicited by songs of Ovenbirds occupying adjacent territories on the one hand, and songs of non-adjacent birds on the other hand.

Adjacent birds were those which occupied neighboring territories not separated by any topographical features. Their territorial boundaries overlapped or were separated by distances up to 70 feet (Stenger and Falls, 1959). Distances between "centres of gravity" (calculated by the method of Odum and Kuenzler, 1955) of neighboring territories ranged from 160 to 440 feet with an average of 325 feet (data from 23 experiments). Six territories in the study area averaged 2.3 acres in extent.

Non-adjacent birds, on the other hand, were those separated by at least one intervening territory or by some topographic feature such as a hill or a large clearing. Distances between territories (centres calculated as above) of non-adjacent birds and territories of birds to which their songs were played ranged from 405 feet to more than a mile and a half.

It is difficult to determine how far away one Ovenbird can hear another. During the period when the experiments were done birds sometimes seemed to react to natural songs heard near their territories but no evidence was obtained about reactions to distant songs. Under favorable conditions in the study area an experienced person might hear an Ovenbird 1000 feet away and could distinguish songs of some individuals at half that distance. If we may judge from these rough

estimates based on human experience, there is little doubt that under natural conditions a bird could easily hear the songs of its neighbors and might hear the songs of the closer non-adjacent birds. However, it is unlikely that the birds tested in these experiments had previously heard the songs of the more distant non-adjacent birds which were played to them.

The equipment used in the experiments covered the frequency range of an Ovenbird's song (about 3,000 to 8,000 cycles per second) and the reproduced songs sounded normal to the experimenters, although more directional than the song of a bird. Thus, reproduced songs were usually louder than normal songs if heard directly in front of the speaker, but were not as loud to the side or behind the speaker. Details of equipment follow:

Songs were recorded with an Electro-voice 635 microphone mounted at the focus of a 30-inch parabolic reflector. In 1955 a Webcor 210 tape-recorder was used at a tape speed of 7½ inches per second. In 1956 an Ampex 600 recorder was used at 15 inches per second. For play-back, a good quality four-watt amplifier was used with the recorder. Loud-speakers were used on cables up to 500 feet long. In 1955 eight-inch cone speakers were used mounted in plywood boxes, and in 1956 Atlas HR-2 metal "tweeters" were used unmounted.

Two types of experiments were carried out and will be referred to respectively as "intensive" and "extensive" experiments. Intensive experiments were done with a few birds in one area with each bird tested many times. Extensive experiments, on the other hand, involved more birds in four widely-separated areas with each bird tested only a few times. Methods and results for the intensive experiments will be given first, followed by those for the extensive experiments.

"Intensive" studies were made of the birds occupying a surveyed plot of about 25 acres on which territorial boundaries were accurately known. Preliminary experiments were done on eight birds from June 17 to July 21, 1955 and a more extended series of experiments was carried out on five birds from May 29 to July 12, 1956. Six of the eight birds used in 1955 and all six birds used in 1956 were tested with songs of both adjacent and non-adjacent birds. Non-adjacent birds were located from 405 feet to more than one and a half miles from the birds tested.

In 1955 the following procedure was used. A loud-speaker was placed on or near the ground at a standard location within a territory. Songs given by the resident male were counted for five minutes before recordings were played. Then recorded songs of one bird were played for four minutes with natural intervals between songs (variable, but averaging about 15 seconds). This was followed by five minutes of silence during which the speaker was moved 132 feet to a new location, still within the territory. The same songs were played again for a final period of four minutes from the new location. During the whole experiment, the number of songs and types of call notes given

by the territory-holder and the number of locations which it visited were noted. Successive experiments on the same bird were separated by at least two hours.

In 1956 some changes in procedure were adopted. A speaker was hung in a tree 20 to 30 feet above the ground (a height at which Ovenbirds normally sing) and only one location was used in each territory. A recorded song was played at regular 15-second intervals (using a loop of tape) for three minutes, followed by three minutes of silence and a final three minutes of playing. The observer hid beneath a blind during the experiments. No bird was tested oftener than every two days.

In analyzing the results of these experiments four responses by a bird were considered—song, call notes, approach to the speaker, and amount of movement in the vicinity of the speaker. A bird was considered to have responded with respect to each category as follows:

Song—If the number of songs per unit of time was greater during the experiment than before and if singing continued after the experiment.

Call notes—If at least two types were given.

Approach—If a bird approached within 30 feet of the speaker.

Movements—If a bird visited more than five locations in the vicinity of the speaker.

Responses of birds to songs of adjacent and non-adjacent individuals are summarized in Table 1. A bird might react to the tape-recorded songs with respect to one, two, three, or four of the foregoing behavior categories, or not at all. The results show that, for the most part, birds reacted in three or four ways to songs of non-adjacent birds, but failed to react, or reacted in only one or two ways, to songs of neighboring birds.

Responses usually included approach and call notes, but most birds showed idiosyncracies of some sort in their reactions. For example, one bird was unusual in that it reacted mainly by singing; another usually performed threat displays; a third usually gave warbling songs.

The "extensive" experiments, it will be recalled, were designed to obtain quantitative data on a larger sample of birds than was possible in the "intensive" experiments, and to minimize the amount of recorded song played in any one area. In these experiments about one-tenth as many songs were played in any one area as in the intensive experiments already described. Fourteen birds in four widely separated areas were studied from June 14 to July 20, 1956. Non-

TABLE 1

NUMBER OF EXPERIMENTS CLASSIFIED BY RESPONSE OBTAINED TO SONGS OF ADJACENT AND NON-ADJACENT BIRDS

	Four categories of response noted	*Three categories of response noted*	*Two categories of response noted*	*One category of response noted*	*No response noted*
1955					
Response to adjacent birds	0	1	4	1	0
Response to non-adj. birds	20	4	0	1	0
1956					
Response to adjacent birds	2	1	4	5	5
Response to non-adj. birds	10	7	5	1	0
Totals					
Response to adjacent birds	2	2	8	6	5
Response to non-adj. birds	30	11	5	2	0

adjacent birds whose songs were used were from a third of a mile to one and a half miles away from the birds tested. It is unlikely, therefore, that the tested birds had heard these songs before.

In these experiments the loud-speaker was placed at one location in each territory about six feet above ground. A song was played every 15 seconds until the territory-holder approached the speaker. A minimum of four songs was played. If the bird did not approach, the test song was played for three minutes followed by three minutes of silence and a final three-minute period of playing. Songs of the territory-holder were counted before, during, and after each experiment. The times which elapsed from the playing of the first song until the bird first reacted by sound and approach were noted to the nearest 15 seconds. Five experiments were performed on each bird, usually at least two days apart, and a different test song was used on each occasion. In the course of these experiments, each bird was exposed to songs of two non-adjacent birds and two adjacent birds, and to its own song. The order in which these songs were used and the order in which birds were tested each day were random.

Results are shown in Tables 2 and 3. In Table 2, time values of zero are given for reactions which occurred between the first and second playings of the recorded song (*i.e.*, in the first 15 seconds),

values of 15 for reactions between the second and third playings and so on. This procedure was adopted because vocal responses usually occurred immediately after a recorded song was played. No results are shown for experiments in which technical failures occurred or the identity of the reacting individual was not established. Only average values for time of approach are given in Table 2 since the detailed data are similar to those presented in the same table for time of the first sound.

It is apparent from Tables 2 and 3 that birds reacted more quickly (by sound and approach) and more strongly (*i.e.*, sang more) to songs of non-adjacent birds than to songs of their neighbors, the differences being statistically significant. Responses of birds to their own songs were intermediate in these respects.

Birds typically responded by uttering call notes and approaching the loud-speaker. On 44 of 66 occasions when responses occurred, the

TABLE 2

TIME ELAPSED BETWEEN FIRST RECORDED SONG AND BIRD'S REACTION

		Recorded songs used				
		Adjacent		*Non-adjacent*		*Bird's*
		No. 1	*No. 2*	*No. 1*	*No. 2*	*own*
First sound by bird						
Area	*Bird*					
A	1	0 sec.	60 sec.	0 sec.	0 sec.	0 sec.
A	2	180	120	75	30	60
A	3	0	75	0	0	360
A	4	75	0	0	15	NR
B	1	15	15	0	0	15
B	2	105	495	45	420	0
C	1	0	—	0	0	120
C	2	30	—	0	15	30
C	3	—	15	0	—	NR
C	4	0	60	0	30	NR
D	1	—	—	15	0	30
D	2	0	45	15	0	0
D	3	0	15	0	0	0
D	4	NR	15	15	90	15
Average		60 sec.		28 sec.		57 sec.
Probability of chance difference*		$P < .01$				
First approach noted						
Average		74 sec.		45 sec.		64 sec.
Probability of chance difference*		$P < .05$				

* "t" test pairing data for adjacent and non-adjacent experiments for each bird. NR indicates no reaction.

TABLE 3

SONGS GIVEN BY BIRD IN FIVE MINUTES FOLLOWING EXPERIMENT MINUS SONGS GIVEN IN FIVE MINUTES BEFORE EXPERIMENT

		Recorded songs used				
		Adjacent		*Non-adjacent*		*Bird's*
Area	*Bird*	*No. 1*	*No. 2*	*No. 1*	*No. 2*	*own*
A	1	10	12	26	31	30
A	2	0	12	11	4	7
A	3	−6	26	8	21	17
A	4	20	0	—	9	NB
B	1	17	16	—	23	22
B	2	9	1	7	8	−1
C	1	12	—	22	26	23
C	2	—	—	11	3	19
C	3	—	3	30	—	0
C	4	7	1	−2	—	NB
D	1	—	—	27	37	12
D	2	8	7	23	2	18
D	3	18	9	10	14	10
D	4	−1	22	—	26	6
Average		9.2 songs		16.4 songs		13.6 songs
Probability of chance difference*		$P < .05$				

* "t" test pairing data for adjacent and non-adjacent experiments for each bird. NB indicates no bird in evidence.

first sounds given were call notes. Most birds eventually sang near the speaker but they often did not sing until the playing of recorded songs was stopped. As in the intensive experiments, marked differences were noted in the way individual birds reacted. Compare, for example, the considerable times taken for birds A2 and B2 to react with the much shorter times for birds A1 and D3 (Table 2).

In both intensive and extensive experiments there was considerable variation in the responses of the same birds on different occasions. Many factors may have contributed to this variability including weather (wind, rain, etc.), stage of the breeding cycle when a bird was tested, and minor variations in technique (for example, loudness at which recorded songs were played).

DISCUSSION AND CONCLUSIONS

In both intensive and extensive experiments birds behaved in much the same way as those observed in natural encounters with other males. In each case approach, movements, songs, call notes, and threat displays were noted. It is reasonable to suppose, then, that the findings of the experiments also apply to natural encounters between birds.

Certain conclusions may be drawn from the results of these experi-

ments. Obviously, song is a sufficient stimulus to elicit an aggressive response from a male Ovenbird, provided it originates within his territory. It is also clear that sounds, particularly call notes, play an important part in the aggressive behavior by which the territory is defended. Apparently, Ovenbirds can distinguish between songs of different individuals of their species and can recognize songs of particular individuals (their neighbors). Moreover, they react more strongly to songs of non-adjacent birds than to songs of their neighbors.

Individual Ovenbirds have constant and distinctive songs. It is not surprising, therefore, that a bird learns to recognize the songs of others which it hears frequently. As Hartshorne (1956) points out, what stimulates animals is change; what deadens response is sameness or persistent repetition. The weak reactions to songs of neighbors noted in these experiments may be an example of a response which has been reduced in intensity by a persistent repetition of the stimulus.

Early in the season, before most of these experiments were done, boundaries of territories are established as a result of encounters between neighboring males. The social adjustment between the birds which results from these experiences may be another factor which tends to reduce the aggressive response of a bird to the songs of its neighbors.

Whatever the factors which bring about the observed differences in response to songs of the non-adjacent and adjacent birds, there would appear to be survival value in a mechanism which reduces strife once territorial boundaries are established. Later in the breeding season, when most of these experiments were carried out, the chief danger of serious encroachment on a bird's territory would presumably come from strangers and it is appropriate that they should elicit a strong aggressive response on the part of a territory-holder.

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SUMMARY

Encounters between male Ovenbirds in the breeding season consisted of vocalizing (songs and call notes), chasing, threat displays, and rarely physical contact. Encounters were prolonged and highly aggressive before the arrival of females, and became briefer and less intense as the breeding season progressed.

When tape-recorded Ovenbird songs were played through a speaker located within an Ovenbird's territory, the territory-holder reacted in much the same way as in a natural encounter with another male.

Birds reacted faster and more strongly to songs of non-adjacent birds than to songs of their neighbors. Probable causes and survival value of this behavior are discussed.

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STOMACH CONTENTS

About 20,000 specimens of bird and mammal stomach contents remaining in the Patuxent Research Refuge Food Habits Collection of the Fish and Wildlife Service have been transferred to the Department of Zoology, University of Massachusetts. The specimens will be available after February, 1960, to qualified research personnel for food habits studies. Address inquiries to Dr. L. M. Bartlett, Associate Professor of Zoology, University of Massachusetts, Amherst, Massachusetts.