RESPONSES OF MALE WHITE-CROWNED SPARROWS TO PLAYBACK OF RECORDED SONGS

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Recent perfections in portable sound recording and broadcasting equipment have led to a growing field of playback studies in which sounds recorded in a natural situation are later replayed in a natural situation while responses of animals to those sounds are observed and described. The purposes of such playback experiments have been varied, and several behavioral changes have been measured to provide indices to the subjects' responses. Such detailed analyses of quantitative and qualitative changes in the behavior of birds under such circumstances show exciting promise as means for measuring, in the field, levels of intensity in animal motivation.

While the behaviors employed have, in most cases, been quantitatively treated (e.g., Falls 1963), no investigation has yet attempted quantitatively to assess the effects of playback on a bird's behavioral repertoire in general. Such an analysis is central to selection of those behavioral changes likely to provide the most useful measures of response intensity. Moreover, no systematic attention has yet been given to the possibility that various environmental factors influence response intensity in various ways.

We report here a portion of the results of a more extensive analysis (Milligan and Verner 1971) of vocal discrimination by White-crowned Sparrows (*Zonotrichia leucophrys*). The central purpose of the present paper is to examine which of the bird's behavioral changes are most useful in measuring the response to playback and to assess the influence of a limited number of environmental factors on that response. While nearly the entire behavioral repertoire examined was altered by playback, only a few behavioral acts were judged to have utility as measures of response intensity. Further, the demonstrated effects of known environmental variables suggest that more attention must be given such variables in future playback studies. Ignorance of the effects of certain variables on the response to playback could lead to serious misinterpretation of results.

The most surprising result of this study was the discovery that male White-crowned Sparrows habituated to the playback situation. In addition to providing evidence of the bird's capacity for discriminating between vocal signals, this fact requires that future playback studies of this species employ only naive subjects and that the occurrence or nonoccurrence of habituation in other species be established before they are used for playback experiments.

STUDY AREA AND PERIOD

Results reported here were obtained in a resident population of White-crowned Sparrows located at the northern tip of Schooner Bay, Point Reyes, near Inverness, Marin County, California. The study period extended from 21 July 1964 through 26 July 1965, including winter months. Comparable studies were conducted in two other resident populations in connection with the analysis of discrimination. Observations in those populations confirm the results reported here.

METHODS

The song used for playback was recorded in July 1964 on a Uher 4000S portable tape recorder, operating at 7½ ips, with a Uher 514 microphone mounted on a 24-inch aluminum parabola. This song was copied on a loop for final copy on the playback tape at a rate of one song every 15 sec for a period of 5 min; thus 20 songs comprised each subject's exposure to playback. Tape speed for playback was 3¾ ips. Comparison of sonagrams of this song played at both speeds revealed no differences. A compact speaker designed and built by W. E. Fish was used for playbacks and was connected to the recorder by a 50-ft lead, thus enabling us to observe from a point removed from the source of sound and yet have control of the recorder.

Each session began with a 5-min silent period (Control), followed by 5 min of playback (Test), and a final 5-min silent period (Residual). One observer described the behavior of the bird in detail while the other, employing symbols to represent each behavior, transcribed the verbal record onto a data sheet. In this system the initial period served as a standard for

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The Condor 73:56–64, 1971

comparison with the test period, and the final period provided a measure of the residual effect of playback on the subject.

A limited banding program, including colored bands, facilitated determination of the number of times a male had been used as a subject.

Selection of a bird as a subject was usually based on location of song perches. While every effort was made to place the speaker well within the subject's territory, it was occasionally located near a boundary. In such cases two males sometimes responded to the playback, and the resulting confusion obscured the true response of the male chosen as a subject. At times even prolonged observation prior to playback was insufficient to avoid the difficulty of placing the speaker near a territorial boundary.

During winter months we normally played to nonterritorial flocks, although in some localities birds that gave every indication of being territorial were used as subjects.

RESPONSE MEASURES

Since male white-crowns were commonly concealed for portions of the observation periods, many responses that might otherwise have been useful were incompletely recorded and could not be utilized as measures of response intensity. Behaviors in this category, each of which was obviously affected by the playbacks, included the following: hopping, pivoting, wing flicking, foraging, resting, preening, and crown erection. Activities that could be recorded with reasonable accuracy at all times, irrespective of the bird's visibility, fell into two groups: vocalizations, and changes in location relative to the speaker.

Song was the most prominent vocalization and was assumed to be confined to males (we obtained no evidence to the contrary, though females reportedly sing, Luis Baptista, pers. comm.). Whistles (Phrase A of normal song, Marler and Tamura 1962) and part songs (the first portion of normal song through the first or second syllable of the trill portion, Marler and Tamura 1962) were separately symbolized. In our analysis, however, these vocalizations have been included with songs, since it seems likely that similar motivation underlies all three.

Chips were common to both sexes but did not prove satisfactory in the measurement of response to playback. First, chips were sometimes delivered at rates too rapid for accurate counting. Second, sometimes both sexes and perhaps even some young were chipping simultaneously, so counting the chips of a single bird was impossible.

Trills were also produced by both sexes but were more commonly delivered by females. This call provided our chief measure of the response of females to playback; these results are described in a paper (Milligan and Verner, 1971) treating vocal discrimination.

Position of the bird in relation to the speaker was recorded regularly. Distances from the speaker were estimated to the nearest foot when the bird was within 10 ft of the speaker, to the nearest 5 ft when it was 10–20 ft from the speaker, and to the nearest 10 ft when it was farther than 20 ft from the speaker. That there was doubtless much subjective error in distances estimated in this way does not preclude the usefulness of the procedure.

Any sustained movement of at least 1 ft was considered to be a *flight*. All observed flights were recorded, and flight lengths were estimated in the manner described above. Since some flights must have occurred that we were unable to see, flight number is a less accurate measure of the response than are songs and location changes. Nonetheless, even short flights could be noted when a bird was nearly obscured behind shrubbery, where most other activities could not be observed at all.

TABLE 1. Number of sessions completed under various experimental conditions.

	Without young		With young		
Exposure	AM	PM	AM	PM	Total
First	7	7	7	5	26
Second	3	1	5	2	11
Third	1	3	1	1	6
Total	11	11	13	8	43

Another measure of the response that could be obtained with reasonable accuracy was the time taken for the bird to approach the speaker. The 15-sec intervals following each song were numbered in reverse order from 20 to 1. By recording the interval number during which a bird came within 30, 20, and 10 ft of the speaker, we have obtained an index of its *approach time*. The higher the score, the more rapidly the bird approached the speaker. Birds already within 10, 20, or 30 ft of the speaker when the playback period began could not be scored for the respective distances.

We have compared the responses of subjects exposed once to playback with those exposed twice and three times, of subjects exposed when they apparently had no young to feed with those exposed when they definitely had dependent young either in or out of the nest, and of subjects exposed in the morning with those exposed in the afternoon. Table 1 summarizes the numbers of sessions conducted in each of the above categories, and tables 2 and 4 present the means, etc., of the various responses measured in each category.

Student's t test was employed to compare differences between sample means, and 0.05 was chosen as the level of significance. For all responses except *flight length* we obtained one score per subject per period, so our sample sizes have been limited by the number of sessions. In these cases we were able to employ t scores for the difference between paired samples. Other t scores are based on means of unpaired samples, and different formulae for t have been used, depending upon results of the F-test of sample variances (see Edwards 1958).

RESULTS

Virtually every aspect of behavior seemed affected by playback. Males typically responded by flying toward the speaker, usually after the first song or two. General and conspicuous increases in locomotor and vocal activities persisted throughout playback, with wing flicking, pivoting, hopping, and flying short distances commonly occurring at high rates. The subjects were clearly hyperactive at these times and might be described as

TABLE 2. Measures of responses by male White-crowned Sparrows to playback of recorded songs.

Measure period	First exposure		Second exposure		Third exposure		No young		With young		Morning		Afternoon	
	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n
Songs per period														
Control	6.3 ± 1.4	26	4.6 ± 2.1	11	3.2 ± 1.8	6	7.3 ± 1.3	22	3.5 ± 1.5	21	5.8 ± 1.4	24	5.0 ± 1.5	19
Test	21.0 ± 2.5	26	11.5 ± 2.3	11	5.3 ± 2.8	6	16.9 ± 3.0	22	15.9 ± 2.5	21	17.7 ± 2.5	24	14.7 ± 3.0	19
Residual	18.9 ± 2.7	26	9.5 ± 2.5	11	5.7 ± 2.6	6	17.7 ± 2.7	22	11.5 ± 2.7	21	15.3 ± 2.5	24	13.8 ± 3.2	19
Greatest distance from speaker														
Control	125 ± 11.6	26	94 ± 13.4	11	78 ± 18.9	6	103 ± 15.9	22	118 ± 7.4	21	112 ± 12.8	24	108 ± 11.2	19
Test	113 ± 14.0	26	121 ± 20.6	11	103 ± 15.2	6	105 ± 17.5	22	123 ± 10.5	21	132 ± 14.8	24	91 ± 11.4	19
Residual	97 ± 14.4	26	97 ± 18.1	11	139 ± 31.6	6	91 ± 15.2	22	116 ± 15.2	21	116 ± 14.4	24	87 ± 15.8	19
Nearest distance from speaker														
Control	62 ± 6.9	26	67 ± 9.4	11	64 ± 20.6	6	78 ± 5.1	22	48 ± 8.4	21	66 ± 5.8	24	60 ± 10.0	19
Test	32 ± 12.8	26	40 ± 10.3	11	33 ± 14.2	6	29 ± 14.5	22	39 ± 8.7	21	38 ± 13.3	24	29 ± 8.6	19
Residual	44 ± 14.0	26	47 ± 10.1	11	48 ± 16.8	6	50 ± 14.0	22	41 ± 11.7	21	48 ± 14.4	24	43 ± 9.6	19
Flights per period														
Control	2.8 ± 0.6	25	0.6 ± 0.2	11	1.3 ± 1.0	6	1.6 ± 0.7	22	2.5 ± 0.5	20	2.0 ± 0.6	23	2.0 ± 0.6	19
Test	9.6 ± 1.6	25	5.7 ± 1.0	11	5.5 ± 1.6	6	6.8 ± 1.7	22	9.3 ± 1.2	20	9.2 ± 1.6	23	6.6 ± 1.2	19
Residual	5.3 ± 0.9	25	3.5 ± 1.0	11	4.3 ± 1.3	6	4.0 ± 0.9	22	5.4 ± 0.8	20	5.3 ± 0.9	23	3.9 ± 0.7	19
Flight length														
Control	61 ± 8.1	71	110 ± 28.7	7	29 ± 7.5	8	47 ± 7.0	35	72 ± 11.2	51	57 ± 12.0	47	69 ± 10.8	39
Test	21 ± 2.3	234	36 ± 6.0	59	38 ± 5.9	35	25 ± 2.8	147	26 ± 3.0	181	23 ± 2.5	208	30 ± 3.4	122
Residual	33 ± 4.0	119	23 ± 7.3	38	33 ± 8.5	28	26 ± 4.3	77	34 ± 4.7	108	31 ± 4.2	113	31 ± 5.1	72
Longest flight														
Control	134 ± 18.8	18	112 ± 41.4	5	45 ± 25.0	2	79 ± 13.6	12	163 ± 24.1	13	124 ± 24.4	13	122 ± 22.3	12
Test	85 ± 13.5	22	89 ± 18.2	11	84 ± 17.0	6	68 ± 10.6	21	107 ± 14.9	18	91 ± 14.3	21	80 ± 11.9	18
Residual	117 ± 43.5	22	65 ± 23.1	10	102 ± 11.1	5	62 ± 10.3	19	142 ± 52.6	18	87 ± 13.7	20	118 ± 56.3	17
Shortest flight														
Control	51 ± 16.4	18	104 ± 41.3	5	8 ± 7.0	2	43 ± 14.0	12	72 ± 25.5	13	72 ± 26.3	13	43 ± 12.1	12
Test	4 ± 1.3	22	8 ± 2.9	11	11 ± 4.0	6	8 ± 2.0	21	5 ± 1.5	18	6 ± 1.6	21	7 ± 2.1	18
Residual	16 ± 6.7	22	14 ± 7.3	10	5 ± 2.6	5	17 ± 7.7	19	11 ± 4.4	18	15 ± 6.7	20	12 ± 5.8	17
Approach time														
30 feet	12.6 ± 1.7	22	5.4 ± 2.4	10	7.8 ± 4.8	4	11.2 ± 2.1	18	8.9 ± 2.0	18	9.0 ± 1.9	20	11.5 ± 2.1	16
20 feet	12.0 ± 1.6	25	3.5 ± 2.0	10	9.3 ± 3.2	6	10.8 ± 1.9	21	8.3 ± 1.8	20	9.1 ± 1.8	22	10.0 ± 2.0	19
10 feet	10.2 ± 1.6	26	1.7 ± 1.3	11	6.5 ± 3.3	6	9.1 ± 1.9	22	5.8 ± 1.6	21	7.5 ± 1.7	24	7.5 ± 1.9	19

TABLE 3. Summary of significantly differing ($P < 0.05$) means of various measures of responses of male White-crowned Sparrows to playback of recorded songs during control (C), test (T), and residual (R) periods, based on data presented in table 2.

	Response measure						
Condition	Songs per period	Greatest distance from speaker	Nearest distance from speaker	Flights per period	Flight length	Longest flight	Shortest flight
1st Exposure	T > C R > C		C > T	T > C R > C T > R	C > T C > R R > T	C > T	C > T
2nd Exposure	T > C		C > T	T > C R > C	C > T		C > R
3rd Exposure							
No young	T > C R > C		C > T C > R R > T	T > C R > C T > R	C > T C > R		C > T
With young	T > C R > C T > R			T > C R > C T > R	C > T C > R		
AM	T > C R > C			T > C R > C T > R	C > T C > R		C > T
PM	T > C R > C		C > T R > T	T > C T > R	C > T C > R		C > T C > R

"nervous" or "jittery." It was not uncommon for a male to perch on the speaker and sing, and infrequently one would peck at the speaker after each song was played.

MEASURED RESPONSES

Examination of the means in table 2 and the summary of significant differences in table 3 reveals that all responses except *greatest distance from the speaker* changed significantly from the control to the test period. *Approach time* does not apply in this connection, since all three measures of this behavior were obtained during the test period. Note, also, that in the first exposure data (table 4) significant differences (table 5) occurred between the means for *songs, flights,* and *flight lengths* during control and residual periods. Further, *flights* and *flight lengths* differed significantly between test and residual periods. Briefly, on the basis of first exposure sessions then, playback resulted in the following: 1) song rate increased; 2) subjects came closer to the speaker; 3) they flew more frequently; and 4) they flew shorter distances.

HABITUATION TO PLAYBACK

Comparison of the numbers of significant differences between means of the various control, test, and residual periods in the first, second, and third exposure columns of table 2 indicates that behavior was less markedly altered when subjects were exposed to playback a second time, and that behavior was not altered significantly when they were exposed a third time. This trend is further substantiated by comparisons of control with control, test with test, and residual with residual periods for each response between first and second exposures, first and third exposures, and second and third exposures (see table 6). While some sample sizes are admittedly small, especially for third exposure, those for *flight length* are substantial in each exposure category.

Although we lack data to examine the possibility that habituation of White-crowned Sparrows to playback is less pronounced, or even lacking, if the time lapse between exposures is lengthened, some of the subjects included here were used only every two weeks or every month.

NO YOUNG VS WITH YOUNG

Results presented in tables 2–6 clearly indicate that birds with dependent young respond differently, in some behaviors, than do birds without young, at least during the afternoon.

MORNING VS AFTERNOON

The data presented in tables 2–6 indicate that responses are very much alike in the morning and afternoon. Nonetheless, birds with young

TABLE 4. Measures of responses by male White-crowned Sparrows on first exposure to playback of recorded songs.

Measure period	With young						Without young					
	AM		PM		All trials		AM		PM		All trials	
	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n
Songs per period												
Control	5.6 ± 2.4	7	2.8 ± 1.7	5	4.4 ± 1.5	12	6.9 ± 2.7	7	9.1 ± 3.4	7	8.0 ± 2.1	14
Test	23.1 ± 6.4	7	14.4 ± 6.5	5	19.5 ± 4.6	12	22.4 ± 2.7	7	22.3 ± 5.0	7	22.4 ± 2.7	14
Residual	19.4 ± 5.6	7	9.4 ± 5.5	5	15.3 ± 4.1	12	23.3 ± 2.8	7	20.9 ± 6.9	7	22.1 ± 3.6	14
Greatest distance from speaker												
Control	137 ± 35.5	7	156 ± 17.5	5	145 ± 21.3	12	111 ± 15.5	7	103 ± 14.1	7	107 ± 10.1	14
Test	153 ± 39.5	7	108 ± 32.9	5	134 ± 26.6	12	107 ± 16.3	7	81 ± 16.4	7	94 ± 11.7	14
Residual	150 ± 30.5	7	78 ± 16.2	5	120 ± 21.2	12	90 ± 26.4	7	65 ± 27.4	7	78 ± 18.6	14
Nearest distance from speaker												
Control	49 ± 7.9	7	31 ± 5.6	5	41 ± 5.6	12	84 ± 7.2	7	74 ± 18.6	7	79 ± 9.7	14
Test	53 ± 41.6	7	29 ± 6.0	5	42 ± 23.9	12	19 ± 15.2	7	25 ± 20.8	7	22 ± 12.4	14
Residual	55 ± 41.0	7	35 ± 10.0	5	47 ± 23.6	12	50 ± 28.9	7	34 ± 20.0	7	42 ± 17.1	14
Flights per period												
Control	5.2 ± 1.7	6	3.0 ± 1.5	5	4.2 ± 1.0	11	1.3 ± 0.8	7	2.1 ± 1.2	7	1.7 ± 0.7	14
Test	15.7 ± 4.3	6	6.8 ± 2.4	5	11.6 ± 2.8	11	8.9 ± 2.5	7	7.1 ± 2.5	7	8.0 ± 1.7	14
Residual	7.8 ± 1.8	6	3.0 ± 1.3	5	5.6 ± 1.3	11	5.9 ± 2.1	7	4.1 ± 1.1	7	5.0 ± 1.7	14
Flight length												
Control	50 ± 12.7	31	100 ± 21.1	16	66 ± 11.4	47	41 ± 16.9	8	57 ± 10.6	15	50 ± 13.1	24
Test	17 ± 3.3	92	48 ± 9.1	32	24 ± 3.5	127	18 ± 4.2	57	16 ± 2.9	43	17 ± 2.6	107
Residual	36 ± 7.3	48	67 ± 12.5	13	43 ± 6.7	60	22 ± 5.1	32	22 ± 8.2	23	22 ± 4.2	59
Longest flight												
Control	155 ± 47.9	5	182 ± 33.7	5	168 ± 28.0	10	90 ± 25.2	3	92 ± 19.3	5	91 ± 14.2	8
Test	115 ± 35.2	5	130 ± 31.4	4	122 ± 22.7	9	80 ± 26.6	6	43 ± 6.4	7	60 ± 13.3	13
Residual	118 ± 27.1	5	295 ± 235.7	4	197 ± 102.1	9	68 ± 16.5	6	57 ± 20.4	7	62 ± 12.9	13
Shortest flight												
Control	54 ± 51.4	5	48 ± 22.5	5	51 ± 26.5	10	48 ± 45.8	3	52 ± 17.6	5	51 ± 18.3	8
Test	2 ± 0.7	5	3 ± 1.0	4	2 ± 0.6	9	3 ± 1.1	6	8 ± 3.9	7	5 ± 2.2	13
Residual	1 ± 0.2	5	14 ± 6.6	4	7 ± 3.5	9	27 ± 18.9	6	18 ± 13.8	7	22 ± 11.0	13
Approach time												
30 feet	10.3 ± 3.9	6	13.0 ± 4.5	4	11.4 ± 2.8	10	13.7 ± 2.8	7	13.6 ± 3.9	5	13.7 ± 2.2	12
20 feet	10.0 ± 3.9	6	9.0 ± 4.0	5	9.5 ± 2.7	11	13.7 ± 2.8	7	14.3 ± 2.8	7	14.0 ± 1.9	14
10 feet	11.0 ± 3.5	7	1.4 ± 1.4	5	7.0 ± 2.5	12	12.9 ± 2.7	7	12.9 ± 3.0	7	12.9 ± 1.9	14

TABLE 5. Summary of significantly differing ($P < 0.05$) means of various measures of responses by male White-crowned Sparrows on first exposure to playback of recorded songs during control (C), test (T), and residual (R) periods, based on data presented in table 4.

	Response measure						
Condition	Songs per period	Greatest distance from speaker	Nearest distance from speaker	Flights per period	Flight length	Longest flight	Shortest flight
With young							
All trials	T > C R > C			T > C T > R	C > T R > T		
AM	T > C R > C				C > T R > T		
PM		C > R			C > T		
No young							
All trials	T > C R > C		C > T C > R	T > C R > C T > R	C > T C > R	C > T	C > T
AM	T > C R > C		C > T	T > C			
PM	T > C		C > T C > R		C > T C > R	C > R	C > R

that were exposed for the first time made significantly longer flights in the afternoon during control, test, and residual periods than they did in the morning. Perhaps larger samples would confirm other significant differences, for example, between the numbers of songs sung by birds with young.

SEASONAL CHANGES IN RESPONSE

Although sessions were continued throughout the fall, winter, and spring, three factors contributed to our failure to obtain adequate data to reach definite conclusions regarding the seasonal changes in responsiveness. First, the response waned gradually during the fall, so that each time we conducted experiments we needed to obtain a sufficient number in one day to characterize the response at that time. That was not accomplished. Second, gradually the situation of an individual male or pair responding gave way to flock responses, so comparison between summer and winter responses was not feasible. Third, and most important, playbacks were begun in late July of 1964, so that when the response soon began to change, we could not be certain this was entirely a normal, seasonal phenomenon and not, at least in part, the result of habituation. Notwithstanding these problems, some general remarks can be made regarding seasonal differences in response, since some of our observations suggest promising lines of continued research.

It was evident that not all aspects of the response to playback were extinguished simultaneously during the fall and winter. The residual response waned before that of the test period. Next the hyperactivity (wing flicking, pivoting, hopping, and excessive flying) declined. Then the approach to the speaker disappeared. The last behavioral change to disappear was increased singing and chipping. This pattern, if it is real, reflects the loss first of the most energetically costly activities, and last of the least costly activities. The significance of such an adaptation, in terms of the bird's energy budget, is obvious. To adequately test these observations, however, would require extensive playback experiments throughout the year, employing naive subjects for each session.

In Berkeley, we used four males that held breeding territories along a row of shrubbery bordering a play field on the University of California campus. These birds were exposed to playback repeatedly, even into the winter months. During the breeding season, the subject holding the territory in which the speaker was placed responded normally. His neighbors came to the edges of their territories nearest the speaker and increased their singing rates.

During the winter, these same four birds apparently continued to occupy their respective "territories" and to sing regularly. Without careful observation, one would assume

TABLE 6. Values of t in comparisons of means of unpaired scores on various measures of responses of White-crowned Sparrows to recorded playback of songs.

Measure Period	Grouped data[a]					First exposure data[b]				
	Exposures					AM vs. PM			Young vs. no young	
	1st vs. 2nd	1st vs. 3rd	2nd vs. 3rd	AM vs. PM	Young vs. no young	Young	No young	Young vs. no young	AM	PM
Songs per period										
Test	2.24*[c] (35)	2.79*** (30)								
Residual	2.03* (35)	2.20* (30)								
Greatest distance										
Test				2.07* (41)						
Nearest distance										
Control					3.01*** (41)			3.40*** (24)		2.21* (10)
Flights per period										
Control	3.23*** (34)							2.06 (23)	2.10 (11)	
Test	2.05* (34)									
Flight length										
Control		2.88*** (77)	2.71** (13)			2.10* (44)				
Test	2.34** (291)	2.69*** (267)				3.18*** (122)				3.34*** (73)
Residual						1.97 (61)		2.65*** (117)		3.04*** (34)
Longest flight										
Control					2.82*** (23)			2.15* (16)		2.32* (8)
Test					2.14* (37)			2.38* (20)		2.72* (9)
Approach time										
30 feet	2.32* (30)									
20 feet	2.92*** (33)									
10 feet	3.10*** (35)									3.46*** (10)

[a] Tests of data in table 2.
[b] Tests of data in table 4.
[c] * $0.05 > P > 0.02$; ** $0.02 > P > 0.01$; *** $P > 0.01$. Unstarred t values approach chosen level of significance, P ranging from 0.054 to 0.051. Degrees of freedom appear in parentheses below appropriate t value.

that they defended these sites all winter. However, when a speaker was placed anywhere near the shrubbery, two, three, or even all four birds approached it. At times two birds perched on the speaker together for periods of over a minute. Never did more than one of these birds sing. However, two birds were observed singing on the ground, within 3 ft of the speaker, and in one such instance the subjects were less than 1 ft apart.

These observations relate to the presumed function of song in territorial defense and suggest that the functional significance of song may change with hormone levels. Playback techniques have promise as a means of obtaining direct evidence on the function of avian song, and situations such as that described here would seem to have promise in this connection.

DISCUSSION

MEASURING THE RESPONSE

Proper use of sound playback as a tool in field experimentation depends upon the identifica-

tion of behavioral responses that can be measured accurately and that exhibit sufficiently large and consistent changes to provide the answers we seek. While the present study indicates that most aspects of the subject's behavior changed in response to playback of recorded songs, not all aspects could be consistently measured, because the birds were concealed from view part of the time. Of those that could be measured with reasonable consistency, only one (*greatest distance from the speaker*) did not vary significantly from the control to the test period.

If the experimenter wished to determine only whether or not a male White-crowned Sparrow would respond to a given song, any of the measures used here would be sufficient. However, of these various measures, *songs, flights,* and *approach time* are the most accurately measured and could be tallied easily by a single observer. If, on the other hand, the experimenter wished to compare the intensities of responses under different, specified conditions, a wider choice of behavioral parameters should be chosen. For example, we found that first and second exposure subjects differed in their song output during both the test and residual periods, in their flights during the test periods, their flight lengths during the test periods, and in their approach times at all three specified distances. Morning and afternoon subjects, with young, and exposed the first time, differed only in their flight lengths during the test and residual periods. Birds with and without young, given first exposures in the afternoon, differed in their flight lengths during the test periods, in their longest flights during the test periods, and in their approach times at the 10-ft distance. In comparisons of this type, *greatest distance from the speaker, nearest distance from the speaker,* and *shortest flights* were essentially useless measures.

Flight length was clearly the most useful measure employed; however, this may be a result of the fact that more than one value was obtained for each subject for each observation period, so the sample sizes were usually much larger than were those for other measures. Combining the evident sensitivity of the various responses as indicators of differences in behavior under different conditions, with the ease and accuracy with which those responses can be recorded in the field, *songs, flights,* and *approach times* are the most feasible measures. Indeed, reliability of the estimate of response intensity is probably increased substantially through measurement of such a combination of qualitative and quantitative behavior differences.

FACTORS AFFECTING THE RESPONSE

Evidence clearly indicates that male White-crowned Sparrows habituated to the playback situation as presented to them in our experiments. It is possible that they learned to recognize the song used for playback through its unique characteristics or through background sounds on the tape. They might also have learned that our association with the sound meant that there was not another male intruding upon their territory. In any case, the fact that their response declined after repeated exposure to the playback situation indicates that, for this species at least, only naive subjects should be employed. Probably each species should be tested for habituation before it is employed in an experimental program. M. Tamura (pers. comm.) reported that Oregon Juncos (*Junco oreganus*) apparently do not habituate to playbacks.

In experiments such as those of Abs (1963) and Falls (1963), the possibility exists that results have been affected by subject habituation to playback, although Falls' experimental design should have eliminated any possible misinterpretations as a result of subject habituation. One of the species (White-throated Sparrow, *Zonotrichia albicollis*) with which Falls worked is congeneric with the White-crowned Sparrow, which may or may not have a bearing on its tendency to habituate to song playbacks.

The facts that subjects respond differently when they are caring for young than when they are not, and that at least under certain conditions they respond differently in the morning than in the afternoon, only add to the problem of adequately controlling the experimental situation. Other factors, e.g., age of subject, pairing status of subject, time since last natural territorial dispute, etc., may be of importance as well. Knowledge of the full range of variables that influence subjects' responses to playback would probably help to explain why those responses are so variable.

The results of the present study indicate that unless the experimenter knows, beforehand, all the variables that affect his subjects' responses to playback, efforts should be made to confine all experiments to naive subjects, to obtain an equal number of sessions in morning and afternoon periods, and to conduct a sufficiently large number of sessions to equalize other variables between groups chosen for comparison.

SUMMARY

The responses of male White-crowned Sparrows to conspecific songs played within their territories were measured in an attempt quantitatively to describe the normal response and to identify some of the variables that influence that response. Nearly the entire behavioral repertoire was markedly altered by playback, but many responses could not be consistently recorded because the subjects were occasionally hidden from view. Of the seven responses measured six differed significantly from control to test periods. Six of eight response types measured were useful in comparing the behavior of different groups of subjects. On the basis of the accuracy with which the various responses could be recorded and the usefulness they serve in comparing behavior, we conclude that the number of songs per period, the number of flights per period, and the time taken to approach the speaker after playback begins are the best measures of this species' behavior.

In comparing the responses of different groups of subjects, it was shown (1) that subjects habituated to the playback situation, with most not responding after their third or fourth exposure; (2) that subjects with dependent young responded differently than those without; and (3) that subjects responded differently in the morning than they did in the afternoon, but only when they had dependent young.

It is recommended that future studies of this sort use naive birds for each playback session, unless it has been previously established that the species concerned does not habituate to playbacks. Further, an equal number of sessions should be conducted during morning and afternoon periods; and samples should be sufficiently large to equalize other variables between groups chosen for comparison.

ACKNOWLEDGMENTS

We are especially indebted to Peter Marler for his encouragement and many useful suggestions during the course of this study. M. Ealey, J. Nelson, and M. Tamura assisted with field work. Support for this research was provided by NSF G-23737, to Peter Marler, by an NIH postdoctoral fellowship to Milligan, and by an NSF postdoctoral fellowship to Verner.

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Accepted for publication 21 July 1970.