Reproductive Condition and the Response of White-Crowned Sparrows (*Zonotrichia leucophrys nuttalli*) to Song

Abstract. *The pattern of responses of both male and female white-crowned sparrows to playback of recorded song depends on whether the female has eggs, nestlings, or fledglings, and on the behavior under consideration. These patterns can be understood in the context of the behavior patterns appropriate during each of the different stages of the reproductive cycle.*

Both naturalistic observations and systematic investigations of the function of birdsong have led to an understanding of some of the functions of song in a variety of avian species (*1*).

The most useful method of studying the function of song has been to play recorded songs to birds and to observe their responses (*2*). Most such studies assess the relative strength of one or a few salient responses selected from the total response repertoire elicited by the recorded songs. In the usual method of data analysis either nominal categories of response strength or contrasts of response levels are used. The sessions are usually of short duration and are, thereby, influenced by momentary fluctuations in responsiveness. We have analyzed an extensive time sample of an almost complete sample of the behavioral responses to recorded songs. This reduces the likelihood that the conclusions drawn reflect only a restricted aspect of the behavior system and reduces the impact of short-term changes in responsiveness.

Songs of territorial males in the local dialect were tape-recorded and played to pairs of territorial white-crowned sparrows (*Zonotrichia leucophrys*) of the sedentary Nuttall race. These birds were all mated, and the females were either brooding eggs (E), caring for nestlings (N), or had newly fledged young (F). The experiments were performed between 22 April and 30 June 1972 ($N = 9$), and between 24 March and 18 June 1974 ($N = 24$) at several sites in California: Point Reyes, Sunset Beach, Twin Peaks, and the Presidio of San Francisco. Before the experimental day the nests were located, the pair was identified, and the territorial boundaries were mapped through observation. On the experimental day, each pair of birds received eight playback trials. Each trial consisted of ten presentations of the 2-second song with an 11-second interval between songs, a 1-minute silent period, another ten song presentations, and a 5-minute silent period (*3*). In 1972, two observers recorded the occurrence of each flight and of each song by the male. In 1974, responses were recorded continuously by two observers, with a portable 20-pen Esterline-Angus event recorder. One observer recorded the following male behaviors: full songs, partial songs, flights, distance from the speaker, fright chinks, trills, wing flutters, and the number and length of attacks on other birds. The other observer recorded the number of counter songs by neighboring birds and the following female behaviors: flights, fright chinks, trills, flutters, and time in view. In addition, we noted the date and the time of day, the distance between the speaker and the nest, the distance between the experimenters and the nest, and whether another bird flew to within 15 m of the speaker (*4*).

Our primary interest was to determine potential differences in the response levels of the three groups (E, N, and F) (*5*), whether the change in the response level is the same across trials for the different groups, and whether this change is significant for each group. A direct way to obtain an answer to these questions is, first, to test for differences between regression coefficients for each of the three groups on each trial, for each of the response measures (*6*). If there are no significant differences, we can conclude that the slopes of the response curves are parallel; if there are significant differences, this means that there is an interaction between group membership and change over trials. If the regression coefficients can be considered to be from the same population, we can then test whether or not the common regression coefficient is significant; that is, whether the response level changes over trials. If the regression coefficients are the same, we can also test whether the intercepts for the groups are different, that is, whether the mean response levels differ.

For the males, the slope of the curves for the number of full songs per minute is common for the three groups and there is a significant decrement in response over trials for all three groups (*7, 8*). The intercepts are significantly different; group E sings the most, group N not as much, and group F the least (Table 1). For partial song, the curves are parallel, the slope is not significant, but the intercepts are different; group E emits more partial songs per minute than either groups N or F, which do not differ from one another. The curves for both trills and flights are paral-

Table 1. Mean number of responses to recorded birdsong by males and females with eggs (E), with nestlings (N), or with fledglings (F), and the significance levels for the common regression coefficient (*R*), intercept (*I*), and slope (*S*). The means are expressed over the 4-minute playback period. The total mean is taken over trials 2 to 8. The interval between songs (ISI) and the time in view are expressed in seconds; N.S., not significant.

Group	Responses							
	Songs			Flights (No.)	Chinks (No.)	Trills (No.)	Flutters (No.)	In view (seconds)
	Full (No.)	Partial (No.)	ISI (seconds)					
				Males				
E								
Trial 2	32.41	5.67	5.95	11.67	1.67	2.67	3.33	
Total	30.27	3.16	6.10	11.02	0.64	1.11	1.50	
N								
Trial 2	28.86	1.43	5.86	7.14	0.57	0.14	1.71	
Total	23.82	1.39	6.64	8.14	2.16	0.31	0.78	
F								
Trial 2	19.50	1.50	8.69	10.75	23.25	0.75	4.00	
Total	15.60	0.96	9.50	7.57	9.50	0.21	1.43	
P values								
R	N.S.	N.S.	< .01	N.S.	< .05	N.S.	N.S.	
I	< .01	< .01		N.S.		N.S.	N.S.	
S	< .05	N.S.		N.S.		N.S.	< .01	
				Females				
E								
Trial 2				1.50	1.33	5.25	2.42	14.50
Total				1.27	0.79	3.11	1.83	26.30
N								
Trial 2				2.43	2.00	0.43	0.00	37.57
Total				2.12	1.10	0.12	0.02	26.84
F								
Trial 2				13.00	24.75	3.00	0.75	136.50
Total				11.18	12.32	4.46	3.71	124.93
P values								
R				N.S.	< .01	N.S.	< .01	N.S.
I				< .01		< .01		< .01
S				N.S.		N.S.		N.S.

lel, there is no change in response rate over trials, and there are no differences between any of the three groups. The curves for flutters are parallel, the decrease in response level over trials is significant, and there are no differences between groups. The slopes are not parallel for either the intervals between songs or fright chinks. This means that there is an interaction between group membership and response. For intersong interval, the interaction results from the fact that group F has a longer interval than groups E and N, and the interval for this group increases slightly, while the interval is constant for the other two groups. With chinks, F is higher and decreases over trials, while the response level for the other two groups is very low.

For the females (*9*) (who do not ordinarily sing), the curves for both flight and the time in view are parallel, the slopes are not significant, and group F is at a higher level than groups E and N, which are the same. The picture for female flutters is the same, except that both groups E and F are the same and are higher than group N. The curves for female chinks are not parallel; group F is higher than E and N, which are both at zero, and there is a significant decrease in the F curve over trials. The curves for female flutters are not parallel; group N is at zero throughout, groups E and F are both at a slightly higher level, and group E significantly decreases over trials.

How are all of these results to be interpreted? First of all, it should be emphasized that, if we had arbitrarily chosen only one or a selected few of these variables as the dependent variables for study, it would be possible to argue that there are no differences in response level as a function of reproductive condition (if we had looked only at male flights, trills, and flutters), that there is a large difference in level (by looking only at song), that birds with eggs respond more than those with young (by measuring only partial song), or that birds with fledglings respond more than any other group (by counting only female flight and time in view). Similarly, by selecting variables, we could conclude that response level does not change over trials (male flight, trill, partial song, female flight, trill, and time in view), that it decreases over trials (male song and flutters), or that females with fledglings show a slight increase, while those with eggs show a slight decrease (female flutters). If no attention were paid to the reproductive condition of the birds, a major modulating influence would be left uncontrolled. This is especially serious since the breeding cycles of these birds tend to be highly synchronous. Therefore, if the research is done during a short segment of the total breeding period, it is likely that most of the birds will be in the same reproductive condition and the outcome will be biased accordingly.

Although the pattern of the above results might seem complex and confusing when considered in isolation, it is more readily understood in the context of the ongoing behavior during the different stages of the reproductive cycle. When the female is brooding eggs, she is not in view a great deal. Having no young to warn, she issues practically no fright chinks but does trill and flutter in response to the playback on the rare occasion when she does come into view. These last two behaviors seem to serve an aggressive function for both males and females; the male does not chink but he trills and flutters at the outset and ceases to do so as the playback progresses. He, then, behaves in a manner similar to that of a paired territorial male prior to the nesting season: he sings and flies about a great deal.

The female with nestlings flies about and is in view very little. She emits few trills, flutters, or chinks. In short, she is cryptic in her behavior; if she was in the nest bush when the recorded song began, she stayed there quietly; if she was out of the nest bush foraging, she remained concealed away from the nest. The male is less responsive at this stage of the reproductive cycle and stays away from the immediate region of the nest.

With fledglings, the female is in view most of the time and flies about issuing a large number of fright chinks. Since the fledglings tend to cease moving and to stop emitting begging calls when either the male or female chinks, this enhances the concealment of the young. The female also flutters and trills at a fairly high rate. The male sings less than in the other two conditions, the interval between songs is longer, he flies less, he initially chinks and flutters at a high rate, but stops doing so as the trials progress. At this stage the male is taking a more active role in the care of the fledglings, and the defensive and warning behaviors (chinks, trills, and flutters) drop out as trials progress; the male often begins to forage for insects to feed the fledglings during the later playback trials.

The data suggest that the response to song is determined by a complex interaction in which internal states may influence the intensity of the response system of both males and females, and the stage of the reproductive cycle influences the response typography.

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References and Notes

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3. Recording and playback equipment are described by L. Petrinovich and H. V. S. Peeke [*Behav. Biol.* **9**, 743 (1973)].
4. In the interest of brevity, only the data for the playback period are presented. Also, for the present purposes, not all of the environmental and behavioral variables were included since they are not germane to the issues considered in this report.
5. J. Verner and M. M. Milligan [*Condor* **73**, 56 (1971)] suggested that there may be some differences in response to playback when the pair have young compared to when they do not. Their data are difficult to interpret, however, since they found the effect only for birds tested in the afternoon, the results are confounded with habituation effects, and the analysis is based on a large number of individual *t*-tests.
6. F. N. Kerlinger and E. J. Pedhazur, *Multiple Regression and Behavioral Research* (Holt, Rinehart and Winston, New York, 1973), pp. 233–238.
7. Instead of presenting the complete figures for each group on a few selected variables, it is more informative and economical to tabulate (Table 1) the initial level as represented by the mean on trial 2 (the level of trial 1 is sometimes depressed by animals with a long first response latency) and the overall level by the mean on trials 2 through 8. Since the curves tend to be linear, and we are using a linear analytic model, a fair estimate of the trend of results for each variable can be obtained by establishing a straight line between the point at trial 2 and the mean point at trial 5.
8. Although these decrements might be an instance of habituation (*3*), a complete and detailed analysis of these data, including a series of experimental manipulations following the playback trials reported here, indicate that the effects might be due to a complex interaction of habituation, sensitization, and associative memory. To avoid the problems inherent in the habituation problem, we prefer the descriptive term response decrement for this report.
9. Although other investigators have either not reported female behavior, or have stated that the females are not responsive to playback (*5*), we observed a systematic pattern of female behavior depending on the tasks to which they were attending as a function of their reproductive condition.
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