

# THE EFFECT OF STIMULUS PRESENTATION SEQUENCE ON THE RESPONSE OF RED-WINGED BLACKBIRDS IN PLAYBACK STUDIES

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**ABSTRACT.**—I studied the responses of territorial male Red-winged Blackbirds (*Agelaius phoeniceus*) to playback of only the introductory notes of a conspecific advertisement song and to playback of the full song. The strength of response to these playbacks differed depending upon the sequence of presentation. When playback of only introductory notes preceded playback of a full song, the introductory components elicited little or no response. When playback of introductory components followed playback of full song, however, the strength of response to the introductions did not differ significantly from that to the full song. A similar effect of playback order was seen when the introductory notes of a Wood Thrush (*Hylocichla mustelina*) song were presented in sequence with a full redwing song in a similar manner. These results suggest that, after arousal by an effective control signal, birds will respond to what was initially a signal of low stimulus value. *Received 17 June 1980, accepted 7 November 1980.*

STUDIES of bird song commonly use playback procedures to determine the effectiveness of acoustic signals. Intensity of response to playbacks, however, may vary both with stage of breeding season and time of day (Verner and Milligan 1971). To minimize variability in response due to these factors and others (e.g. social interactions, territorial status, weather conditions), control and experimental stimuli should be played to an individual in rapid succession (see Shiovitz 1975). Presenting both stimuli within a short time period, however, may result in a decreased response to the second signal due to a generalized adaptation following exposure to the first signal (see Verner and Milligan 1971, Petrinovich and Peeke 1973, Krebs 1976). Conversely, a bird may show a strong response to a normally nonstimulating signal as a residual effect (Verner and Milligan 1971) of prior exposure to a signal that produced great arousal. In two complementary playback experiments involving Red-winged Blackbirds (*Agelaius phoeniceus*), I examined how the sequence of presentation of an experimental signal relative to a control stimulus may affect the intensity of response to the experimental signal.

The redwing advertisement song consists of one to six brief introductory components followed by a longer concluding trill (Marler et al. 1972; see Fig. 1). There is considerable individual variation of frequency and temporal parameters in the introductory components (Yasukawa 1981), but little in the concluding trill (pers. obs.). An earlier study demonstrated that playback of only the trill to territorial males was as effective in eliciting an aggressive response as was playback of the full song (Brenowitz in prep.). This result suggested that the trill conveys information on species identity. The first of the present experiments was initiated to investigate whether the remainder of the redwing song, the introductory components, also encodes species identity. The second experiment attempted to determine the cause of the variability in response strength with stimulus presentation sequence that was observed in the first experiment.

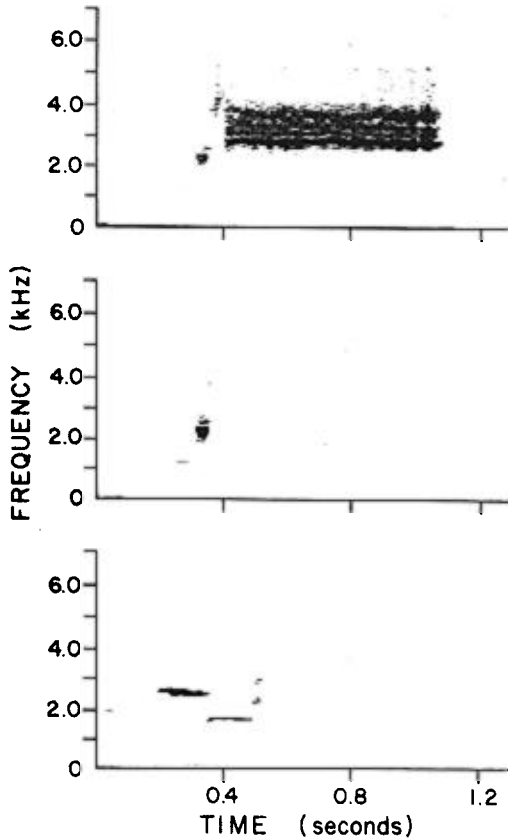


Fig. 1. Narrow-band sound spectrograms of the signals used in playbacks. **Top:** full Red-winged Blackbird advertisement song, used as the control stimulus in all experiments; **middle:** introductory components of the same full song as above, used as the experimental signal in the first set of playbacks; **bottom:** introductory components of a Wood Thrush song used as the experimental stimulus in the second series of playbacks.

### EXPERIMENT 1

*Methods.*—The first series of playbacks was performed during the breeding season, from 25 April to 21 May 1979, either in early morning (0600–0900 EDT) or early evening (1800–2000), in an upland area near Ithaca, New York. Approximately 20 male redwings, most of which were individually color-banded, defended territories in this area. The control signal used was the full song of a “stranger” blackbird, which defended a territory about 10 km from the study site. The song of this bird was recorded with a Gibson electronic parabolic microphone and a Nagra IV-D recorder and was used to minimize the chance of prior habituation to the control signal. The experimental stimulus was only the introductory components of this song (Fig. 1).

A playback procedure similar to that of Brooks and Falls (1975) was used, which allowed me to compare the responses to the introductions and to the full song both before and after exposure to the song. Tape loops were prepared of the control and of the experimental signals. A Nagra DH speaker-amplifier was placed in the center of a male’s territory. When the bird no longer appeared to react with alarm to my presence, I took 1 min of baseline observations of the three behavioral categories listed in Table 1, and I recorded the number of songs given. The redwing introductions alone were then played at 15-s intervals for 3 min at a maximum RMS sound pressure of 91 dB SPL at 1 m. Field measurements indicate that this is a typical pressure level at which redwings sing. The behavior of the focal male was monitored

TABLE 1. Behavioral hybrid index used in quantifying strength of response to signal playbacks. The numbers in parentheses are the scores assigned to each level of response. For the number of song spreads,  $D$  = the difference, regardless of sign, between the number of signals observed during the 3-min playback plus 1-min postplayback period and the number of signals expected if the playback produces no change in behavior. This expected number is generated by multiplying by four the number of times each signal was given during the 1-min baseline period.

Percentage of songs accompanied by song spread	Number of song spreads	Percentage of high-intensity song spreads
(0) None	(0) None	(0) None
(1) 1-25	(1) $0 < D \leq 5$	(1) 1-25
(2) 26-50	(2) $5 < D \leq 10$	(2) 26-50
(3) 51-75	(3) $D > 10$	(3) 51-75
(4) 76-100		(4) 76-100

during the playback period as well as during a subsequent 1-min post-playback period. After a silent interval of 5-15 min, the full song was played back in the same manner, and similar data were recorded. After another interval of 5-15 min, the introductions were again played to the same bird. No male was tested more than once.

Silent intervals between stimuli varied from 5-15 min depending upon male behavior. Males commonly left their territories for brief periods to feed, drink, or bathe nearby. If a male returned to his territory more than 15 min after termination of the previous playback period, the experiment was aborted.

The birds' responses to these signals were measured using a behavioral hybrid index scale (Emlen 1972) constructed on the basis of observations during preliminary playbacks. Table 1 presents the behavioral categories used, along with the intensity scales established for each category. The song spread, a graded visual display, constitutes the basis for the measurement of response strength, because it is the most common and conspicuous display of territorial redwings (Orians and Christman 1968), and studies have shown that gradation of its intensity indicates corresponding gradation of aggressive arousal of the bird (Nero 1956; Orians and Christman 1968; Peek 1972; Yasukawa 1978, 1981; W. Searcy and K. Yasukawa pers. comm.). In the present experiment, I rated each song spread observed as either low or high in intensity (see Orians and Christman 1968, Figs. 5 and 6). In a high intensity spread, the epaulets were completely flared and the wings fully extended. All other spreads were scored as low intensity.

The number of song spreads given by a bird during the playback period was scored in comparison with the 1-min baseline level as described in Table 1. For each male the scores for this as well as the other two categories in Table 1 were summed to give one composite estimate of response strength to playback of full song and to each of the two playbacks of introductory components.

All data were tested with a Wilcoxon matched-pairs signed-ranks test (Siegel 1956). The Wilcoxon test is a paired test that in this case was used to compare each individual's responses to the two signals. Two-tailed tests were used because the alternative hypotheses were nondirectional.

**Results.**—Table 2 presents composite scores of response for male blackbirds exposed first to playback of redwing introductions, then to full conspecific song, and finally to redwing introductions again. There was a significant difference ( $P < 0.01$ ) in the strength of response to the initial playback of the introductions and to subsequent playback of full song. A different pattern was found, however, upon comparison of scores of responses to the presentation of introductions following playback of full song. When the two signals were presented in this order, playback of introductory components evoked a response that did not significantly differ in strength from that produced by playback of full song ( $P > 0.10$ ). Furthermore, the strength of response to playback of introductions following full song was significantly greater than the response to playback of introductions before full song ( $P < 0.05$ ). Preliminary control experiments involving repeated playback of introductions, but without intervening playback of full song, failed to show any increase in responsiveness.

**Discussion.**—The introductory components of redwing song by themselves apparently do not encode species identity. This is suggested by the observation that

TABLE 2. Composite scores of response shown by Red-winged Blackbirds to playbacks of only the introductory components of conspecific song both before and after playback of full conspecific song. Asterisk (\*) indicates birds that left territory before second playback of Redwing introductory components.<sup>a</sup>

Bird number	Redwing introductorics (RI <sub>1</sub> )	Full redwing song (RS)	Redwing introductorics (RI <sub>2</sub> )
1	6	9	7
2	3	10	*
3	0	11	8
4	0	6	*
5	10	10	8
6	2	7	9
7	2	11	9
8	3	9	*
9	2	11	8
10	5	8	*
$\bar{x}$	3.3	9.2	8.2

<sup>a</sup> RI<sub>1</sub> vs. RS: Wilcoxon signed rank (two-tailed)  $T = 0$ ,  $n = 10$ ,  $P < 0.01$ . RS vs. RI<sub>2</sub>: Wilcoxon signed rank (two-tailed)  $T = 2.5$ ,  $n = 6$ ,  $P > 0.10$ . RI<sub>1</sub> vs. RI<sub>2</sub>: Wilcoxon signed rank (two-tailed)  $T = 2$ ,  $n = 6$ ,  $P < 0.05$ .

response to playback of introductorics is weak when this signal precedes the full song in the experimental sequence.

Two hypotheses can be proposed to explain elevation in strength of response to the introductorics following exposure to full song. (1) The trill portion may be necessary for species identification, but, once this identification has been made, the introductorics of that same song by themselves may be sufficient for birds to recognize the song. Particularly, redwings may be predisposed to such learned recognition of introductorics if the introductorics fulfill an important function such as the communication of individual identity. This idea is supported by consistent interindividual variation in spectral and temporal parameters of song introductorics (Yasukawa 1981; pers. obs.). (2) After a bird becomes aroused by exposure to full song, it may generalize its aggressive response to what was previously a signal of low stimulus value. The second experiment, described below, was designed to discriminate between these two hypotheses.

## EXPERIMENT 2

If the variation in response strength to introductorics before and after full song seen in Experiment 1 was due to learned recognition (hypothesis 1 above), then substituting an unrelated signal for the redwing introductorics should prevent an enhanced response to the experimental stimulus after exposure to full song. Alternatively, if the effect is due to generalized arousal (hypothesis 2), then variation in response with playback order will still be observed.

*Methods.*—This series of playbacks was conducted from 18 May to 12 June 1979 at the same study site and at the same times of day as in Experiment 1. The control signal in the present playbacks was the same full redwing song as in the preceding experiment, but the experimental signal consisted of the introductory components from the song of a Wood Thrush (*Hylocichla mustelina*) recorded in Ithaca (Fig. 1). This signal was chosen because it is generally similar in its spectral and temporal parameters to introductorics of eastern redwing songs but differs in several specific ways from those found in the particular redwing song used as a control in this investigation. In addition, it is unlikely that the two species often come into direct contact because they occupy different habitats, and so the introductorics of thrush song would be of low stimulus value to blackbirds.

TABLE 3. Composite scores of response shown by Red-winged Blackbirds to playbacks of heterospecific (Wood Thrush) introductory song components both before and after playback of full conspecific song. Asterisk (\*) indicates birds that left territory before second playback of Wood Thrush signal.<sup>a</sup>

Bird number	Thrush introductions (TI <sub>1</sub> )	Full redwing song (RS)	Thrush introductions (TI <sub>2</sub> )
1	6	6	*
2	2	0	*
3	0	8	9
4	2	11	10
5	0	11	11
6	0	6	0
7	0	9	8
8	3	0	*
9	0	9	11
10	0	10	2
$\bar{x}$	1.3	7.0	7.3

<sup>a</sup> TI<sub>1</sub> vs. RS: Wilcoxon signed rank (two-tailed)  $T = 3$ ,  $n = 9$ ,  $P < 0.02$ . RS vs. TI<sub>2</sub>: Wilcoxon signed rank (two-tailed)  $T = 6$ ,  $n = 6$ ,  $P > 0.05$ . TI<sub>1</sub> vs. TI<sub>2</sub>: Wilcoxon signed rank (two-tailed)  $T = 0$ ,  $n = 6$ ,  $P = 0.032$ .

The playback procedure used in this series was the same as that described for the first set of playbacks, with the Wood Thrush introductions substituted for the redwing introductions. The same behavioral categories were used in measuring strength of response. Data were tested with two-tailed Wilcoxon matched-pairs signed-ranks tests.

**Results.**—Response to the initial presentation of thrush introductions was significantly weaker than that to full redwing song ( $P < 0.02$ ; Table 3). No significant difference ( $P > 0.05$ ) was found, however, between strength of response to full redwing song and to subsequent presentation of thrush introductions. Thus, when Wood Thrush introductions followed full redwing song in the playback sequence, the level of response to the thrush signal was elevated significantly above that seen when this signal preceded the full redwing song ( $P = 0.032$ ).

**Discussion.**—Intensity of response of blackbirds to both redwing and Wood Thrush introductory song components depended upon order of presentation relative to full conspecific song. For both experimental signals, an aggressive response comparable in strength to that elicited by full song was observed only after previous exposure to this full song. It therefore seems that the elevation in response strength was not due to learning of redwing introductory components during prior exposure to the entire song, but rather to the fact that the control stimulus aroused the males and sensitized them to subsequent presentation of what were previously nonstimulating signals.

An arousal response such as I propose here may be adaptive for territorial male redwings. Playback of an unfamiliar redwing song to a territorial male may represent a conspecific trespasser. Allowing a trespasser to remain on his territory exposes the territory holder to the disadvantages of cuckoldry, because the intruder could copulate with the male's mates (Bray et al. 1975). If the test bird cannot visually locate an intruder after acoustically detecting one, it might be beneficial for the territory holder to remain in an aroused state and to react aggressively to any stimuli that are suggestive of a conspecific intruder for some time after the initial detection. It may be well worth the relatively low time and energy expenditure involved in unproductive aggressive behavior, which consists mostly of songs and visual displays, if a possible reduction in reproductive success from cuckoldry can be prevented.

The results of this study can be of practical value to investigators using playback methods (see also Verner and Milligan 1971). If the researcher wants to determine whether birds are being sensitized to what are actually neutral stimuli, he or she can vary the order in which signals are presented and compare the responses from the different sequences in the way I have described. The effect of such sensitization may be reduced by increasing the interval between presentation of the different signals. Further research should be conducted to test this prediction. In addition, response strength in playback studies should always be quantified relative to baseline levels measured immediately preceding presentation of the first signal.

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