

TESTS OF HABITUATION TO SONG REPERTOIRES BY CAROLINA WRENS

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ABSTRACT.—In a series of playback experiments with Carolina Wrens (*Thryothorus ludovicianus*), each with 25–43 song types, I tested the effect of song repertoires on habituation in simulated long-range countersinging between territorial neighbors by playing back songs 75 m or 100 m outside the territorial boundary of each subject. One experiment tested differences in response to six repertoire sizes during 15-min continuous playbacks. A second experiment tested habituation to four different repertoire sizes over 2 h of intermittent playbacks. In both experiments birds sang more in response to playbacks than to controls. The response to playbacks of single song types did not decline over time. The subjects did not respond differently to large repertoires compared to single songs, nor did different sizes of repertoires affect the changes in the birds' responses over time. The results provide no evidence for an effect of song repertoires in reducing habituation to neighboring intruders. Species like the Carolina Wren, in which individuals communicate over long distances by repeating the same song, might in fact evolve resistance to habituation to acoustically simple, repeated signals. Received 11 April 1983, accepted 20 October 1983.

SINCE Hartshorne's exposition of the "anti-monotony" hypothesis (Hartshorne 1956, 1973), there has been interest in whether or not birds use song repertoires to reduce the effects of habituation (Dobson and Lemon 1975, Falls 1978, Kroodsma 1978, Catchpole 1979, Krebs and Kroodsma 1980). The hypothesis predicts that birds that sing for extended periods of time use repertoires of different song types and that such behavior reduces habituation to the signal by listeners. In this study, I use a new method to test empirically the responses of Carolina Wrens (*Thryothorus ludovicianus*) to repertoires of different numbers of songs played back outside their territorial boundaries. Here, habituation is operationally defined as a decrement over time in frequency or intensity of a response to a continuous or repeated stimulus (Thorpe 1963, Hinde 1970).

One way to evaluate the effect of habituation to song is to test the response of listeners to different repertoires of song types. Several workers have examined habituation to repeated single songs and repertoires by territorial birds (Lemon et al. 1981, references cited below). In these studies, birds responded to

played-back songs with an initial increase in rate of response, followed by a decrease in response over time, a pattern characteristic of the dual processes of sensitization and habituation (Thompson et al. 1973). In the White-crowned Sparrow (*Zonotrichia leucophrys*), a species with one song per bird, the number of flights and songs used in response to playbacks of repeated song declined over time (Verner and Mulligan 1971, Petrinovich and Peeke 1973); the reproductive state of the female and "response state" of the male influenced the pattern of the response curve (Patterson and Petrinovich 1979; Petrinovich and Patterson 1979, 1980). Great Tits (*Parus major*), each with 2–7 song types per bird, habituated more slowly to played-back repertoires of 4 song types than to single songs (Krebs 1976). Experiments with Red-winged Blackbirds (*Agelaius phoeniceus*) compared the effects of repertoires of 2, 4, or 8 song types to single songs and found presentation of multiple song types slowed the rate of habituation of song-spread display intensity (Yasukawa 1981).

These studies of responses of territorial birds to played-back songs used similar methods. In all cases the playback apparatus was erected inside the territory of the subject and thus permitted the subject to approach closely. Other workers using playbacks of songs have shown how the location of the playback speaker in the territory affects the behavior of the subject (Falls

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and Brooks 1975, Wiley and Wiley 1977, Mellemis and Falls 1982). The effect of repertoires was enhanced when Krebs (1976) alternated presentation through two speakers at two sites in the territory instead of one speaker at one site. Changing the source of the stimulus caused a renewal of response in other habituation tests as well (Shalter 1975).

In response to playbacks inside its territory, the resident typically approaches the playback speaker, flies back and forth in an agitated fashion, sings, and displays other territorial behaviors. Carolina Wrens respond with a silent approach, followed by repeated songs and short flights near the speaker (Richards 1981b, pers. obs.). In testing habituation, investigators have measured the latency to approach, the number of flights near the speaker, the number of songs, and the intervals between songs. Although the waning of these behaviors suggests habituation, once the bird approaches the speaker it can gain experience about the playback situation in addition to the acoustic stimulus. In particular, the bird can learn that the expected visual stimulus is not present. The playing back of songs from a speaker inside the subject's territory thus leaves open the possibility that this additional experience, rather than habituation, might explain the decreased response.

One solution to this problem is to present the stimulus outside the bird's territory, where the bird will not approach. In this way, the playback simulates a nearby territory holder. Such experiments also test birds' responses to songs played back over long distances when the strength of the signal is lowest and habituation should be most rapid (Hinde 1970). In the following experiments I tested the responses of Carolina Wrens to different sizes of repertoires of song played back outside their territorial boundaries and thus simulated the stimulus of a new neighbor.

Carolina Wrens are highly territorial, monogamous, woodland birds. Males use their repertoires of 25–43 song types to countersing with neighbors throughout the year. They countersing with played-back song in a similar way. Typically birds sing at a rate of 9 songs/min. Songs consist of 2–12 (usually 4–6) identical syllables, each 0.169–0.620 s in duration (Borror 1956, Richards 1978, Simpson 1982). On mornings in spring, during 1 h, wrens sing on average 14 min of song in seven bouts of 2 min each. Birds commonly use 3–6 different song

types per hour in long-range countersinging. At short-range, wrens use their songs quite differently, switching rapidly between songs (Simpson 1982).

Territory sizes of Carolina Wrens vary with the density of wrens. In spring, density is a function of the severity of the preceding winter (pers. obs. 1978–1981, Morton 1982). During the spring of 1980 and 1981 when these experiments were conducted, territories averaged about 1 ha; center-to-center distance between territories was 100–150 m.

Two series of playback experiments are described separately below. Both Experiment A and Experiment B tested the responses of wild Carolina Wrens to different sizes of repertoires played back outside their territorial boundaries from distances usual for neighboring wrens in long-range interactions.

GENERAL METHODS

The experiments were conducted at the Behavioral Research Station at the North Carolina Botanical Garden and adjacent woodlands (Wiley 1977). The study area consisted of mature woodlands and fields in varying stages of succession. In spring, wrens held territories in the forests and along margins of woods, old fields, and streams. No territories included the centers of the fields, although later in the year young birds attempted to set up territories in those areas. To minimize responses of the subjects' neighbors and to simulate a new territory-holder, I set up the playback apparatus in these fields, 75 m (Experiment A) or 100 m (Experiment B) from each subject's territorial boundary. Experiments were conducted from 17 April through 23 June 1980 (Experiment A) and from 23 May through 5 June 1981 (Experiment B) on sunny days between 0600 and 0900.

The playback apparatus consisted of a Sony TC45 cassette tape recorder, an Amplivox S-610C portable amplifier, and a Realistic Minimus 7 speaker. The speaker was erected on a tripod 1.5 m above the ground and directed toward the bird's territory. Peak volume for played-back songs was 85 dB (re: 0.0002 dynes/cm²) measured at a 1-m horizontal distance from the speaker with a Realistic 42-3019 sound level meter (settings: fast response, C weighted). The song types used in playback tapes had been recorded in 1979 (Experiment A) or 1980 (Experiment B) from wrens captured from the local population. All songs were recorded within 1 m of a singing bird. The song types occurred in repertoires of at least 50% of the wrens previously recorded in the study area. None of the playback songs was recorded from the experimental subjects or neighbors of the subjects to avoid confounding the results with the "neighbor-stranger" recognition effect (Lemon 1967, Brooks and Falls

TABLE 1. Protocols for Experiment A, consisting of 6 parts. As described in the text, each 15-min playback period was preceded by a 15-min pre-experimental period and followed by a 15-min postexperimental period.

Experiment	Playback period
A-1	1 song type for 15 min
A-2	5 song types, each for 3 min
A-3	8 song types, each for 1.9 min
A-4	15 song types, each for 1 min
A-5	2 song types, alternating for 15 min
A-6	15 song types, alternating for 15 min

1975, Kroodsmma 1976, Wunderle 1978, Schroeder 1980, Yasukawa et al. 1982). The number of syllables per song type varied from three to four. All song types were played back at a rate of 10 songs/min.

In each year, for several weeks before the presentation of the experiments, I determined the boundaries of each bird's territory by plotting its singing locations on a map of the area. Each subject, individually marked with colored leg bands, was a mated adult male territory holder. Although I did not control for reproductive state, all birds of known reproductive stage (50% of the subjects) were caring for nestlings or fledglings.

EXPERIMENT A

METHODS

Experiment A (Table 1) tested the responses of Carolina Wrens to different sizes of repertoires of played-back song. I used a protocol of three 15-min periods: a pre-experimental period, a playback period, and a postexperimental period. The 15-min playback period corresponded to the maximum time I had recorded a wren singing one song type without interruption. During the pre-experimental and postexperimental periods, I monitored the songs given by the subjects in the absence of playback. I could compare each experimental trial with the pre-experimental control and evaluate any residual effects of the experiment by comparing it with the postexperimental period. This experimental design has been used by other investigators (Brooks and Falls 1975, Falls and Brooks 1975, Krebs 1976, Richards 1981a, Searcy et al. 1982) and thus permits comparisons across species. Because each bird served as its own control, individual differences in response attributable to reproductive stage or other "state" variable are taken into account.

There were six playback protocols, each with a different number of songs or a different sequence of

switching song types. In all cases, the playback ran for 15 min continuously. In Experiment A-1, the playback consisted of one song type played for 15 min. In Experiment A-2, the playback consisted of five song types, each played for 3 min. In Experiment A-3 there were eight song types, each played for 1.9 min. In Experiment A-4 the playback had 15 song types, each played for 1 min. In Experiment A-5, there were two song types alternating after each rendition. Such alternations are occasionally used by wrens for 1 or 2 min. In Experiment A-6, the playback switched to a new song type after each rendition; the tape included 15 different song types.

At times, wrens switch rapidly among many song types. I predicted that if repertoires were important in long-range communication, the response to Experiment A-6 would be greater than the response to Experiment A-4, which in turn would be greater than the response to A-3 and so on, with the lowest response to Experiment A-1. Comparing the results of Experiment A-5 with Experiment A-6 would separate the effects of rapid switching rate and low recurrence interval with rapid switching rates and high recurrence interval. Recurrence interval is the number of songs between any occurrence of one song type and its next occurrence.

For Experiment A-1, I randomly selected among three tapes so that I could compare the effects of particular song types (types #9, #28, #57, Fig. 1). For Experiments A-2 through A-6, I used the same tape for each experiment. I was also able to test whether or not birds habituated to one type played back for 15 min (Experiment A-1).

The subjects were 10 adult male Carolina Wrens. I set up the playback apparatus 75 m outside the subject's territory. For each subject, I randomized the order of presentation of experiments. If during the first trial the subject approached the speaker or did not respond with countersinging during the first 5 min of the playback experiment, I terminated the experiment, then took several days to recalculate his territory before retesting him with a different tape. Each subject received one experiment on each of six sequential days, weather permitting. Because I was primarily interested in comparing each bird's responses to the different playbacks, I tested each bird at the same time of day, although times varied between birds. Birds on neighboring territories were never subjects of successive experiments until at least one week had passed.

I recorded the vocalizations of the experimental subjects continuously during the 45 min of each experiment (10 birds \times 6 trials/bird \times 0.75 h/trial = 45 h of experimental data). The recording equipment consisted of a Sennheiser directional microphone (ME 80 and K2-U battery pack) and a Nagra 4.2 reel-to-reel tape recorder or a Dan Gibson parabola with microphone and a Uher Report L reel-to-reel tape recorder. In the laboratory I edited the tapes by play-

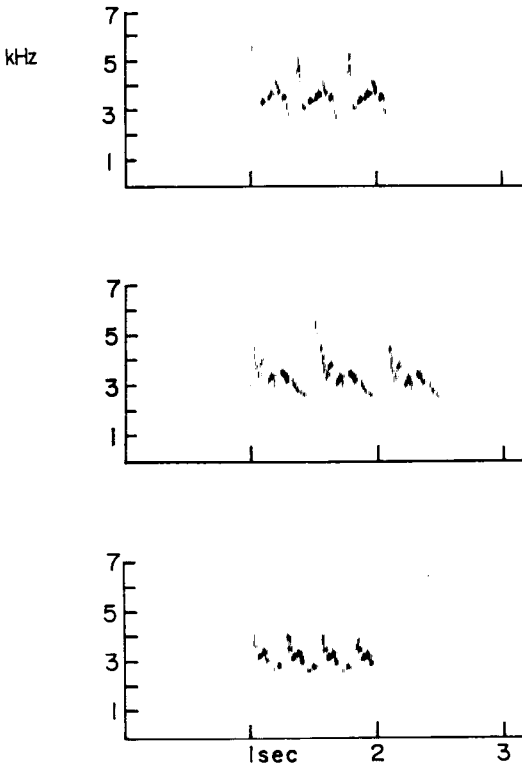


FIG. 1. Three song types used in Experiment A.

ing them back on a Tandberg Series 15 reel-to-reel tape recorder. A sample of each song type was analyzed on a real time spectrum analyzer (Spectral Dynamics Corporation, Model SD 301D, analysis range 50k limited to 10k, band width 150Hz, memory period 10ms; Hopkins et al. 1974).

I cataloged each song type by overlaying an acetate trace of its spectrographic pattern on one of 150 different reference types previously recorded. Because of environmental noise and degradation of song types over distance, I was not able to classify all songs, although I could always distinguish changes from one song type to the next. From detailed notes taken during the experiments and data from tapes, I determined the number of minutes of song (rounded to the nearest 0.25 min) and the number of different song types. When possible, I noted whether or not a neighbor's song matched the song of the subject or playback.

RESULTS

There was no effect of the order of experiments on the total number of minutes of song (Page's Test for Ordered Alternatives, $n = 10, k = 6, L = 666.5, NS$; Hollander and Wolfe 1973).

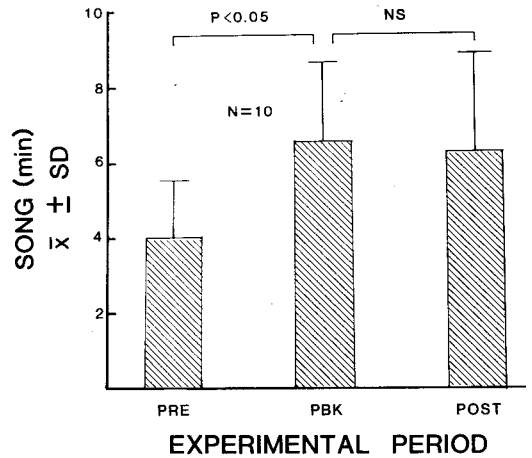


Fig. 2. Mean minutes of song by each of 10 birds during pre-experimental periods (PRE), playback periods (PBK), and postexperimental periods (POST) for six experiments each of Experiment A. Birds sang more in playback periods than in pre-experimental periods (Wilcoxon Matched-pairs Signed-ranks Test, $n = 10, T = 6, P < 0.05$, two-tailed). Birds did not sing more during playback periods compared to postexperimental periods (same test, $n = 10, T = 24.5, P \gg 0.05$, two-tailed, NS).

Subjects responded clearly to the playbacks, regardless of the pattern of song types included. Over all experiments, birds sang for more minutes during playback periods and postexperimental periods than during pre-experimental periods; birds did not sing more during playback periods than during postexperimental periods (Fig. 2). There were more song types used during playback periods than during pre-experimental periods (Wilcoxon Matched-pairs Signed-ranks test, $n = 10, T = 1, P < 0.01$, two-tailed), but no more than in postexperimental periods (same test, $n = 10, T = 14, P > 0.05$, two-tailed).

In contrast to the clear responses to playbacks, regardless of the patterns of song types included, there were no differences in responses to the six different protocols for playback (Fig. 3). Birds did not sing more song types in response to playbacks of larger repertoires (Experiment A-6 versus Experiments A-1, A-2, A-3, A-4, or A-5, Sign Test, $n = 10, P \gg 0.05$, two-tailed, for all pairwise comparisons) or with faster switching rate (Experiment A-5 versus Experiments A-1, A-2, A-3, A-4, or A-6, Sign

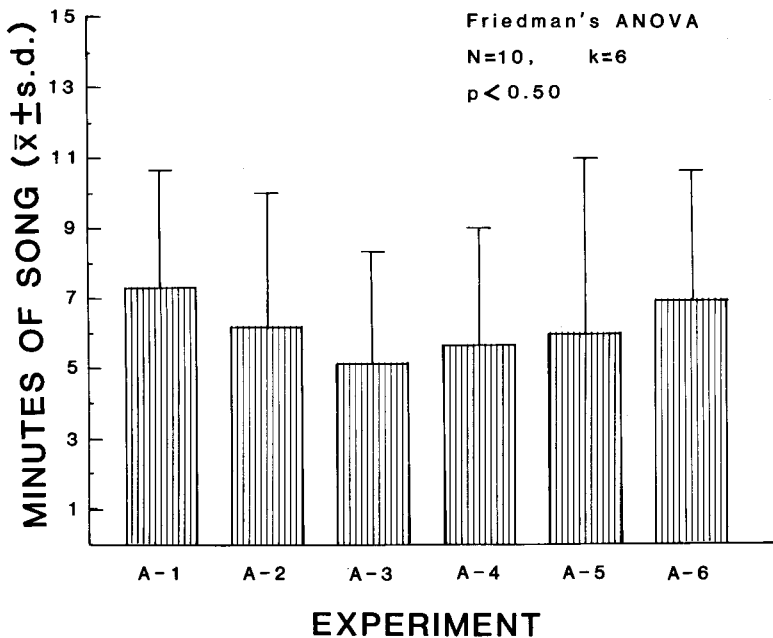


Fig. 3. A comparison of the minutes of song in response to six protocols of playback in Experiment A (see Table 1). There were no differences between experiments (Friedman two-way ANOVA, $n = 10$, $k = 6$, $P < 0.50$, NS).

Test, $n = 10$, $P \geq 0.05$, two-tailed, for all pairwise comparisons).

There was no difference in the amount of singing in response to the three different song types used in Experiment A-1 (Mann-Whitney *U*-Test, comparing number of minutes of song in response to song type #9 and song type #57, $n_1 = 3$, $n_2 = 4$, $U = 3$, $P = 0.40$, two-tailed; comparing #9 and #28, $n_1 = 3$, $n_2 = 3$, $U = 3$, $P = 0.70$, two-tailed, NS; comparing #28 and #57, $n_1 = 3$, $n_2 = 4$, $U = 3$, $P = 0.40$, two-tailed, NS). There was no habituation during Experiment A-1. The number of minutes of song did not decline over the three 5-min periods of the playback (Page's test, $n = 10$, $k = 3$, $L = 121$, NS).

Matching in response to played-back song types occurred rarely during the 60 experimental periods. Two birds matched one song type each during Experiment A-3, and two birds matched one song type each during Experiment A-4. One bird matched song types twice with a neighbor during Experiment A-3. Of the bouts of countersinging with neighbors that I noted, two birds matched song types with neighbors during pre-experimental periods, and three birds matched song types with neighbors

during postexperimental periods, once after Experiment A1 and twice after Experiment A-3. I was not always able to monitor singing by neighbors during the experiments, however.

DISCUSSION

In Experiment A, Carolina Wrens responded to playbacks by increasing the number of minutes of song and the number of song types used during pre-experimental periods. There were no differences in responses to six played-back songs of six repertoire sizes when playbacks were set 75 m outside the boundary of the subject's territory. Repertoires were no more effective than one song at distances comparable to those between neighbors. Although wrens rarely used song types that matched the playbacks, the capacity to match particular song types suggests that birds can distinguish them at far distances. This provides indirect evidence that the similarity in response to the six experiments is not due to the inability of wrens to recognize differences between songs. Because I did not obtain the complete repertoires of the subjects, I was not able to calculate the

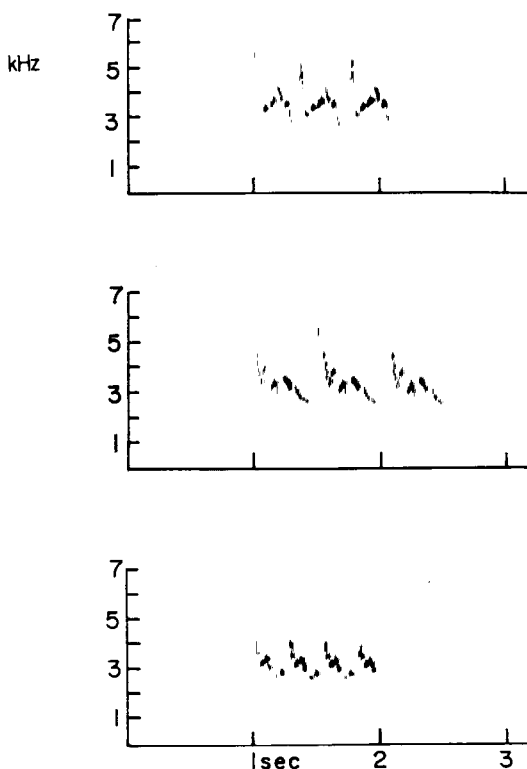


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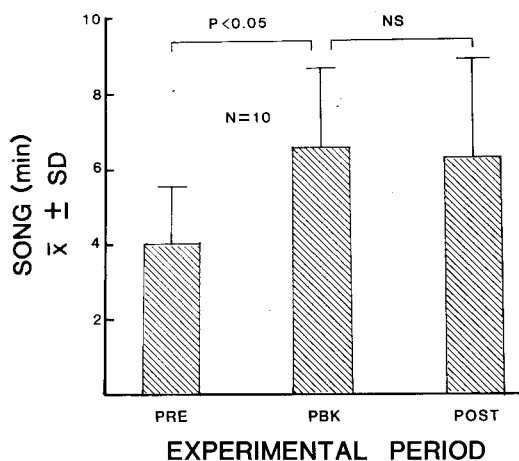


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Subjects responded clearly to the playbacks, regardless of the pattern of song types included. Over all experiments, birds sang for more minutes during playback periods and postexperimental periods than during pre-experimental periods; birds did not sing more during playback periods than during postexperimental periods (Fig. 2). There were more song types used during playback periods than during pre-experimental periods (Wilcoxon Matched-pairs Signed-ranks test, $n = 10$, $T = 1$, $P < 0.01$, two-tailed), but no more than in postexperimental periods (same test, $n = 10$, $T = 14$, $P > 0.05$, two-tailed).

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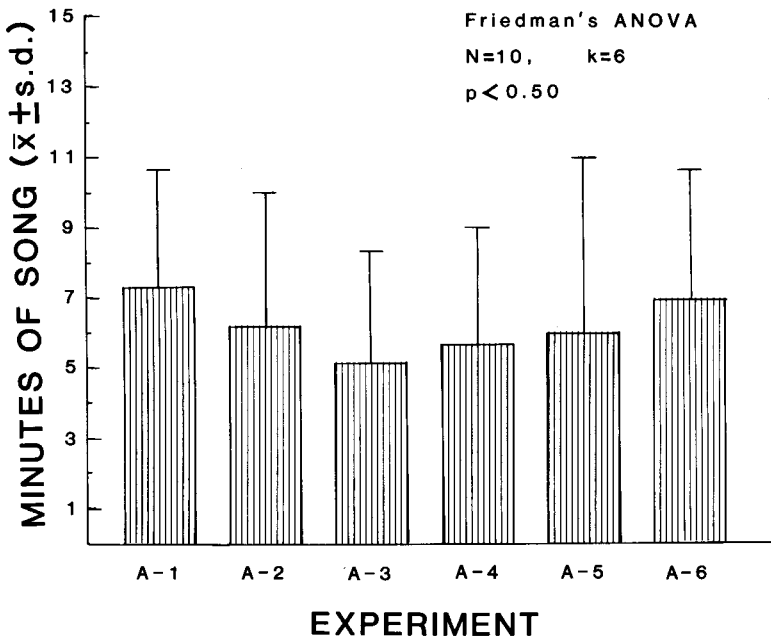


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Test, $n = 10$, $P \gg 0.05$, two-tailed, for all pairwise comparisons).

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DISCUSSION

In Experiment A, Carolina Wrens responded to playbacks by increasing the number of minutes of song and the number of song types used during pre-experimental periods. There were no differences in responses to six played-back songs of six repertoire sizes when playbacks were set 75 m outside the boundary of the subject's territory. Repertoires were no more effective than one song at distances comparable to those between neighbors. Although wrens rarely used song types that matched the playbacks, the capacity to match particular song types suggests that birds can distinguish them at far distances. This provides indirect evidence that the similarity in response to the six experiments is not due to the inability of wrens to recognize differences between songs. Because I did not obtain the complete repertoires of the subjects, I was not able to calculate the

probabilities of matching the playbacks. In previous studies (Simpson 1982), however, in which I controlled the distance between captive wrens, males matched more often than expected by chance at even greater distances than used in these experiments (140 m).

There was no evidence of habituation to a single song type played back for 15 min, the maximum time I had recorded a wren singing one song type continuously. Wrens often sing one song type intermittently for longer periods, however. Fifteen minutes may be too brief to test the hypothesis that birds habituate to one song over time. Experiment B was designed to examine the effect of repertoires on habituation to songs played back intermittently for 2 h.

EXPERIMENT B

METHODS

In this experiment, the effects of four repertoire sizes played back intermittently for 2 h were examined. As in Experiment A, normal singing rates for wrens were simulated, and methodological conventions for habituation experiments established in the literature were followed (Krebs 1976), except that playbacks were presented outside the subject's territory. Subjects were six adult male Carolina Wrens.

I set up the playback apparatus 100 m from the edge of each bird's territory. This distance was chosen to reduce the occurrence of a subject leaving its territory to approach the speaker. On each test day, I conducted either a control observation or one of four experiments on the experimental subject (Table 2). If instead of remaining on its territory and countersinging with the tape, the bird flew to the speaker, I discontinued the test and reassessed the bird's territorial boundaries before restarting the series (one occasion). In addition, I abandoned the experiment if the subject failed to sing within 24 min after start (eight occasions).

I presented one experiment or control in a randomly assigned order on alternate days. After the conclusion of one series of experiments, birds with territories within approximately 200 m of playbacks were not used as subjects for at least 1 week.

Playbacks followed the pattern of 2 min of song followed by 6 min of silence. There were 15 of these 8-min periods in each experiment. During each 2-min playback period, only one song type was played.

Experiment B-1 consisted of one of four randomly selected song types played for 2 h. Habituation, if it occurs, should be most pronounced during Experiment B-1. For Experiment B-2, I played four different song types in four sequential 8-min periods; there-

TABLE 2. Protocols for Experiment B, consisting of 4 parts and a control period. Each 2-h playback consisted of 15 time periods. Each time period included 2 min of playback followed by 6 min of silence. Song types are indicated below by letters.

Experiment	Number of song types	Time periods														
		1	2	3	4	5	6	7	8	...	15					
B-1	1	A	A	A	A	A	A	A	A	A	...	A				
B-2	4	A	B	C	D	A	B	C	D	...	C					
B-3	2	A	B	A	B	A	B	A	B	...	A					
B-4	2	A	A	A	A	A	A	A	A	B	...	B				
Control	0	No playback														

after, I repeated the same sequence of song types for 2 h. If repertoires reduce habituation, response to Experiment B-2 should decline less rapidly than response to Experiment B-1. Experiment B-3 consisted of two song types alternating in each 8-min period. Thus, Experiment B-3 was similar to Experiment B-2, but it included fewer song types. During Experiment B-4, I played one song type for 1 h and a second song type for the 2nd hour. If habituation occurred in the 1st hour, there should be a recovery of response when I switched song types at the start of the 2nd hour.

For controls, I monitored the singing rate of each bird from the playback site in the absence of playback. Controls allowed me to determine any effect of the time of day that might confound interpretation of the results.

For each experiment and control, I noted the number of songs given by the subject and the occurrence of song matching the playback.

RESULTS

Each bird sang more songs during experiments regardless of the pattern of playbacks than during the control periods (Fig. 4). On the other hand, there were no differences between the number of songs in response to the four experimental treatments (Friedman two-way ANOVA, $n = 6, k = 4, X^2 = 5.2, P < 0.20, NS$).

Changes within the 2-h control and experimental periods could result from habituation or from normal changes with the time of day. To facilitate analysis of these changes, I combined the 15 8-min periods for each experiment or control into five longer periods of 24 min each. The absence of a decline in the number of songs over time during control periods indicated that there was no effect of the time of

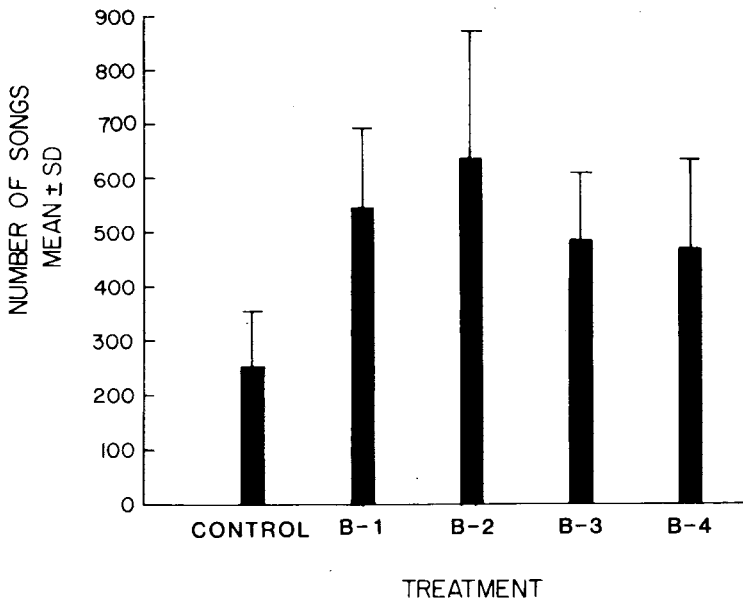


Fig. 4. Number of songs in response to four experimental conditions and controls (mean \pm SD) in Experiment B. Response to each experiment was greater than the control (Wilcoxon Matched-pairs Signed-ranks test, $n = 6$, $T = 0$, $P < 0.05$, two-tailed, for all pairwise comparisons). There were no differences between experiments (Friedman's ANOVA, $n = 6$, $k = 4$, $X^2 = 5.2$, $P < 0.20$, NS).

day during the 2 h employed for experiments. Similarly, for each of these experiments, there was no significant decline in the number of songs over time (Fig. 5). When I combined all experiments in a *post-hoc* analysis, however, I did find a significant decrease in the number of songs over time (Page's test, $n = 4$ experiments, $k = 5$ time periods, $L = 256$, $P < 0.0001$). It is possible that the controls would yield comparable results if sample sizes were similarly increased four-fold. Alternatively, there might have been an overall reduction in the stimulatory effect of the playbacks over time.

There was also a decline in responsiveness over the entire experimental series. The birds responded less to the presentation on the last day than on the first day. When order of tests was statistically controlled in a main-effects model, however, the experimental outcome was not altered. The number of songs during each experiment differed significantly from control periods (Statistical Analysis System, General Linear Model, each experiment versus control, $n = 6$, $df = 14$, two-tailed; Experiment B-1, $t = 3.76$, $P < 0.002$; Experiment B-2, $t = 3.03$, $P < 0.009$; Experiment B-3, $t = 2.08$, $P < 0.056$; Ex-

periment B-4, $t = 2.29$, $P < 0.038$). The results of the four experiments were not significantly different (ANOVA, $df = 3$, $F = 1.58$, $P > 0.05$, NS).

To determine the effect of switching song types after 1 h in Experiment B-4, I tested whether or not there were fewer songs during the 16 min before the switch of song compared to the 16 min after the switch of song. There was no tendency for birds to increase singing rates after the switch (Wilcoxon Matched-pairs Signed-ranks Test, $n = 6$, $T = 12$, $P > 0.05$, one-tailed, NS).

Birds matched played-back songs only three times during the 48 h of playbacks, one time each to Experiments B-2, B-3, and B-4.

DISCUSSION

In summary, these experiments demonstrate a clear effect of playbacks outside a bird's territory compared to controls. They provide no empirical support, however, for the hypothesis that song repertoires reduce habituation in long-range interactions of territorial Carolina Wrens.

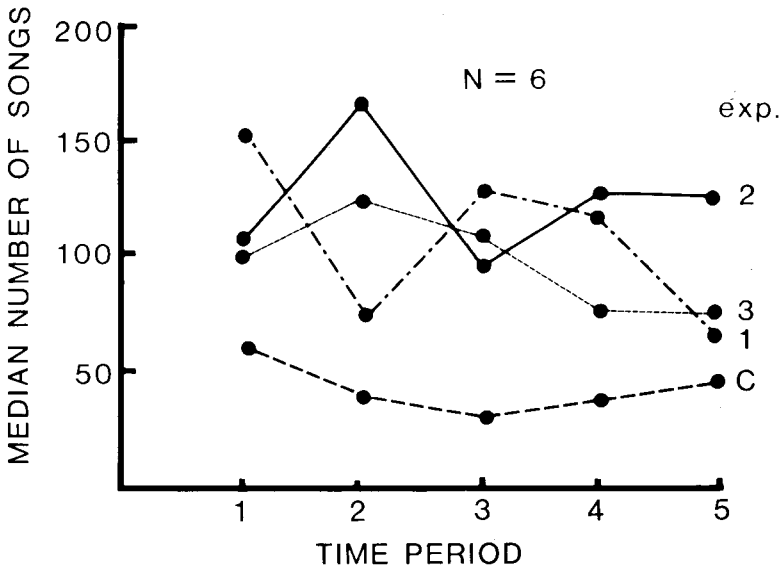


Fig. 5. Median number of songs during experiments and controls for six birds. Each trial, lasting 2 h, was divided into five equal time periods of 24 min each. There was no significant decline in number of songs over time for the controls (Page's test, $n = 6, k = 5, L = 258, NS$) or Experiments B-1 through B-3 (Page's test, for each experiment, $n = 6, k = 5$; Experiment B-1, $L = 259, NS$; Experiment B-2, $L = 256, NS$; Experiment B-3, $L = 246, NS$). In addition, none of the slopes differed from zero (Thiel Nonparametric Regression Test, Control, $C = -4, P = 0.242$; Experiment B-1, $C = -6, P = 0.592$; Experiment B-2, $C = 0, P = 0.059$; Experiment B-3, $C = -6, P = 0.117$, all NS, Hollander and Wolfe 1973).

GENERAL DISCUSSION

Unlike previous investigations, these experiments test habituation by means of songs played back outside the territory of the subject. This method (1) avoids possible effects of additional experience gained by the subject's approach to the playback speaker and (2) more realistically simulates long range communication in which the effect of habituation to a stimulus should be strongest. When tested for time periods at the limits of normal singing by wrens, the results fail to confirm that habituation affects response, as measured by the number of songs. There was no evidence of habituation to single song types played back for 15 min continuously (Experiment A) or 2 h intermittently (Experiment B). In all cases birds increased song rates in response to Experiments A and B compared to controls. When all trials of Experiments B were pooled, this response declined over time.

It is possible that birds could not differentiate song types at long range. This would explain the similar responses to all sizes of play-

back repertoires in Experiments A and B. Convergence of signals with different frequencies over distance might mask differences between them (Brenowitz 1982). In Experiment A, I found it impossible to classify sonograms of bird songs recorded from 100+ m, because classifying the songs required recognition of similarities in fine structure, which degraded over distance. Even though I could not always classify the song types, however, I could recognize audible and spectrographic differences when song types changed even at great distances; it is likely that the wrens can do at least as well. The ability of Carolina Wrens to match long-range signals (Simpson 1982) is evidence that they can distinguish particular song types. The rarity of matching the playback might indicate that it is not always possible for wrens to do so or that in Carolina Wrens matching does not have a role in long-range communication, as in other species (Krebs et al. 1981, Payne 1982, Schroeder and Wiley 1983).

These experiments do not eliminate the possibility that Carolina Wrens habituate to con-

specific songs. In fact, the total number of songs used in response to playbacks of Experiment B declined over the period of a week. Because the playback simulated a new neighbor, habituation to song may explain the reduction in response to the songs of neighbors compared to strangers, which has been demonstrated in other species (Brooks and Falls 1975, Wiley and Wiley 1977, Wunderle 1978). In addition, these experiments cannot exclude the possibility that habituation is important during seasons or to age and sex classes not tested. The data do cast doubt on the hypothesis that song repertoires influence short-term habituation by Carolina Wrens when tested in biologically relevant ways.

In response to playbacks outside territories, wrens approached the boundaries and countersang with the tape. Subjects did not remain at the same site throughout the trial, however. After the initial response, each bird moved around its territory, periodically returning to the edge nearest the playback. During controls, birds similarly moved around their territories and countersang with neighbors.

The differences between these results and the results of other investigators might be attributed to species differences, methodological differences, or both. These experiments for the first time tested responses of Carolina Wrens to repeated songs. Individuals of this species differ from those of other species that have been used in habituation tests in one or more of the following ways: (1) in their large repertoires, (2) in their use of repeated songs over long distances, and (3) in their ability to distinguish degraded from undegraded song. Thus, species differences might account for the lack of corroboration between these experimental results and those of previous investigators. Alternatively, methodological differences might explain the disparate results. These experiments, for the first time, test birds' responses to playbacks outside their territories. Results of extended playbacks to birds inside their territorial boundaries might have alternative explanations. Specifically, the tendency for birds to approach the playback speaker leaves open the possibility that the birds obtain additional information about the playback stimulus.

Carolina Wrens respond to nearby playbacks very differently than to distant playbacks. In response to nearby playbacks of undegraded

songs inside their territories, wrens approach silently as if to attack and sing only after investigating the source (Richards 1981b, pers. obs.). If a caged wren is positioned at the playback speaker, residents attempt to attack it (pers. obs., E. S. Morton pers. comm.). When approaching a speaker inside its territory, the bird appears to be searching for an intruder (pers. obs., Richards 1981b, Melemis and Falls 1982, Morton 1982).

Carolina Wrens normally use songs to countersing with neighbors over long distances. There is theoretical (Wiley and Richards 1978) and empirical (Richards 1981b, Gish and Morton 1981) evidence that Carolina Wrens songs are well adapted for long-range communication. Their songs are quite intense, up to 110 dB at 1 m (Morton 1982), structurally simple, and repetitious. In addition, syllables contain frequency sweeps (2–6 kHz), which could be used to compare reverberations or attenuation of high- and low-frequency components in estimating distance. In a simple but elegant experiment, Richards (1981b) showed that Carolina Wrens can use cues other than absolute attenuation to estimate distance. Gish and Morton (1981) provide evidence that song types used by Carolina Wrens might be adapted for long-range transmission in the habitats in which they occur.

Songs of the Carolina Wren are repetitious, both within songs and between songs. When countersinging over long distances, Carolina Wrens tend to repeat the same song type many times (Kroodsma 1977, Simpson 1982). Such repetition is effective in increasing the detectability of a signal (Cherry 1966, Brown and Lemon 1979, Wiley and Richards 1982), particularly a signal used over long distances. In fact, given the importance of redundancy in transmission of long-range signals, there could be selection against habituation by listeners to distant songs. In other territorial species living in woodland habitats, such as Northern Cardinals (*Cardinalis cardinalis*, Lemon and Chatfield 1971), Tufted Titmice (*Parus bicolor*, Schroeder 1980), and Rufous-sided Towhees (*Pipilo erythrophthalmus*, Richards 1981a), individuals repeat song types many times before switching to a new song type, although they have repertoires of 2–12 song types. The songs of such species, like those of Carolina Wrens, consist of identical repeated units.

Long-range countersinging by neighbors

could provide information about the presence and location of conspecifics. The degradation of the signal and the necessity for redundancy might limit the information in the signal to species identification and location. Coordinated countersinging and matching might allow birds to direct songs to one particular neighbor at a time (Lemon 1968).

To investigate the adaptations animals have made for communication, it is necessary to test responses within the context of the social organization and spacing of the species (Lemon 1968, Petrinovich 1973, Schleidt 1973, Wiley and Richards 1978). These experiments simulated normal spacing of Carolina Wrens in tests of habituation to song. The results demonstrate that Carolina Wrens are resistant to habituation to repeated songs played back in these conditions and suggest a strong correspondence between the behavior of singers and the responses of listeners (Searcy and Marler 1981, Searcy et al. 1982). Such a system would allow birds to use repetitious signals adapted for effective transmission over long distances.

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LITERATURE CITED

- BORROR, D. J. 1956. Variation in Carolina Wren Songs. *Auk* 73: 211-229.
- BRENOVITZ, E. A. 1982. Long-range communication of species identity by song in the Red-winged Blackbird. *Behav. Ecol. Sociobiol.* 10: 29-38.
- BROOKS, R. J., & J. B. FALLS. 1975. Individual recognition by song in white-throated sparrows: I. Discrimination of songs of neighbors and strangers. *Can. J. Zool.* 53: 879-888.
- BROWN, R. M., & R. E. LEMON. 1979. Structure and evolution of song form in the wrens *Thryothorus sinaloa* and *T. felix*. *Behav. Ecol. Sociobiol.* 5: 111-131.
- CATCHPOLE, C. K. 1979. Vocal communication in birds. Baltimore, Maryland, Univ. Park Press.
- CHERRY, C. 1966. On human communication. Cambridge, Massachusetts, M.I.T. Press.
- DOBSON, C. W., & R. E. LEMON. 1975. Re-examination of the monotony hypothesis in bird song. *Nature* 257: 126-128.
- FALLS, J. B. 1978. Bird song and territorial behavior. *Advances Study Comm. Affect* 4: 61-89.
- , & R. J. BROOKS. 1975. Individual recognition by song in white-throated sparrows: II. Effects of location. *Can. J. Zool.* 53: 1412-1420.
- GISH, S. L., & E. S. MORTON. 1981. Structural adaptations to local habitat acoustics in Carolina Wren songs. *Z. Tierpsychol.* 56: 74-84.
- HARTSHORNE, C. 1956. The monotony threshold in singing birds. *Auk* 73: 176-192.
- . 1973. *Born to sing*. Bloomington, Indiana Univ. Press.
- HINDE, R. A. 1970. Behavioral habituation. Pp. 3-40 in *Short-term changes in neural activity and behavior* (G. Horn and R. A. Hinde, Eds.). Cambridge, Cambridge Univ. Press.
- HOLLANDER, M., & D. A. WOLFE. 1973. *Nonparametric statistical methods*. New York, J. Wiley & Sons.
- HOPKINS, C. D., M. ROSETTO, & A. LUTJEN. 1974. A continuous sound spectrum analyzer for animal sounds. *Z. Tierpsychol.* 34: 313-320.
- KREBS, J. R. 1976. Habituation and song repertoires in the Great Tit. *Behav. Ecol. Sociobiol.* 1: 215-227.
- , & D. E. KROODSMA. 1980. Repertoires and geographical variation in bird song. *Adv. Study Behav.* 11: 143-177.
- , R. ASHCROFT, & K. VAN ORDSODOL. 1981. Song matching in the Great Tit *Parus major*. *Anim. Behav.* 29: 918-923.
- KROODSMA, D. E. 1976. The effect of large song repertoires on neighbor "recognition" in male song sparrows. *Condor* 78: 97-99.
- . 1977. Correlates of song organization among North American wrens. *Amer. Natur.* 111: 995-1008.
- . 1978. Continuity and versatility in bird song: support for the monotony-threshold hypothesis. *Nature* 294: 681-683.
- LEMON, R. E. 1967. The response of cardinals to songs of different dialects. *Anim. Behav.* 15: 538-545.
- . 1968. The relation between organization and function of song in cardinals. *Behaviour* 32: 158-178.
- , & C. CHATFIELD. 1971. Organization of song in cardinals. *Anim. Behav.* 19: 1-17.
- , M. A. FIELDS, & J. STRUGER. 1981. Testing the monotony threshold hypothesis. *Z. Tierpsychol.* 56: 359-379.
- MELEMIS, S. M., & J. B. FALLS. 1982. The defense function: a measure of territorial behavior. *Can. J. Zool.* 60: 495-501.
- MORTON, E. S. 1982. Grading, discreteness, redundancy, and motivational-structural rules. Pp. 183-212 in *Acoustic communication in birds* (D.

- Kroodsma and E. H. Miller, Eds.). New York, Academic Press.
- PATTERSON, T. L., & L. PETRINOVICH. 1979. Field studies of habituation: II. Effect of massed stimulus presentation. *J. Comp. Physiol. Psych.* 93: 351-359.
- PAYNE, R. B. 1982. Ecological consequences of song matching: breeding success and intraspecific song mimicry in Indigo Buntings. *Ecology* 63: 401-411.
- PETRINOVICH, L. 1973. A species-meaningful analysis of habituation. Pp. 141-162 in *Habituation I: behavioral studies* (H. V. S. Peeke and M. J. Herz, Eds.). New York, Academic Press.
- , & T. L. PATTERSON. 1979. Field studies of habituation: I. Effect of reproductive condition, number of trials, and different delay intervals on responses of the White-crowned Sparrow. *J. Comp. Physiol. Psych.* 93: 337-350.
- , & ———. 1980. Field studies of habituation: III. Playback contingent on the response of the White-crowned Sparrow. *Anim. Behav.* 28: 742-751.
- , & H. V. S. PEEKE. 1973. Habituation to territorial song in the White-crowned Sparrow (*Zonotrichia leucophrys*). *Behav. Biol.* 8: 743-748.
- RICHARDS, D. G. 1978. Environmental acoustics and song communication in passerine birds. Unpublished Ph.D. dissertation, Chapel Hill, North Carolina, Univ. North Carolina.
- . 1981a. Alerting and message components in songs of rufous-sided towhees. *Behaviour* 76: 223-248.
- . 1981b. Estimation of distance of singing conspecifics by the Carolina Wren. *Auk* 98: 127-133.
- SCHLEIDT, W. M. 1973. Tonic communication: continual effects of discrete signs in animal communication systems. *J. Theor. Biol.* 42: 359-386.
- SCHROEDER, D. J. 1980. Whistled song as communication in the Tufted Titmouse (*Parus bicolor*). Unpublished Ph.D. dissertation, Chapel Hill, North Carolina, Univ. North Carolina.
- , & R. H. WILEY. 1983. Communication with shared song themes in Tufted Titmice. *Auk* 100: 414-424.
- SEARCY, W. A., & P. MARLER. 1981. A test for responsiveness to song structure and programming in female sparrows. *Science* 213: 926-928.
- , M. H. SEARCY, & P. MARLER. 1982. The response of swamp sparrows to acoustically distinct song types. *Behaviour* 80: 70-83.
- SHALTER, M. D. 1975. Lack of spatial generalization in habituation tests of fowl. *J. Comp. Physiol. Psychol.* 89: 258-262.
- SIMPSON, B. S. 1982. Communication with complex vocal repertoires by a territorial passerine, the Carolina Wren. Unpublished Ph.D. dissertation, Chapel Hill, North Carolina, Univ. North Carolina.
- THOMPSON, R. F., P. M. GROVES, T. J. TEYLER, & R. A. ROEMER. 1973. A dual-process theory of habituation: theory and behavior. Pp. 239-271 in *Habituation I: Behavioral studies* (H. V. S. Peeke and M. J. Herz, Eds.). New York, Academic Press.
- THORPE, W. H. 1963. *Learning and instinct in animals*. London, Methuen Press.
- VERNER, J. I., & M. MILLIGAN. 1971. Responses of male White-crowned Sparrows to playback of recorded songs. *Condor* 73: 56-64.
- WILEY, R. H. 1977. Census No. 33. *Amer. Birds* 31: 41.
- , & D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3: 69-94.
- , & ———. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. Pp. 131-181 in *Acoustic communication in birds* (D. Kroodsma and E. H. Miller, Eds.). New York, Academic Press.
- , & M. S. WILEY. 1977. Recognition of neighbors' duets by Stripe-backed Wrens *Campylorhynchus nuchalis*. *Behaviour* 62: 10-34.
- WUNDERLE, J. M. 1978. Differential response of territorial Yellowthroats to the songs of neighbors and non-neighbors. *Auk* 95: 389-395.
- YASUKAWA, K. 1981. Song repertoires in the red-winged Blackbird (*Agelaius phoeniceus*): a test of the Beau Geste hypothesis. *Anim. Behav.* 29: 114-125.
- , E. I. BICK, D. W. WAGMAN, & P. MARLER. 1982. Playback and speaker-replacement experiments on song-based neighbor, stranger, and self discrimination in male Red-winged Blackbirds. *Behav. Ecol. Sociobiol.* 10: 211-215.