

**RECOGNITION OF NEIGHBORS'
DUETS BY STRIPE-BACKED WRENS
*CAMPYLORHYNCHUS NUCHALIS***

by

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(With 4 Figures)
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Experiments in the field with playbacks of tape recordings have demonstrated that territorial passerines of a number of species can recognize the advertising songs of their neighbors. Two related abilities have been documented by these procedures. First, a territorial resident reacts less intensely to any neighbor's vocalizations, broadcast near the appropriate boundary of the subject's territory, than to any stranger's vocalizations. This result indicates an ability to discriminate individual differences in vocalizations and to recognize familiar ones. Second, a territorial resident responds differently to a particular neighbor's vocalizations broadcast from the correct and the opposite side of the subject's territory, a result that indicates an ability to recognize the vocalizations of different neighbors.

Habituation of responses to familiar associates could produce different reactions to sets of more and less familiar individuals. Because a resident's reactions wane during repeated playbacks of vocalizations (VERNER & MILLIGAN, 1971; PETRINOVICH & PEEKE, 1973; BROOKS & FALLS, 1975), the different responses of residents to neighbors' and strangers' vocalizations might indeed result from habituation (BEER, 1970). Once a stable boundary is established between neighbors, the waning of responses to each other's vocalizations would permit territorial residents to save their time and energy for other purposes.

If habituation explains the decreased responsiveness to neighbors' vocalizations, then complex repertoires of advertising vocalizations should impede

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recognition of neighbors. Most demonstrations of discrimination between neighbors' and strangers' songs have involved species with one song pattern per individual (WEEDEN & FALLS, 1959; FALLS, 1963, 1969; KREBS, 1971; EMLÉN, 1971; GOLDMAN, 1973; BROOKS & FALLS, 1975). Recently, KROODSMA (1976) has verified that male song sparrows (*Melospiza melodia*), which have over 10 song patterns each, also respond less to neighbors' songs than to strangers'. Discrimination between neighbors' and strangers' vocalizations is thus possible even when individuals have complex repertoires. Because of the problems in comparing studies by different authors, it is still not clear whether or not multiple song patterns would at least retard habituation to neighbors' songs.

The songs of many territorial passerines include enough variation among individuals to permit recognition of each neighbor, not only a binary discrimination of neighbors and strangers. Evidence that territorial residents actually can recognize different neighbors' vocalizations is available only for white-throated sparrows (*Zonotrichia albicollis*). Territorial males of this species respond to tape recordings of a neighbor's song broadcast from the wrong boundary as intensely as to a stranger's song (FALLS, 1969; FALLS & BROOKS, 1975). Rather than differentiating only familiar and unfamiliar vocalizations, these territorial sparrows recognize each neighbor's vocalizations and associate each with a location.

If the usual location of a stimulus contributes to the total configuration to which a territorial resident habituates, then the increased response to a neighbor's song from an unusual direction could result from partial recovery of the response when one parameter of the stimulus, the location, changes. The resident must discriminate the characteristics of neighbors' vocalizations and associate each vocalization with a customary location. Complex repertoires might retard habituation to song-location patterns and thus increase the difficulty of recognizing the songs of different neighbors.

Individual recognition of neighbors by a territorial white-throated sparrow involves differentiation of several other individuals. A simpler form of individual recognition would require that a subject differentiate by a particular reaction only two sets of other individuals, provided that one of these sets contained only a single individual. For instance, reactions specific to a mate would require no more than discrimination between two sets of individuals, the mate and all others. Recognition of parents or young might also involve only a binary discrimination between the objects and all others. White-throated sparrows provide the best available evidence that individual recognition by birds can involve more than such binary discriminations between one individual and all others.

The experiments reported here show that territorial stripe-backed wrens *Campylorhynchus nuchalis* (Troglodytidae), like white-throated sparrows, respond more vigorously to strangers' than to neighbors' vocalizations and also respond differently to neighbors' vocalizations on the correct and the wrong side of the subject's territory. In two series of experiments, we used matched pairs of tests in a symmetrical design to compare responses to neighbors' and strangers' vocalizations and then responses to neighbors' vocalizations on the correct and opposite sides of the subject's territory.

The advertising vocalizations of stripe-backed wrens, unlike those of any previous subjects for similar experiments, are stereotyped duets, which are performed by the principal pair, and less frequently by other members, in a stable group of individuals that jointly defend a territory. The principal pair of each group has five or more duet patterns. It is clear from our results that these duets are used in much the same situations and have much the same effects on territorial residents as do the advertising songs of many individually territorial passerines.

THE SPECIES AND STUDY AREA

Stripe-backed wrens inhabit savanna and second-growth habitats at low elevations across northern Columbia and Venezuela, where they often are familiar birds in parks and residential areas. Through the courtesy of Tomás BLOHM, we studied populations at Fundo Pecuario Masaguaral, a ranch in the Venezuelan llanos approximately 45 km south of Calabozo, Edo. Guárico. The savanna vegetation in this area varies from nearly treeless grasslands with scattered palms (*Copernicia tectorum* Mart.) to areas with groves of contiguous trees and intervening grassy openings. Most of these areas flood with 0.1 to 1 m of water during the late rainy season, August to November. In addition, groves of trees border several hundred hectares of mowed pastures on low sandy ridges near the center of the ranch. Wherever trees grow in scattered groves, these wrens occupy contiguous territories. Unlike most species of wrens, they forage primarily in the foliage of trees, usually at least 2 m above ground.

In three study areas on the ranch, we mist-netted and marked with colored bands and leg flags over 70 wrens, about three-quarters of the members of 14 groups. Ten easily accessible groups with contiguous territories near the headquarters of the ranch served for the experiments reported here.

Stripe-backed wrens live in stable groups. In our study areas between June and November 1974, these groups included 2 to 14 members (mean 7.1), of which 2 to 11 (mean 5.8) were independent adults older than about 6 months and 0 to 3 were juveniles, still fed by other group members. Juveniles have dark irides, evenly dark crowns, and less heavily marked underparts than do adults. The members of a group spend the night together in one roosting nest. We could easily census a group as its members left the roosting nest one by one at dawn.

Each group occupies an exclusive area. Overlap with neighboring groups is limited to boundary zones only 2 to 5 m wide, while the territories are usually 100 to 200 m in diameter. Boundaries are the sites of vocal duels between neighboring groups and occasional episodes of chasing and supplanting by individuals in neighboring groups.

One principal pair in each group performs most of the duets. These two birds remain within 10 m of each other, usually within 5 m, whereas other group members often wander farther from each other. The major pair is also most vigorous and prompt in

responding to neighbors' duets and in accepting challenges at a boundary, behavior that became very apparent during our playback tests.

The female of the major pair incubates the eggs, and generally only she has an incubation patch. In one group, a second female had partial defeathering of the abdomen. All adult members of the group feed the nestlings; and all *except* the major pair feed the young after they leave the nest for at least 3 months until the young begin to acquire adult plumage.

The principal pair in each group duets frequently. Other group members sometimes join to produce a chorus by three to five individuals. Occasionally two auxiliary adults in a group will begin a duet, but the principal pair always joins them, except on infrequent occasions when auxiliary members duet at a distance of 30 m or more from the principal pair.

The duets consist of precisely timed, repeated cadences of harsh notes. The energy in each note spreads over a broad spectrum, but differences in predominant frequencies add slight variations in pitch to the primary sensation of staccato harshness. By observing pairs at close range, we could confirm that two duetters alternate or at least intercalate their contributions, but only sound-synchronized filming will identify the contributions of the partners.

The major pair of each group has a repertoire of 5 or more different cadences. Most of these cadences differ from those of other groups, but sometimes one or two in a pair's repertoire closely approximate a neighboring pair's cadences. We have a number of questions about these vocalizations under investigation. Do the duets by auxiliary group members match those of the major pair? If any group member can sing any cadence with any other member, then each must be able to sing either part in the cadence. Chorusing, involving three or more birds, occurs frequently. What parts do individuals sing in choruses? By ear there seems not to be any clear temporal organization of chorusing, so individuals or pairs might sing separate parts or duets simultaneously but without precise reference to each other. For the studies reported here, we have selected duets of major pairs, each consisting of two repetitions of a cadence distinctive for that pair.

PROCEDURES

Our first series of experiments compared a subject group's responses to duets of a neighboring pair and a strange pair (First Series: N and S tests); a second series compared responses to duets of neighboring pairs on the correct side and the opposite side of the subject group's territory (Second Series: N and XN, cross-neighbor, tests) (Table 1).

TABLE 1

Outline of the two series of experiments

Series	Kinds of Tapes*	Subject Groups**	Dates
I	S, N	MR, RW, TB BT, HS, TK	24 Aug- 29 Sept
II	XN, N	RW, TB, CC BT, CN, HS	23 Sept- 9 Oct

* S, strangers' duet; N, neighbors' duet on the correct boundary; XN, neighbors' duet on the opposite boundary.

** Each group is designated by a symbol of two letters.

In each series, we administered four tests to each subject group, two tests on each of two days. The two tests of a subject group on the same day included one with each kind of playback (either N and S, or N and XN, depending on the series) presented at the same location. The first test began between 07.00 and 08.00, and the second began 30 to 65 min after the first ended. Thus these two tests were matched for subject group, date, and location. For each subject group, the two test days were at least a week apart. On the two days, we used different locations, near boundaries with different neighbors, and presented the two kinds of tapes in the opposite order. Half of the subject groups received N tapes first on the first test day and half received S tapes first (or XN tapes in the second series). In each series, the order of presentation for the two kinds of tapes was thus permuted across groups and days to yield a symmetrical experimental design (Table 2). This design allowed us to examine the effects of one signal on subsequent responses to the other and the differences in responses to the two kinds of signals in matched tests.

TABLE 2

Design for each series of experiments

n (Subject Groups)	Day (Location) 1		Day (Location) 2	
	Test 1	Test 2	Test 1	Test 2
3	Tape A*	Tape B	Tape B	Tape A
3	Tape B	Tape A	Tape A	Tape B

* Series I, A=N, B=S; Series II, A=N, B=XN.

For each test, we placed a speaker (Magitran E51, 11 × 22 cm, 80 Hz to 15 kHz ± 5 dB, 10 watts rms) 2.5 to 3 m above the ground on a pole, partially concealed within the lower branches of a tree, approximately 5 m inside the subject group's territorial boundary. One of us played the recorded test tape on a Uher 4000 tape recorder from an inconspicuous position 20 to 30 m from the speaker. A 30-m lead connected the Uher to the speaker, which was aimed toward the center of the subject group's territory.

Each test tape consisted of a short segment of a duet, 3 to 4-s long, repeated 10 times at 30-s intervals. A test lasted 15 min. During each 30-s interval, one of us noted each duet or chorus by the subject group, whether or not the major pair performed the duet or joined the chorus, whether or not the duet began in flight, and the time to the nearest 10 s whenever the major pair approached within 10 m of the speaker or left this perimeter. The other person recorded the same data for the neighboring group that shared the boundary nearest the speaker. The test tape was played during the middle 5 min of the test. Each test thus consisted of ten 30-s intervals preceding the test tape, ten 30-s intervals each initiated with a brief playback, and finally ten 30-s intervals following the playbacks: 5 min before, 5 min during and 5 min after playback.

To control the intensity of the playback, we standardized both the recording and the playback levels. Each test tape was prepared from a short segment of a recording in the field on a Nagra IVD tape recorder at 19 cm/s with a Sennheiser MKH815 directional microphone. We then recorded a test tape on a Uher 4000, after adjusting the record level to obtain a standardized displacement of the Uher VU meter. Then during our tests, we played the test tape at a standardized setting of the Uher volume control. The same tape recorder was used to record and playback all test tapes. Oscilloscope tracings of the test tapes revealed later that the ratio of peak amplitudes in the loudest and softest tapes was 1.9 (2.8 dB).

The intensity of the playbacks in line with the axis of the speaker seemed comparable by ear to the intensity of a pair of wrens duetting at the same distance. The intensity

fell off appreciably to either side of the axis of the speaker. We explored the sound field of our speakers more quantitatively with the Sennheiser MKH815 microphone and Nagra IV recorder, on which a modulometer calibrated in dB displays the peak level of the input. At 90° in a horizontal plane from the axis of each speaker, the intensity was 10 and 14 dB lower respectively than on the axis; at 180°, the levels were 9 and 10 dB lower respectively than on the axis. These values varied by no more than 1 dB in repeated determinations. The playback intensities along the axis of the speaker were similar to those obtained with the same equipment from duetting wrens at comparable distances.

Our tests followed the period of increased activity during the first hour after the groups left their roosting nests between 06.00 and 06.15. By 07.00 the group members had often dispersed through the territory in smaller groups and engaged in steady foraging through the crowns of trees. The major pair rarely separated more than 10 m, but not infrequently the rest of the group wandered away from them. The major pair usually had favorite locations within the territory where they spent much of their time, behavior that allowed us to standardize their approximate position with respect to the speaker at the start of our tests. Before starting a test, we usually waited until the major pair duetted once, so that we could ascertain that they were in a suitable location.

Some attempt to standardize the birds' initial locations proved important. If the major pair were on the far boundary of a large territory, they could not hear the playbacks. In all but one of our tests (see Discussion), the major pair started near the center of their territory, within 30 degrees of the axis of the speaker, and 20 to 50 m away depending on the shape of the group's territory. Usually for the two matched tests on one day, we could start with the major pair within 10 m of the same location each time. In a minority of tests, we waited 10 to 30 min until the major pair returned to their habitual location. In addition, if any group member was within 20 m of the speaker site, we waited until they had moved at least that far away before starting our test.

As a pair's excitement increased during playback or during natural boundary encounters, they increasingly flew short (5 to 10 m) distances near the boundary and often began duets during these flights. Duets begun in flight characteristically started with a rapid series of abrupt harsh notes before the pair settled into repetitions of one of their regular cadences just before or after landing. This characteristic of duets begun in flight allowed us to identify them by ear even when the birds were out of sight. The frequency of duets begun in flight is an index of the pair's activity, since almost all flights during our playback periods were accompanied by these duets. As a pair responded more intensely to the playback, they flew more frequently, duetted more frequently, and started a greater proportion of their duets in flight.

The tendencies of pairs to approach the speaker within 10 m were strongly influenced by the arrangement of trees near the speaker. Consequently, the latencies to approach within 10 m and the time spent within this perimeter were not useful measures of the birds' responses. Activities by auxiliary group members contributed little to the responses to our tests (see Discussion). The following analyses consider only the number of perched duets and flying duets by the principal pair before, during and after playback. The symbols B, D, and A represent the number of duets in these three periods respectively.

RESULTS

First series: stranger, neighbor comparisons.

The activity of the principal pair in the subject group increased during playback in both N and S tests, although the increase was not statistically significant during N tests presented first (Figs. 1 and 2, Table 3). The increased frequency of duetting involved primarily an increase in the fre-

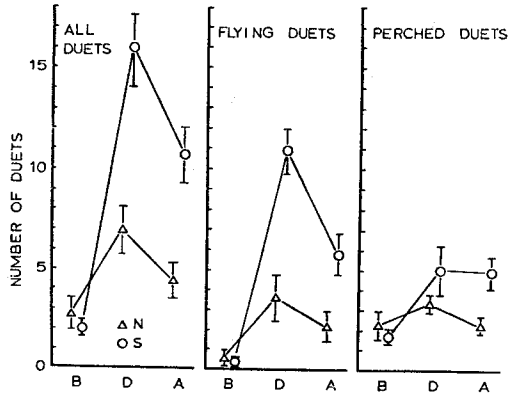


Fig. 1. First series of experiments: number of duets by the principal pair of the subject group before, during, and after playback. Triangles, N, tests with neighbors' duets; circles, S, tests with strangers' duets. Symbol indicates the mean ($n = 12$); vertical lines indicate one SD around the mean. Left, all duets; middle, flying duets; right, perched duets. B, 5 min before playback; D, 5 min during playback; A, 5 min after playback.

quency of flying duets. During the five minutes following playback, the principal pair's frequency of duetting declined but still remained higher than prior to playback. Except for N tests presented first, the differences between the before and after periods were statistically significant.

To obtain a measure of the principal pair's response to playback, we subtracted their frequency of duetting before playback from their frequency

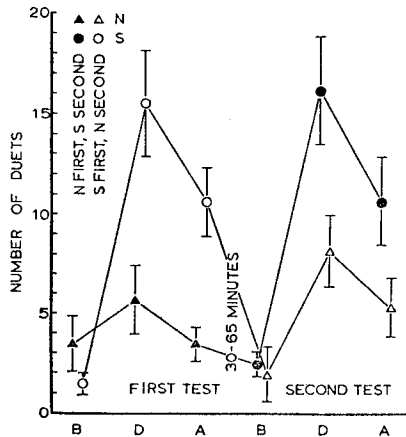


Fig. 2. First series of experiments: number of duets by the principal pair of the subject group before, during, and after playback for tests presented first and second on the same day. For explanation of symbols see Fig. 1. Black symbols, N presented first, S presented second; open symbols, S presented first, N presented second. For each symbol, $n = 6$.

TABLE 3

Changes in subjects' rates of duetting within tests in the S, N series

	T	n	P (1-tailed)
<i>N Tests, all duets</i>			
$H_0: D = B^*$			
N first	3	5	NS
N second	0	5	<.05
Combined	3	10	<.005
$H_0: A = B$			
N first	8	5	NS
N second	0	5	<.05
Combined	14	10	<.025
<i>S Tests, all duets</i>			
$H_0: D = B$			
S first	0	6	<.025
S second	0	6	<.025
Combined	0	12	<.005
$H_0: A = B$			
S first	0	6	<.025
S second	0	6	<.025
Combined	0	12	<.005

* B, D, and A denote the number of duets before, during and after playback, respectively.

Significance of increase in duetting during (D) and after (A) playback in comparison with the period before (B) playback (Wilcoxon Matched-pairs Signed-ranks Test).

of duetting during or after playback (D minus B or A minus B). These measures incorporated some control for differences in the pair's initial level of activity.

The wrens' reactions to N and S playback were not appreciably affected by the order of presentation. Although the wrens increased their frequency of duetting more in N tests presented second than in N tests presented first (Fig. 2), this difference is not statistically significant (Table 4). In comparisons of first and second presentations of S tests, no differences in the principal pair's responses approached statistical significance.

The differences between paired N and S tests, matched for subject group, date, and location, provide the most sensitive indication of any differences in the wrens' responses to N and S stimuli. The responses during and after playback in S tests reliably exceeded the responses in matched N tests (Table 5; Figs. 1 and 2). Significant increases occurred in perched, flying, and total duets, both during and after playback. The greatest difference in

TABLE 4

Subjects' responses to the same kind of stimulus when presented first or second

	U	(P (2-tailed))
<i>S, N Series</i>		
N Tests		
D minus B†, all duets	7½	>.09*
No other significant differences		
S Tests		
No significant differences		
<i>XN, N Series</i>		
N Tests		
No significant differences in D minus B, D (first half) minus ½B, D (second half) minus ½B, or A minus B for perched, flying or all duets		
XN Tests		
D minus B, perched duets	17	NS
flying duets	2	<.02**
all duets	6½	<.10**
D (first half) minus ½B, all duets	2½	<.02**
D (second half) minus ½B, all duets	12½	NS

* Presentation first > presentation second.

** Presentation first < presentation second.

† B, D, and A denote the number of duets before, during and after playback, respectively.

Significance of differences between first and second presentations for each kind of test (Mann-Whitney U Tests, $n_1 = n_2 = 6$; H_0 : presentation first = presentation second).

the wrens' responses to N and S playbacks appeared in the frequencies of flying duets.

If we consider separately the 12 tests presented first and the 12 presented second, we can compare 6 N tests presented first (or second) with 6 S tests presented first (or second), rather than 12 matched pairs of N and S tests. Highly reliable differences still appear in the wrens' responses to N and S tests (Table 6). Any systematic differences among the days of testing or in the efficacy of playback in different locations would tend to obscure differences to N and S tests not matched for these variables. The difference in responses to N and S tests was greater for first presentations than for second presentations, because of the greater response to N tests when presented second (see Fig. 2).

TABLE 5

Comparison of subjects' responses to matched S and N tests

	T	N	P (1-tailed)
<i>D minus B*, perched duets</i>			
N first	1	6	<.025
S first	10½	6	NS
Combined	12	12	<.025
<i>D minus B, flying duets</i>			
N first	1	6	<.025
S first	0	6	<.025
Combined	3	12	<.005
<i>D minus B, all duets</i>			
N first	1	6	<.025
S first	0	5	<.05
Combined	2	11	<.005
<i>A minus B, perched duets</i>			
	9	12	<.01
<i>A minus B, flying duets</i>			
	8	12	<.01
<i>A minus B, all duets</i>			
	1	10	<.005

* B, D, and A denote the number of duets before, during and after playback, respectively.

Significance of differences between pairs of S and N tests matched for subject group, location and date (Wilcoxon Matched-pairs Signed-ranks Tests).

TABLE 6

Comparison of subjects' responses to S and N tests when first and second presentations are separated

	U	P (1-tailed)
<i>First presentations</i>		
D minus B*, all duets	1½	<.005
flying duets	½	<.002
	3	<.01
<i>Second presentations</i>		
D minus B, all duets	5½	<.03
flying duets	5½	<.03
A minus B, all duets	6	<.04

* B, D, and A denote the number of duets before, during and after playback, respectively.

Significance of differences between S and N tests for the first and second presentations (Mann-Whitney U tests, $n_1 = n_2 = 6$, $H_0: N = S$).

The neighboring group that shared the boundary near the speaker might have reacted to the playbacks as well, so the subject group might have responded in part to their neighbors. The position of the speaker, about 5 m inside the subject group's territory and its orientation directly away from the neighboring territory meant that the neighboring group would receive a less intense stimulus. During N tests, which employed a recording of one of their own duets, the neighboring group did not increase their duetting during playback (H_0 : duet frequency during playback equals duet frequency before playback, $N = 11$ matched pairs that showed a difference, $T = 16$, not significant in a one-tailed Wilcoxon Matched-pairs Signed-ranks Test). During S tests, the neighboring group did increase their duetting during playback (in a statistical test analogous to the preceding, $T = 10\frac{1}{2}$, $N = 12$, $P < .025$, one-tailed, mean increase = 4.0 duets). However, the difference in responses during N and S tests matched for subject group, date, and location lacked statistical significance (Table 7). The possibility of interactions with the neighboring group, provoked by the playback, thus cannot explain the responses of the subject groups to the N or S tests or the large difference in their responses to N and S tests.

TABLE 7

Neighbors' responses during playback: mean differences between matched tests

<i>S, N series; mean difference between S and N for matched pairs of tests</i>	
D minus B**, all duets	3.1*
<i>XN, N series; mean difference between XN and N for matched pairs of tests</i>	
D (first half) minus $\frac{1}{2}$ B, all duets	-0.8
D (second half) minus $\frac{1}{2}$ B, all duets	-0.7
D minus B, all duets	-1.5

* $T = 12$, $n = 10$, $p > .05$, Wilcoxon Matched-pairs Signed-ranks Test.

** B, D, and A denote the number of duets before, during and after playback, respectively.

In conclusion, the wrens clearly differentiated the two kinds of playback by their much stronger responses to strangers' duets.

Second series: cross-neighbor, neighbor comparisons.

In this series of experiments, differences in the wrens' responses to the two classes of stimuli were much less pronounced, and the order of presentation had a greater effect.

TABLE 8

Changes in subjects' rates of duetting within tests in the XN, N series

	T	n	P (1-tailed)
<i>N Tests, all duets</i>			
$H_0: D = B$			
N first	0	6	<.025
N second	0	5	<.05
Combined	1	11	<.005
$H_0: D \text{ (first half)} = \frac{1}{2}B$			
N first	1	6	<.025
N second	0	6	<.025
Combined	2	12	<.005
$H_0: D \text{ (second half)} = \frac{1}{2}B$			
N first	0	6	<.025
N second	1	6	<.025
Combined	1	15	<.005
$H_0: A = B$			
N first	2	5	NS
N second	2	5	NS
Combined	7	10	<.025
<i>XN Tests, all duets</i>			
$H_0: D = B$			
XN first	0	6	<.025
XN second	0	6	<.025
Combined	0	12	<.025
$H_0: D \text{ (first half)} = \frac{1}{2}B$			
XN first	0	6	<.025
XN second	0	6	<.025
Combined	0	12	<.005
$H_0: D \text{ (second half)} = \frac{1}{2}B$			
XN first	0	6	<.025
XN second	0	6	<.025
Combined	0	12	<.005
$H_0: A = B$			
XN first	0	6	<.025
XN second	1	6	<.025
Combined	1½	12	<.025

Significance of increases in duetting during (D) and after (A) playback in comparison with the period before (B) playback (Wilcoxon Matched-pairs Signed-ranks Test).

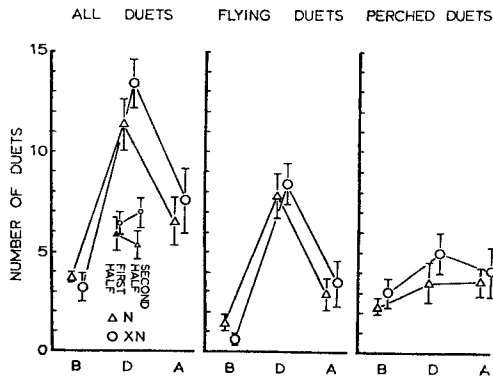


Fig. 3. Second series of experiments: number of duets by the principal pair of the subject group before, during, and after playback. Triangles, N, tests with neighbors' duets on the correct boundary; circles, XN, tests with neighbors' duets on the opposite boundary. For further explanation see Fig. 1. For each symbol, $n = 12$.

The frequency of duetting during and after playback exceeded the frequency before playback in both N and XN tests (Fig. 3, Table 8). As in the first series, the increase during playback primarily involved an increase in the frequency of flying duets. The responses to playback during N tests in this series exceeded those in the preceding series of experiments (compare Figs. 1 and 3). This discrepancy, discussed further below, might have resulted from our use of different sets of subject groups, test duets, and locations for the two series.

The wrens' responses to playback are again best indicated by subtracting the frequency of duetting by the subject group before playback from their frequency of duetting during or after playback (D minus B or A minus B). As an indication of the latency of maximum response, we calculated separate measures of the response in the first and second halves of playback: the frequency of duetting during the first or second five 30-s intervals of the playback period minus one-half the frequency of duetting in the 5 minutes preceding playback: D (first half) minus $\frac{1}{2}B$ or D (second half) minus $\frac{1}{2}B$ (Table 9).

Responses to N tests did not depend on whether the test was presented first or second on any one day (Table 4). Responses to playback in XN tests, however, were significantly greater when the XN test was presented second rather than first. The difference primarily resulted from a higher frequency of flying duets in the first half of the playback period during second presentations. Responses in the second half of the playback period did not differ in comparisons of first and second presentations. Evidently,

TABLE 9

Mean responses to playback in XN, N series

	D minus B†	D (first half) minus ½B	D (second half) minus ½B
N tests			
N first (n = 6)	9.3	4.58	4.75
N second (n = 6)	5.8	3.50*	2.33*
Combined (n = 12)	7.6	4.04	3.54
XN tests			
XN first (n = 6)	7.7	3.25**	4.42**
XN second (n = 6)	12.8	6.42	6.42
Combined (n = 12)	10.2	4.83	5.42
XN minus N for matched pairs of tests			
N, XN order (n = 6)	3.5	1.83	1.67
XN, N order (n = 6)	1.8	-0.25	2.08
Combined (n = 12)	2.7	0.79	1.87

* T = 2, n = 6, P < .10, Wilcoxon Matched-pairs Signed-ranks Test.

** T = 1½, n = 5, P < .10, same test.

† B, D, and A denote the number of duets before, during and after playback, respectively.

the wrens responded more rapidly to XN tests when these were presented after an N test rather than first.

XN and N tests matched for subject group, date, and location evoked different responses from the wrens: the increase in the frequency of all

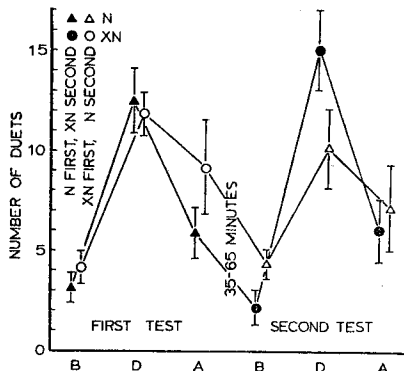


Fig. 4. Second series of experiments: number of duets by the principal pair of the subject group before, during, and after playback for tests presented first and second on the same day. For explanation of symbols see Fig. 1. Black symbols, N presented first, XN second; open symbols, XN presented first, N second. For each symbol, n = 6.

TABLE 10

Comparison of subjects' responses to matched XN and N tests

	T	n	P (1-tailed)
D minus B*, all duets			
N first	1½	6	<.05
XN first	4½	6	NS
Combined	12	12	<.025
D (first half) minus ½B, all duets			
N first	5	5	NS
XN first	9½	6	NS
Combined	28	11	NS
D (second half) minus ½B, all duets			
N first	0	6	<.025
XN first	2½	6	NS
Combined	5½	12	<.005
A minus B, all duets			
N first	8	6	NS
XN first	3½	5	NS
Combined	20	11	NS

* B, D, and A denote the number of duets before, during and after playback, respectively.

Significance of differences between pairs of XN and N tests matched for subject group, location, and date (Wilcoxon Matched-pairs Signed-ranks Test).

duets during playback was significantly greater during XN tests (Table 10). Further examination, however, suggests that the wrens did not differentiate these two stimuli immediately.

The differences between responses to matched N and XN tests lie primarily in the frequency of duets during the second half of the playback period, and the differences are greater with the N test presented first and the XN second (Table 10). Furthermore, there is no difference between N and XN tests in the set of 12 first presentations (6 N and 6 XN tests not matched for group, date or location) (Table 11). In the set of second presentations, significant differences appear in the wrens' responses during both the first half and the second half of the playback period.

To understand these patterns, consider the trends in the mean responses during playback in XN and N tests (Table 9). During first presentations, the wrens' mean responses increased from the first to the second half of the playback period, in both N and XN tests. However, in XN tests the response

TABLE 11

Comparisons of subjects' responses to XN and N tests when first and second presentations are separated

	U	P (1-tailed)
<i>First presentations</i>		
No significant differences		
<i>Second presentations</i>		
D minus B*, all duets	3	<.01
D (first half) minus $\frac{1}{2}$ B all duets	3	<.02
D (second half) minus $\frac{1}{2}$ B all duets	6	<.04
flying duets	5	<.03
No other significant differences		

* B, D, and A denote the number of duets before, during and after playback, respectively.

Significance of differences between XN and N tests for first and second presentations (Mann-Whitney U Tests, $n_1 = n_2 = 6$, $H_0: N = XN$).

increased proportionately more. During second presentations, responses to XN stimuli in the first half of the playback period exceeded responses during either half of first presentations, while responses to N stimuli were lower than those in either half of first presentations. Responses to N stimuli waned markedly during the second half of the playback period during second presentations, while responses to XN stimuli showed no decrease during playback. Consequently, the N, XN order of presentation resulted in the largest difference in the wrens' responses during playbacks matched for group, date, and locations, and this difference is greatest during the second half of the playback periods.

In effect, prior experience with playback on the same day and at the same location increased the wrens' response to an XN stimulus, while prior experience reduced responsiveness to an N stimulus. Responses to XN stimuli were initially lower than responses to N stimuli but increased proportionately more with additional exposure to playback.

DISCUSSION

Control of extraneous variables in playback experiments.

An experimentalist in the field always encounters difficulties in controlling variables extraneous to his study. Previous playback experiments have often

randomized subjects with respect to extraneous variables. However, an experimenter, suspecting the importance of an extraneous variable at the outset, would do best either to match or to permute experimentals and controls with respect to this variable, rather than to randomize them. Particularly with relatively few replications, randomizing would not avoid the chance of systematic bias from the variable. Sufficient replication must accompany randomization to insure a valid experiment (HOEL, 1962). In these experiments, we attempted to match tests for certain variables and to permute tests with respect to others.

We permuted the order of presentation of two tests in one locality. In addition, each subject group received two pairs of tests, one with each sequence, at two localities in each series of experiments. Each pair of tests was matched for the identity and approximate initial position of the subject group, date, and location. We attempted to control the time of day and the weather by testing at nearly the same time each morning and only in good weather. In addition, we attempted to minimize any long-term effects from previous days of testing by scheduling pairs of tests for any one group at least 7 days apart. There were no indications that exposure to 20 tape recorded segments of duets a week earlier in a different location had any systematic effect on the wrens' responses.

One relevant variable left uncontrolled is the initial position and response of the neighboring group nearest the playback site. Our results suggest, however, that the responses of neighboring groups did not differ for N and S or N and XN playbacks.

Although we attempted to control the location of the speaker with respect to the subject groups' boundary, it is likely that the valence of the location varied among the twelve pairs of tests matched for location in each series. The frequency of nearby encounters with the neighboring group or the frequency of visits to the vicinity by the subject group might influence the responses to playback at a particular location.

The cadences selected for playback might have differed somewhat in their inherent valence, a variable beyond our control. In addition, the cadences used for N tests probably differed somewhat in familiarity to the respective subjects.

The initial positions of the principal pair also varied to some extent, although we tried to control the subject group's approximate initial position. The importance of this variable was emphasized to us once when we seriously misjudged a group's initial location during an S test in the first series. An auxiliary member of the group arrived within 20 m of the speaker, by chance we believe, about half way through the playback period. After the first

succeeding playback, this individual immediately returned toward the rest of the group. Within 30 sec the principal pair flew toward the speaker from 50 m away in a direction perpendicular to the axis of the speaker, where they undoubtedly had not heard the playback. This S test evoked less response from the subject group than its matched N test an hour earlier, the only such exception in the first series. The differences in this series were so dramatic that this single contrary result had little effect on our conclusions.

Because the two series of experiments employed different sets of subject groups and locations, comparisons between the series would in part reflect differences among groups, locations, or cadences selected for playback. In the second series, for instance, responses to N playback substantially exceeded the responses to N playback in the first series (Figs. 1 and 3). This discrepancy is particularly marked in comparisons of N tests presented first (Figs. 2 and 4). We have no explanation for this greater responsiveness during the second series. Significant seasonal changes in the birds' behavior between the series seem unlikely. During the first series, one group fed nestlings and two groups (not the same) in each series tended dependent fledglings, but the major pair in each of these groups responded typically for the series. Possibly, the locations or cadences chosen for playback in the second series had by chance greater valence for the subject groups.

Importance of the temporal parameters of playback.

Our experiments, and all similar ones, attempt to demonstrate the subjects' ability to discriminate between two sets of stimuli by measuring a difference in the *intensity* of the subjects' responses to them. The results of such experiments depend strongly on effects of the temporal parameters of playback on the intensity of subjects' responses. The intensity of response is known to wane with repeated or continuing exposure to playback (VERNER & MILLIGAN, 1971; PETRINOVICH & PEEKE, 1973; BROOKS & FALLS, 1975). The dynamics of these responses, however, are undoubtedly more complicated than monotonic habituation.

HINDE'S (1960) studies of chaffinches' reactions to simulated predators indicate some of the complexities in the dynamics of an animal's response during repeated exposure to a stimulus and in the interacting effects of stimuli during successive exposures. Response frequencies do not change monotonically either with time after the initiation of exposure to a stimulus or with the duration of short intervals between exposures. Exposure to one stimulus has long-term effects on responses to another stimulus evoking the same response. Stimulus-specificity in the long-term effects became clear, in HINDE'S experiments, only after prolonged (24 h) initial experience with a

stimulus. Responses to a second stimulus were depressed even 24 hours after an initial 12-min exposure to a different stimulus. Clearly the durations of exposure and intervals between exposures will have complex influences on the intensity of responses.

In selecting temporal parameters of playback tests, we intended to evoke a moderate response to a recording of neighboring groups' duet. Our protocol of 10 approximately 3 or 4-sec recordings at 30-sec intervals seemed to evoke such a response. The playback roughly mimicked a series of brief flying duets at a rate not unusual for an actively duetting pair. A 30-minute interval between tests insured that the subject group's duetting frequency had returned to the level before the initial test (Figs. 2 and 4).

Interactions between successive tests.

In our procedure of matching two tests for date, location, and subject group, the first test might affect responses during the second. We found no evidence of an interaction between matched tests during the first series; responses to N or S playbacks were the same, regardless of their order of presentation (Table 5). Other playback experiments with territorial birds have also failed to find significant interactions between successive stimuli (BROOKS & FALLS, 1975). The stimulus-specificity of the wrens' responses emphasizes the distinctiveness of N and S stimuli for these territorial wrens.

In the second series, with XN, N comparisons, the first presentations in matched pairs had an effect of contrast enhancement on the second presentations. A prior presentation increased subsequent responses to the more effective stimulus and depressed subsequent responses to the less effective. If the N and XN playbacks had the same effects on the wrens' behavior, there would have been no differences in response to N and XN playback in either the first presentations or the second. Even though differences in responses to N and XN playbacks appeared primarily in second presentations, we can conclude that these two kinds of stimuli had different effects on the subjects' responses and consequently that the wrens could discriminate the two.

The increased differentiation of responses to XN and N tapes in second tests might have resulted from either (1) a general effect of the first experience with any playback at a particular location on the wrens' later responses, or (2) specific effects of each kind of stimulus on later responses. A conclusive resolution of this question would require doubling the number of matched tests to allow comparisons between N, N and XN, N and between XN, XN and N, XN orders of presentation, in order to determine whether the kind of preceding stimulus affected the later responses. However, our

information on the course of the wrens' responses in the second series suggests that the increased reaction to XN tapes actually began during the second half of the first presentation and resulted from the wren's experience with general features of the playback tests at a particular location.

The wrens responded promptly to XN playbacks during second presentations. Even during first presentations, the response to XN playback increased from the first to the second half of the playback period relatively more than during N playback (Table 10). Thus, experience with either XN or N playback increased subsequent responses to XN. Without prior experience with playbacks at a particular location, the wrens perhaps were slow to notice the direction of the playbacks. Among trees and at a distance of 20-50 m, locating the direction of the speaker might have presented difficulties. In addition, the wrens might not have attended promptly to the directional cues from the playbacks. Experience with our playbacks in a particular location might thus have increased the promptness with which the wrens located the direction.

Other explanations for the increased contrast in responses to N and XN tapes during second presentations seem less likely. The first series of S, N comparisons, for instance, eliminates the possibility that the wrens could not discriminate between different duet cadences. The wrens might localize the playbacks promptly, even in first presentations, and also recognize the recording as a neighbor's duet, but only gradually associate the duet cadence with the location. Under this hypothesis, however, one would expect the response to XN playback during second presentations to increase as slowly as during first presentations, contrary to the actual results. The evidence thus indicates that although the wrens could differentiate N and XN playbacks, they either experienced some difficulty at first in locating the broadcasts or only gradually attended to directional cues. Sequential effects of presentations appear in our XN, N series but not in our S, N series because the two discriminations require different operations, which are affected differently by prior presentations. Most important, XN, N discrimination necessitates locating and using the direction of the stimulus.

Recognition of different neighbors' duets.

Different responses to playbacks of N and XN duets require that the wrens (1) recognize the cadence as a familiar one from some neighboring group, (2) determine the direction from which the stimulus arrives, and (3) recognize the unfamiliar association of cadence and direction. These processes, which all must occur during playback, require that the wrens have previously (4) developed an association of each neighboring group's cadences with their

usual directions. Our interest for the XN, N experiments was in capability (4). The preceding discussion suggested that the wrens in our experiments were slow at (2). These indications of the wrens' delay in determining the direction of the playback and the critical importance of the temporal parameters of playback make it premature to conclude that the wrens have only marginal abilities to recognize different neighbors' duets.

These wrens probably have optimal opportunities for learning their neighbors' vocalizations. Our studies have shown that they have permanent territories and high survival rates. Their duets have stereotyped patterns like the songs performed by individual territorial residents in many other passerines. On the other hand, stripe-backed wrens have a larger repertoire of duet cadences than white-throated sparrows have song types. A larger repertoire of patterns would presumably increase the difficulty of learning each neighbor's vocalizations.

FALLS & BROOKS' (1975) experiments with white-throated sparrows demonstrated much clearer differences in the response of territorial residents to N and XN playbacks, but their procedures differed from ours in two important respects that might influence the magnitude of the difference in subjects' responses to N and XN stimuli. They directly compared responses to XN and S stimuli, not XN and N as in our experiments. If S stimuli promptly attracted the subject's attention to the playback location, FALLS & BROOKS' procedure might enhance differences in subsequent responses to N and XN playback. Their experiments also involved multiple presentations at one site, either at least one day apart or 12 minutes apart. If responsiveness to XN stimuli increased after some delay as a result of cumulative effects of preceding playback, this procedure would again increase the subjects' responses to XN playback in comparison with N. The indications in our experiments that the subjects did not react promptly to XN playback suggest that, if we had adopted FALLS & BROOKS' protocol, we would have obtained much larger differences in reactions to N and XN stimuli. Consequently, stripe-backed wrens and white-throated sparrows might well have comparable capabilities for recognizing different neighbors' vocalizations.

Individual variation in the advertising vocalizations of territorial birds clearly serves other purposes in addition to any individual recognition of neighbors. Besides its probable importance in heterosexual affiliations, individual variation in advertising vocalizations might provide the easiest way for territorial residents to differentiate neighbors from strangers. Individual neighbors are almost always easily differentiated by their locations without regard to vocalizations. An ability to recognize neighbors out of place would confer little advantage if such situations were infrequent and tem-

porary. It is perhaps not surprising that territorial residents would not evolve a capability for responding promptly to a neighbor's vocalizations in the wrong place.

Biological significance of duetting by stripe-backed wrens.

In almost all respects, duetting by the major pair of a group resembles singing by individual territorial males of many temperate zone passerines. The duets are highly stereotyped in their temporal and spectral features, include both species-specific and pair-specific cues, and normally carry at least the diameter of a territory. The wrens perform duets especially frequently early in the morning just after the groups leave their roosting nests. They occur apparently spontaneously throughout the day, as expected for acoustic displays in long-range advertisement (MARLER, 1969). In addition, neighboring groups engage in "counter-duetting", much like the "counter-singing" familiar in individually territorial species; one group duets in immediate response to a neighboring group's duet. Duetting is also a prominent component of boundary encounters between neighboring groups. The responses to tape recordings of strangers' and neighbors' duets closely match the patterns established for a number of individually territorial passerines (WEEDEN & FALLS, 1959; FALLS, 1963, 1969; KREBS, 1971; EMLLEN, 1971; GOLDMAN, 1973; BROOKS & FALLS, 1975).

The responses to our playbacks came primarily from the major pair of the subject group. Considering the two series together, we sampled a total of 4 hr (48 5-min periods) before playbacks and equal amounts of time during and after playbacks. In all, we recorded only 6 duets by auxiliary members of the subject group before playbacks, 10 during, and 4 after. In a number of tests, auxiliary members arrived near the speaker, either along with or shortly after the major pair, but never duetted or joined the major pair's duets. The auxiliary members duet or join choruses more frequently earlier in the morning, during the first hour after the wrens leave their roosting nest. In addition, during naturally occurring boundary encounters with neighboring groups, auxiliary members chorused with the major pair of their group or with other group members and joined in the supplanting and chasing at the boundary. Indeed, auxiliary members were often more active in chasing, while the major pair hung back 5 or 10 m from the fray and initiated most of the groups' choruses or duets. Our playback experiments evidently indicate that auxiliary members need stronger provocation, perhaps the actual presence of a rival group, before actively engaging in chorusing at a boundary.

Investigators have previously emphasized the importance of duetting for integration of the pair's activities rather than its importance in territoriality. Few reports document the contexts of duetting in enough detail to determine how prevalent duetting might be in territorial contexts. The use of duetting for territorial maintenance by stripe-backed wrens resembles certain uses of duets by *Laniarius* shrikes of Africa (HOOKER & HOOKER, 1969; THORPE, 1972). In particular, the Hookers report "counter-duetting" between neighboring pairs.

The use of duetting for territorial maintenance recurs in other tropical species with permanent pair bonds and territories. For instance, in our study areas for stripe-backed wrens, pairs of the white-bearded flycatcher *Myiozetetes inornatus* (Tyrannidae) occupied well-defined territories and performed duets in the same situations listed above for the wrens. Their duets had simpler acoustic structure than the wrens but equally striking coordination. Two pairs, not 5 m apart on either side of their mutual territorial boundary, would counter-duet repeatedly for minutes at a time. Like the wrens, pairs of these flycatchers usually began their duets while perched within 1-2 meters of each other.

Although the duets of stripe-backed wrens clearly operate in territorial maintenance, they probably have other important effects for the major pair as well. Our studies have provided evidence for two other effects of duetting: maintenance of close spatial association between the paired individuals; and notification of auxiliary members' locations. In addition, it seems likely that duetting would provide mutual stimulation for the pair and other group members that could strengthen their bonds with each other. The lack of any clear seasonal association of duetting with the start of breeding probably excludes any important regulation of the pair's reproductive status. Spatial coordination and mutual stimulation of the pair are probable effects of duetting in other species as well (DIAMOND & TERBORGH, 1968; BERTRAM, 1970; PAINE, 1971; THORPE, 1972; KUNKEL, 1974; WILEY, 1976a, b).

The selection pressures that would favor the evolution of such mechanisms of pair affiliation and territoriality might include the intense competition for territories in tropical species with low adult mortality and both sexes on permanent territories. Development of a duet repertoire might provide a cue to advertise a pair in residence and thus discourage single trespassers, particularly interlopers seeking a mate. In the absence of its partner individual *Laniarius* shrikes sing both parts of the pair's duets but cease this false duetting after one or two days alone (THORPE, 1972). Pair formation that involved development of precise duets would take an appreciable time, at least a number of days, unlike the situation in many individually territorial

passerines in temperate zones, in which a male often seems to stabilize a bond with a mate within hours. The additional time and uncertainty involved in mastering a duet repertoire during pair formation would in the end provide a signal, in the form of the crystallized duets, that a stable breeding pair had established residence.

SUMMARY

Stable groups of stripe-backed wrens *Campylorhynchus nuchalis* occupy exclusive territories and perform stereotyped duets and choruses in the same contexts in which many individually territorial passerines sing. When duets are broadcast from a speaker just inside a group's territorial boundary, the principal pair in the subject group reacts much more strongly to playbacks of strangers' duets than neighbors' duets. In addition, they respond slightly more intensely to a neighbor's duet on the wrong side of the subject group's territory than to the same duet on the correct side of the territory. These results indicate that stripe-backed wrens can differentiate neighboring groups' duets and associate each with a customary direction. The duets of this species have nearly the same effects on territorial residents as do the advertising songs of passerines with individual territories.

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ZUSAMMENFASSUNG

Stabile Gruppen von *Campylorhynchus nuchalis* (Aves, Troglodytidae) bewohnen genau begrenzte Reviere und singen in stereotypen Duetten oder im Chor zu den gleichen Anlässen wie viele einzel-territoriale, nicht gruppenbildende Passeriformes. Wenn ein Duettgesang mit einem Lautsprecher knapp innerhalb der Reviergrenzen einer Gruppe abgespielt wird, reagiert das leitende Pärchen dieser Gruppe wesentlich stärker auf Aufnahmen von Duetten von fremden Gruppen als auf solche seiner Nachbargruppen. Darüberhinaus war festzustellen, daß sie auf den Duettgesang der Nachbargruppe etwas stärker reagierten, wenn dieser auf der falschen Seite ihres Revieres rückgespielt wurde. Diese Ergebnisse weisen darauf hin, daß diese Vögel die Duettgesänge ihrer Nachbargruppen unterscheiden können und sie mit gewohnheitsgemäßen Richtungen verbinden. Die Duettgesänge dieser Art haben auf Revierbewohner den selben Effekt wie territorialer Gesang von Passeriformes mit Einzel-territorien.