

## Effects of location in territory and distance from neighbours on the use of song repertoires by Carolina wrens

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**Abstract.** By capturing territorial Carolina wrens (*Thryothorus ludovicianus*) and housing them in portable cages on their territories, I could control each one's location in its territory and distance from neighbours in experiments on the use of song repertoires. Experiment 1 demonstrated that these wrens sang more songs in the centre of their territories than at the edge, but that they did not use more song types or different song types at the centre than at the edge. In experiment 2, in which I played tape-recorded songs at two distances from wrens caged in the centres of their territories, birds responded more strongly to songs at 25 m, simulating an intruder, than to songs at 165 m, simulating a territorial neighbour. Birds also switched more frequently between song types and sang more song types per 100 songs in response to the nearer playback. Experiment 3 compared captive wrens 140 m, 80 m, 20 m, or 0 m apart on adjacent territories. As the distance between neighbours decreased, birds sang less, but also switched more frequently between song types, used more song types per 100 songs, and matched songs with neighbours more frequently. There were no differences in the kinds of song types sung at different distances from neighbours. A comparison of the results from experiments 1 and 3 confirms that the use of song repertoires is influenced by distance from conspecifics and not by location in the territory.

### INTRODUCTION

A noteworthy study correlating ecological variables with repertoire use by nine species of wrens suggested that large repertoires and complex songs have evolved in species with dense populations and high encounter rates between males (Kroodsma 1977; see also Kroodsma 1983). Ecological considerations might similarly affect the use of song repertoires within a single species. For example, males living in large territories might use more song types in direct close-range encounters with other males than in interactions over long distances. It was the purpose of this study to evaluate the use of song repertoires as a function of the location within a male's territory and the distance to neighbours in one species, the Carolina wren (*Thryothorus ludovicianus*).

The amount of singing is affected by the location of a bird in his territory. Some birds sing more in the centre of their territories than at the edges (Weeden 1965; Wiley & Wiley 1980), although such differences are largely due to the greater amount of

time birds spend in the centre than at the edge (Wiley & Wiley 1980). Responses to playbacks often vary with location as well (review by Waser & Wiley 1980). For instance, when the distance of the bird from a playback inside its territory is controlled, unmated male American redstarts (*Setophaga ruticilla*) respond more strongly to playbacks at the centre than at the edge of their territories (Ickes & Ficken 1970). White-throated sparrows (*Zonotrichia albicollis*) also respond more strongly to playbacks at or near to the centre of their territories than those at the edges or outside the boundaries (Melemis & Falls 1982).

In some species, individuals use certain song types preferentially at the centre or edge of their territories (Lein 1978; Smith et al. 1978; Schroeder & Wiley 1983a). In other species, different song types are used equally in different parts of the territory (Krebs et al. 1978; Smith & Reid 1979). Differences in behavioural tendencies at the centre and edge could be due to differences in familiarity or previous experience with these locations (Waser & Wiley 1980; Wiley & Wiley 1980).

Distance from a neighbour might also influence a bird's use of his song repertoire. In some species, particular song types are used in encounters with males or females (Smith 1959; Morse 1966, 1967,

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1970; Ficken & Ficken 1970; Lein 1972, 1978; Baptista 1978; Smith et al. 1978; Payne 1979; Sossinka & Bohner 1980; Schroeder & Wiley 1983b). The use of repertoires might also change with distance between opponents. As the probability of direct confrontation between males increases, song sparrows (*Melospiza melodia*) tend to switch more rapidly between song types (Kramer & Lemon 1983). Northern cardinals (*Cardinalis cardinalis*) switch song types more frequently in close-range boundary disputes than in normal singing ( $N=2$  birds), and even more frequently in response to the simultaneous presentation of a caged intruder and playbacks ( $N=1$  bird) (Lemon 1968). However, these experiments are difficult to interpret since they confound the effects of distance and location: the boundary disputes occurred only at the edges of territories and the response to presentation of an intruder occurred within the territory of the subject.

During boundary encounters, increased use of repertoires might be a response either to the bird's location in its territory or to the proximity of conspecifics. In this study, using a new technique whereby I moved captive wrens to different locations in their territories, I separate the effects of location and distance from neighbours on the use of song repertoires. Carolina wrens are ideal subjects for such a study. They are aggressively territorial throughout the year (Morton & Shalter 1977), so that seasonal differences are minimized. In this species, pairs have permanent pair bonds: thus song is less likely to have importance for mate attraction. Indeed, young males form pair bonds before they develop adult song (Simpson 1982). Males sing repertoires of 25–43 song types year-round. They counter-sing by alternating songs with neighbours or playbacks. Observational study of the birds led me to believe that they used repertoires differently in close-range and far-range interactions with conspecifics. In addition, Carolina wrens are tolerant of captivity and sing normally when placed in cages on their territories (Simpson 1982). I exploited this tolerance in three series of experiments to separate the effects of location and spacing on singing.

Experiment 1 tested the effects of each bird's location in his territory on his use of song and repertoires. Experiment 1 also established a baseline for song use at the centre and periphery of a territory. Experiment 2 tested the response to playbacks from two distances: 25 m, simulating an

intruder inside the resident's territory, and 165 m, simulating a long-range interaction with a neighbour. In experiment 3, which tested the effect of distance from a neighbour, I moved pairs of territorial wrens progressively closer together, from the centres of their territories (140 m apart) to their boundary (0 m apart).

## GENERAL METHODS

All experiments were conducted between 12 July and 25 November 1981. Subjects were territorial Carolina wrens in woodlands at the Behavioral Research Station of the University of North Carolina (see Wiley 1977 for description of the study area). I selected the subjects, all previously individually marked, primarily on the basis of the suitability of their territories for use in the experiments. All territories used in the experiments were approximately 140 m in diameter. Prior to the experiments, I determined the boundaries of the subjects' territories by following their movement and locations of singing.

For the experiments, males (experiment 1) or pairs (experiments 2 and 3) were captured and each was placed in a portable cage ( $0.6 \times 0.6 \times 1.0$  m) in the centre of its own territory, 70 m from the territorial boundary of the nearest neighbour. Cages were placed on predator-proof stands 1 m above the ground. I provided the birds with water, vitamins, and live food, beetle larvae (*Tenebrio*) and moths captured in light traps each night. Birds vocalized normally by the second day of captivity. All birds were able to maintain their territories while caged (4 days, experiment 1; 13 days, experiments 2 and 3), although in July, first-year birds occasionally entered the territories and approached the cages. At the conclusion of the experiments subjects were released in the centres of their territories. I located all birds on their original territories 1 month after release.

I recorded all vocalizations given by the subject of each experiment. The recording equipment consisted of a Sony TC-110A or TC-56 cassette tape recorder and a Sony ECM-16 or F-27 microphone mounted on a tripod 1 m in horizontal distance from the cage.

In the laboratory, I monitored all the tapes on Superscope CD-330 cassette tape recorder. Samples of each song type were analysed on a real-time spectrum analyser (Spectral Dynamics Corp)

ration, Model SD-301-D; analysis range 50 kHz limited to 10 kHz, band width 150 Hz, memory period 10 ms; Hopkins et al. 1974). For each experiment, I calculated the total number of songs, number of song types, number of transitions between song types, and occurrence of matching (counter-singing with identical song types). Because Carolina wrens occasionally switch repeatedly between two song types, the number of transitions from one song type to the next is not always a direct measure of the number of song types used (Kroodsma & Verner 1978). I also calculated the number of song types per 100 songs and the number of transitions between song types per 100 songs, values independent of the number of songs used by the birds.

In addition, I measured the mean syllable length for each song type and used this value to classify song types into three categories: those with fast syllables,  $< 0.29$  s/syllable; medium syllables,  $0.30-0.39$  s/syllable; and slow syllables,  $> 0.40$  s/syllable. These categories were chosen by measuring the syllable lengths of all songs from control periods and selecting three categories with equal frequency. I compared the number of songs in each category for each experiment to determine if wrens used song types with fast syllables in different locations or social situations, more often than they used slower syllables. Of particular interest was whether or not they used fast syllables in simulated close-range encounters and slower syllables in distant counter-singing. Slower syllables might be less susceptible to degradation by reverberations, and thus might be used preferentially during counter-singing at long distances (Wiley & Richards 1978). For experiments 1 and 2, I tested whether or not rare song types were associated with location or playback distance. For each bird, rare song types were defined as those recorded during only one trial, regardless of the number of times a rare song type occurred during that trial.

## EXPERIMENT 1: USE OF SONG AT THE TERRITORY CENTRE AND EDGE

### Methods

Trials conducted from 12 July to 27 July 1981, I compared the singing rates of captive territorial adults at the centres of their territories and at the edges 70 m away. In July, young birds in their first

few months of life attempt to establish territories, so territorial behaviour is vigorous. I used the following protocol for each of five birds. One day before the start of each trial, I captured the experimental subject and placed him in a cage in the centre of his territory. To avoid interference with late reproductive activities, females were not confined. However, the mate of each subject could be heard nearby during the experiments. Neighbours were not caged. The day after capture, I moved the caged bird along a 70 m lane which I had cleared in a randomly selected direction to the edge of his territory. There I placed the cage on a stand 1 m above the ground for 1 h. I moved the bird back to the centre of his territory for a second hour. Then I repeated the sequence, returning him to the edge for the third hour, then back to the centre for the fourth and final hour. Afterwards I moved the bird to the edge of his territory where he remained for the night. This last move allowed me to determine whether or not remaining overnight at a site had an effect on singing. On the next day, I reversed the order of the trials: the first hour at the centre, the second hour at the edge, the third hour at the centre, and the fourth hour at the edge, for a total of 8 h of experimental data per bird.

Of the 7076 songs which I analysed, I recorded 26-34 song types per bird ( $N=5$  birds, mean =  $28.4 \pm 4.3$  songs). For each bird, I produced a saturation curve of the number of new types as a function of the number of hours of recording. For birds NW (26 types recorded), ES (24 types recorded) and NP (27 types recorded), the curves did not reach an asymptote in the 8 h of recording per bird, so presumably I did not obtain the complete repertoires of these birds. For birds NF (30 types recorded) and SH (35 types recorded), the curves reached an asymptote.

### Results

The total number of songs at all sites did not differ on the two days of the experiments (sign test,  $N=5$ ,  $P>0.50$ , two-tailed). There was also no significant difference in the number of songs at the location where the subject spent the night in comparison to the other location, during the first 2 h of the experiment when the effect should be most pronounced (Wilcoxon matched-pairs signed-ranks test,  $N=10$ ,  $T=27$ ,  $P>0.05$ , two-tailed). More songs occurred during the first 2 h of each day's experiments than during the last 2 h (rando-

mization test,  $N=10$ ,  $P<0.02$ , two-tailed, Siegel 1956), although there were no more songs recorded during the first hour than the second hour (Wilcoxon matched-pairs signed-ranks test;  $N=10$ ,  $T=18$ ,  $P>0.50$ , one-tailed). Because of the effect of time of day, only data from the first 2 h of the experiments are analysed below.

Birds sang more at the centre of their territories than at the edge (Table I). On the other hand, the features of the songs at each site did not differ (Table I). Birds sang no more song types at the centre than at the edge. When the number of song types is adjusted for difference in number of songs, birds used no more song types per 100 songs at the centre than at the edge. Birds sang no more bouts, and no more songs/min of singing, at the centre compared to the edge (Table I).

Song types with longer syllables were not used more frequently at the centre of the territory, where the bird might counter-sing at greater distances from neighbours. There were no differences in the number of songs of short, medium, or long syllable lengths for centre and edge sites (Friedman's ANOVA,  $N=5$  birds,  $k=3$ : centre  $\chi_r^2=5.2$ ,  $P=0.093$ ; edge  $\chi_r^2=2.8$ ,  $P=0.367$ ). There were no differences in the use of the three categories at centre and edge sites (Kruskal-Wallis  $\chi^2$ ,  $\chi^2=1.80$ ,  $df=1$ ,  $P>0.10$ ).

To determine whether or not different sets of song types were used in different locations, I classified songs into three categories on the basis of syllable patterns that appeared distinctive to my ear. Category 1 included song types in which the dominant frequencies of the notes of each syllable ranged sequentially from high to low. Category 2 included song types in which the notes of syllables ranged from high to low to high frequencies. Category 3 included all other songs. Subjects

differed individually in the use of these three categories both at the centre and the edge (Friedman's two-way ANOVA,  $N=5$ ,  $k=3$ : centre  $\chi_r^2=7.6$ ,  $P=0.024$ ; edge  $\chi_r^2=7.6$ ,  $P=0.024$ ). At both sites, half of the song types were classified in category 2. There was no difference in the use of the three categories at the centre compared to the edge (Kruskal-Wallis  $\chi^2$ ,  $\chi^2=2.06$ ,  $df=1$ ,  $P>0.10$ ). I did not separately analyse each of the 64 different song types recorded.

On the possibility that rare and common song types might differ in frequency with location, I compared the use of rare and common song types at the two sites. Among five subjects, there were 46 instances of rare types at the centre, compared to 34 instances at the edge. However, when I compared matched experiments at centre and edge, there was no tendency for birds to use more rare types at the edge compared to the centre (sign test;  $N=15$ ,  $P=0.5$ , one-tailed).

On several occasions, young birds approached the cages of captives and an impromptu territorial encounter ensued. A comparison of 1-h time periods which included these interactions, with the 1-h time periods preceding them, shows the changes in song use which occurred (Table II). Birds did not consistently sing more songs during the encounters, but they did use more song types than during the 1 h prior to the encounter.

## EXPERIMENT 2: RESPONSE TO PLAYED-BACK SONGS FROM NEAR AND FAR DISTANCES

### Methods

In experiments carried out from 15 October to 26 November 1981, I captured six pairs of Carolina

Table I. Use of songs at the centre and edge of the singer's territory

Measure of song use (mean $\pm$ SD)	Centre	Edge	<i>T</i>	<i>P</i> *
Total no. of songs	249 $\pm$ 121.8	162.0 $\pm$ 106.3	7.5	0.05
No. of song types	8.2 $\pm$ 8.2	6.1 $\pm$ 2.0	25.5	NS
No. of types/100 songs	4.1 $\pm$ 3.8	4.9 $\pm$ 3.3	18.0	NS
No. of song bouts	11.5 $\pm$ 9.8	8.6 $\pm$ 3.5	24.5	NS
No. of songs/min	7.8 $\pm$ 1.6	8.1 $\pm$ 1.9	23.0	NS

\* Wilcoxon matched-pairs signed-ranks test,  $N=10$ , two-tailed.



**Table II.** Number of songs, song types and bouts sung by captive birds when they were approached by 'intruders' during the 1-h experimental trial and during the 1 h prior to the approach of an 'intruder'

Bird	Intruder				No intruder			
	No. of songs	No. of song types	No. of types/100 songs	No. of bouts	No. of songs	No. of song types	No. of type/100 songs	No. of bouts
SH	205	13	6	15	127	4	3	6
SH	344	31	9	39	362	3	8	4
NP	170	8	5	7	80	5	6	10
NF	114	8	7	16	96	4	4	7

wrens on their territories and placed each pair in a portable cage in the centre of its own territory, 70 m from the territorial boundary of the nearest neighbour. Maintaining each male with his mate allowed me to control for the location of the female during the trials.

The subjects constituted three replicates, in each of which the territory of one pair was adjacent to the territory of another pair. I captured the birds for each replicate on the same day and began experiments 2–5 days later.

The experiments compared the vocal responses of two pairs of wrens, each located in the centre of its territory, to near and far playbacks of wren songs. A near playback, 25 m from the subject's cage, simulated an intruder within the subject's territory. A far playback, 165 m from the subject's cage, simulated a bird singing from a neighbour's territory.

Playback tapes included one or four song types, all present in the repertoires of all experimental subjects (Fig. 1). Thus this experiment consisted of four playbacks to each subject (two sizes of playback repertoire  $\times$  two distances). For playbacks of a single song type, I selected one of two songs in a permuted order. For playbacks of four song types, I used the same tape for all playbacks. Playbacks were matched for the number of songs per minute (10) and the number of syllables per song (3). The playback apparatus consisted of a Sony TC-45 cassette tape recorder, an Amplivox S-610C portable amplifier and a Realistic Minimus 7 speaker. The speaker was mounted on a tripod 1.5 m above the ground facing the subjects. At the start of each trial, I adjusted the playback volume to 85 dB (maximum reading at 1 m) with a sound pressure level meter (Realistic sound level meter 42-3019, C-weighting, fast response setting).

On successive days, I alternated presentation of near and far playbacks to each pair. I set the playback apparatus in a line 25 m from one pair and 165 m from the adjacent pair and tested two adjacent pairs simultaneously. The playback alternated 2.0 min of song, followed by 6.5 min of silence for 1 h, which approximated the wrens' normal singing rate. Prior to each playback, I collected 1 h of control data, from 0600 to 0700 hours. During control and experimental periods, I recorded all the songs of the experimental birds.

## Results

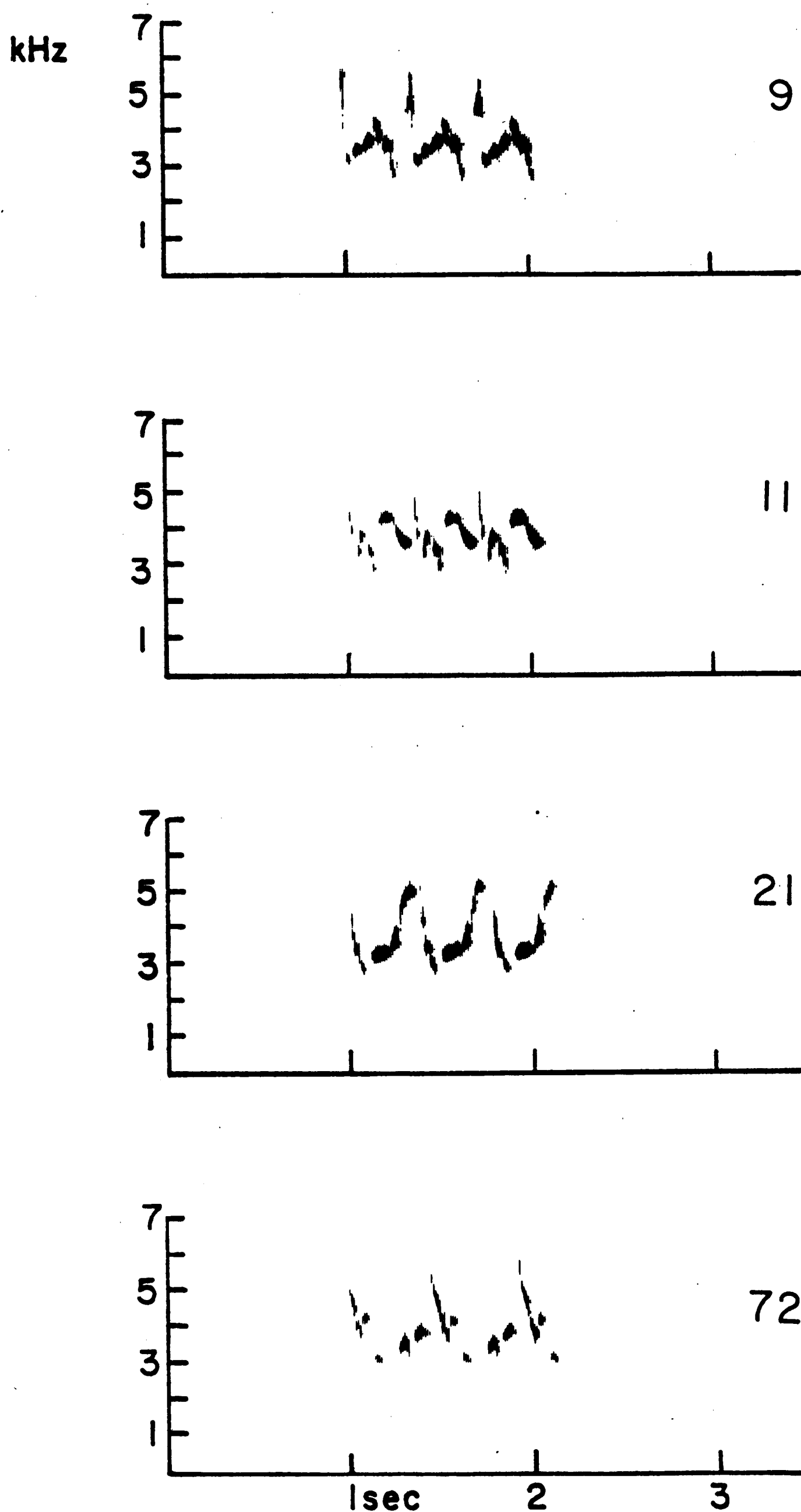
### *Interactions between neighbours*

The singing responses of two birds treated simultaneously were not correlated during control periods (Spearman rank correlation;  $N=12$ ,  $r_s = -0.0356$ ,  $P > 0.05$ ) or experimental periods ( $N=12$ ,  $r_s = 0.220$ ,  $P > 0.05$ ). Compared to controls, two birds tested simultaneously did not both increase or decrease the number of songs used during playbacks (Sign test;  $N=12$ ,  $P=0.774$ , two-tailed). For these reasons, I considered pairs tested at the same time to be independent of each other.

### *Effect of order*

The number of songs did not change on successive days for the four control periods (Page's test for ordered alternatives;  $N=6$ ,  $L=161$ ,  $k=4$ ,  $P > 0.05$ , two-tailed, Hollander & Wolfe 1973), nor did the order of presentation affect responses in the four experiments (Page's test;  $N=6$ ,  $L=148.5$ ,  $k=4$ ,  $P > 0.05$ , two-tailed).

At 25 m, an individual's responses in the two trials were highly correlated (Spearman rank correlation;  $N=6$ ,  $r_s = 0.926$ ,  $P < 0.05$ ), and so for each



**Figure 1.** Song types used in playback experiments. Song type numbers 9 and 11 were used for playbacks of one song type. Song type numbers 9, 11, 21 and 72 were used for playbacks of four song types. Playback songs were recorded in 1980 from captive birds taken from the local population. No songs were recorded from the subjects of the present experiments, although all song types used in playbacks were present in the repertoires of all experimental subjects.

bird I used the mean for two trials in further tests. At 165 m, an individual's responses in the two trials were not correlated ( $N=6$ ,  $r_s=0.20$ ). Thus for analysis of responses at the long distance, I used a sample of 12 playbacks (6 birds  $\times$  2 trials per bird).

#### *Effect of repertoire size in playbacks*

There were no significant differences between the number of songs, song types, or transitions between song types used in response to playbacks of one and four song types at either the 25 m (all comparisons, sign test;  $P>0.376$ , two-tailed) or 165 m distances (all comparisons, Wilcoxon matched-pairs signed-ranks test,  $P>0.344$ , two-tailed). It should be noted that five of the six birds used more song types and switched song types more frequently in response to playbacks of repertoires compared to single songs at 25 m. However, since there were no significant differences between the responses to playbacks of one and four song types, I considered playbacks of different repertoire sizes at one distance to be replicates.

#### *Effect of distance*

There were no differences in the number of songs or the number of song types delivered in response to playbacks at 25 m compared to 165 m (Table III). There were more song types per 100 songs, more transitions between song types, and more transitions per 100 songs in response to playbacks at 25 m than to playbacks at 165 m (Table III). Birds also matched playbacks more frequently at 25 m than at 165 m (seven versus two instances, respectively), although the infrequent occurrence of matching prevented statistical analysis. Thus, although birds did not sing more, they did use their songs differently in response to playbacks at the two distances.

Birds did not sing more songs during playbacks than during control periods, at 25 m (Wilcoxon test;  $N=6$ ,  $T=12$ ,  $P>0.05$ , two-tailed), or at 165 m ( $N=12$ ,  $T=31$ ,  $P>0.05$ , two-tailed). At 25 m, birds typically responded to playbacks by either increasing their singing rate or ceasing to sing entirely, as do wild wrens in response to playbacks inside their territories. At 165 m responses were much less dramatic: birds appeared to counter-sing with the distant tape as they would with an adjacent territory holder. In order to compare such disparate responses, I calculated the change in response between the playback and the preceding control period, regardless of its direction. The mean change

**Table III.** Responses to playback at two distances from the subject\*

Response to playback (means $\pm$ SD)	25 m	165 m	$P^\dagger$
No. of songs	103.90 $\pm$ 128.13	103.83 $\pm$ 57.92	0.812
No. of song types	4.90 $\pm$ 1.71	4.40 $\pm$ 1.78	0.500
No. of song types per 100 songs	11.87 $\pm$ 10.52	5.62 $\pm$ 2.84	0.031
No. of transitions	10.90 $\pm$ 13.60	3.50 $\pm$ 1.69	0.031
No. of transitions per 100 songs	14.75 $\pm$ 9.90	3.97 $\pm$ 1.76	0.031

\* Bird NW<sub>2</sub> was omitted from analysis since he did not sing during trials at 25 m.

† Sign test for mean of 2 trials at 25 m  $>$  mean of 2 trials at 165 m;  $N=5$ , one-tailed.

in response between control and playback at 25 m was greater than at 165 m (Wilcoxon test;  $N=6$ ,  $T=0$ ,  $P<0.05$ , two-tailed): thus the birds responded more strongly to nearby playbacks than to distant playbacks.

#### *Use of song categories*

As in previous playbacks outside the territories of Carolina wrens (Simpson 1982), there were no differences in the response to different song types. There were no more songs used in response to playbacks of song type no. 9 compared to song type no. 11 at the near distance (Mann-Whitney  $U=2$ ;  $N_1, N_2=3$ ;  $P=0.40$ , two-tailed) or far distance ( $N_1, N_2=3$ ,  $U=4$ ,  $P>0.99$ , two-tailed).

For each bird, I compared the number of songs with short, medium or long syllables used during playbacks. There were no differences in the number of songs of the three categories delivered in response to playbacks of one song type (Friedman's ANOVA;  $N=4$ ,  $k=3$ ,  $\chi_r^2=0.50$ ,  $P=0.931$ ) or four song types ( $N=4$ ,  $k=3$ ,  $\chi_r^2=4.50$ ,  $P=0.125$ ) at near distance ( $N=5$ ,  $k=3$ ,  $\chi_r^2=1.6$ ,  $P=0.522$ ) or far distance ( $N=5$ ,  $k=3$ ,  $\chi_r^2=1.6$ ,  $P=0.522$ ). Thus there was no tendency for birds to select song types with rapidly repeated syllables in response to playbacks at the near distance, and slower song types in response to playbacks at the far distance.

Finally, I tested for preferential use of rare song types in response to playbacks from 25 m. There was no tendency for birds to prefer rare song types in response to playbacks in comparison to controls (Sign test;  $N=5$ ,  $P=0.50$ ). Thus, for the categories

I employed, these experiments provide no evidence for the preferential use of different song types by Carolina wrens in response to playbacks.

### EXPERIMENT 3: EFFECT OF THE DISTANCE FROM A NEIGHBOUR ON THE USE OF SONG

#### Methods

This series of experiments compared the responses of wrens to artificially staged territorial encounters, by moving caged neighbours closer together toward their common territorial boundary. All trials were conducted from 0630 to 0915 hours from 8 October to 20 November 1981. The subjects for these experiments were the same birds used in experiment 2. As described in the previous experiment, one territorial pair was matched with another pair on an adjacent territory. Along a 140-m lane cleared between the cages at the centres of the two territories, I placed stands for portable cages at eight sites so that the birds could be placed 140 m, 80 m, 20 m or 0 m apart. At 0 m apart, cages were adjacent at the common territorial boundary. At each distance, pairs were equidistant from the common boundary of their territories. Prior to each treatment, I partially covered the cages and moved them to the designated sites. Handling times were controlled by moving each pair the equivalent of 70 m prior to each trial.

On the first day, at least 2 days after the end of experiment 2, as a control, I tested the birds 140 m apart by carrying the cages the prescribed 70 m and setting each back in its original position. I repeated this procedure three times (periods 1–3), once every 45 min, reversing the order of handling of the subjects each time. On the second day, I moved the matched pairs to sites 80 m apart for 45 min, then 20 m apart for 45 min, then 0 m apart for 45 min (periods 1–3 respectively). On the third day, I moved the birds 20 m apart for 45 min, 80 m apart for 45 min, and 0 m apart for 45 min, and also reversed the order of handling of the subjects.

#### Results

##### *Effects of order*

The order of handling had no effect on the birds' singing. For instance, the first male moved at the start of each trial did not sing more or fewer songs

than the second male (sign test;  $N=9$ ,  $P=0.746$ , two-tailed). Time of day did affect singing during control periods. At 140 m, birds sang less during period 3 than during periods 1 or 2 (Wilcoxon test; period 1 versus period 2,  $N=6$ ,  $T=5$ ,  $P>0.05$ , two-tailed; period 2 versus period 3,  $N=6$ ,  $T=0$ ,  $P=0.05$ , two-tailed). Thus the trials at 80 m and 20 m were presumably not influenced by the time of day or the duration of the experiment, since they occurred within the first two periods each day. The responses of individuals were correlated in the first and second periods at 140 m (Spearman rank correlation;  $N=6$ ,  $r_s=0.83$ ) but not in successive trials at other distances (80 m,  $N=6$ ,  $r_s=0.60$ , NS; 20 m,  $N=6$ ,  $r_s=0.71$ ; 0 m,  $N=6$ ,  $r_s=0.51$ ). Consequently, for analysis of these experiments, I considered repeated trials independently.

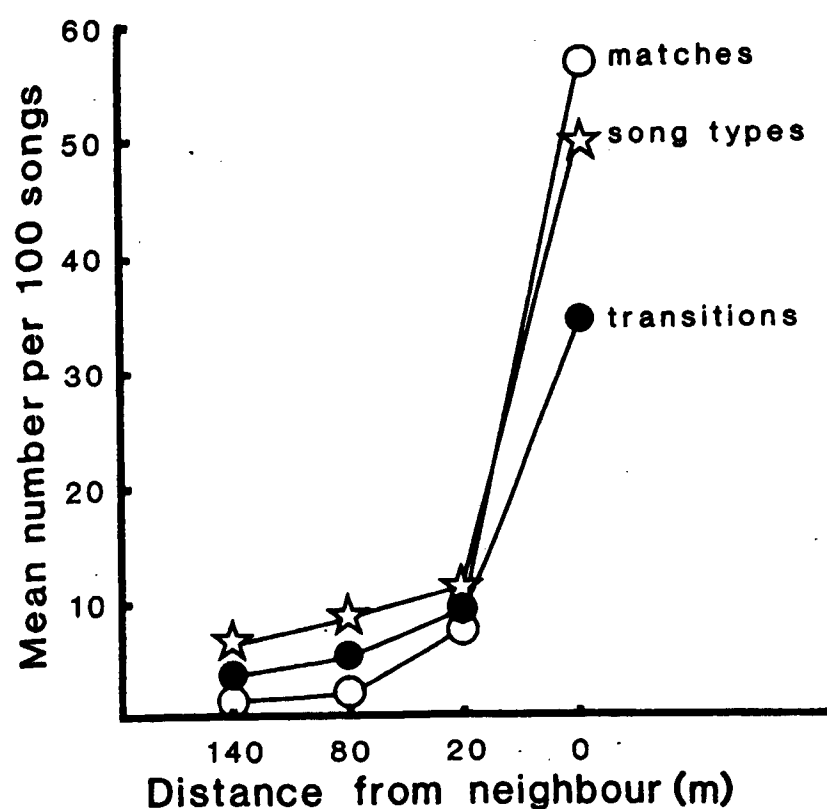
##### *Effect of distance*

For all birds, the number of songs was positively correlated with the distance from the neighbour (Page's test;  $L=348$ ,  $N=12$ ,  $k=4$ ,  $P=0.001$ ). The total number of song types was also positively correlated with distance (Page's test;  $L=190$ ,  $k=4$ ,  $P=0.05$ ). To control for the number of songs used by different birds, I calculated numbers per 100 songs of song types, transitions between song types, and matched song types. All three of these measures were inversely correlated with distance (Fig. 2), an indication that although birds sang less at decreased distances from neighbours, they altered the way they used their songs. When I moved two cages closer together, birds typically engaged in counter-singing bouts, which consisted of rapid transitions between song types. At short range, birds frequently matched songs with opponents. In addition to counter-singing, they frequently simultaneously matched songs by singing the same song type at the same time. This temporal overlap of the song of one bird over the song of his neighbour occurred only when birds were adjacent at their common boundary. Often at 0 m, they would not sing again after an initial song bout, but would call instead.

##### *Categories of songs*

On the basis of the duration of syllables, I calculated the percentage of fast, medium and slow songs for each trial. I thus tested whether or not birds used these categories equally at four different distances from neighbours. There were no differences in the use of these three categories at the





**Figure 2.** Mean number of song types/100 songs, transitions between song types/100 songs, and occurrence of matching song types/100 songs at four distances of the subject from a captive neighbour. Birds which did not sing at 0 m were omitted from the analysis. Page's test for ordered alternatives,  $k=4$  distances: song types,  $N=7$ ,  $L=193$ ,  $P=0.010$ ; transitions,  $N=4$ ,  $L=118$ ,  $P<0.001$ ; matching,  $N=4$ ,  $L=118$ ,  $P<0.001$ ).

different distances (Friedman two-way ANOVA; for each distance  $P>0.20$ ).

## DISCUSSION

### Effect of Location

In contrast to other studies on the effects of a subject's location in its territory (Weeden 1965; Waser & Wiley 1980), experiment 1 controlled the amount of time the subject spent at the centre and the edge. The experiment confirmed that Carolina wrens sing more at the centre than the edge. However, they use their song repertoires similarly at both sites.

### Effect of Distance from Playback

Experiment 2 controlled for location by confining each pair of birds in the centre of its territory and playing back songs from two distances. In response to playbacks from 165 m which simulated singing by a neighbour from an adjacent territory, the birds' singing rates and use of repertoires were indistinguishable from those during the control periods. Previous playbacks to unconfined Carolina wrens from unoccupied areas outside their territories did result in clear changes in singing rate

(Simpson 1984). In the present experiments, songs played from familiar locations might have successfully represented the neighbours.

That there were no differences in response to playbacks of one or four song types at 165 m substantiates previous evidence that in this species repertoires are not important in long-range communication (Simpson 1984).

In response to playbacks from 25 m, simulating an intruder inside the territory, subjects fell into two groups: some increased their singing rates, others decreased their singing rates. The difference in response reflects some unidentified difference in the 'states' of the birds (Petrinovich & Patterson 1980; Dabelsteen 1982) or valence of the playback locations. The total silence of several of the birds in response to near playbacks confounded the analysis, by reducing the sample for comparisons of song use. However, if I calculated the absolute value of the change in response to playbacks compared to the control periods, response was greater to near than to far playbacks. There was a trend, though not statistically significant, toward an increase in the use of song types and transitions between song types among birds which sang in response to repertoires of four song types, compared to single song types, at the nearer distance. In sum, experiment 2 demonstrates a clear effect of the distance of the playback.

### Effect of Distance from Neighbour

In experiment 3, I attempted to simulate territorial encounters by pairs of Carolina wrens. Previous observations of such events led me to expect that wrens would use their large repertoires in close-range encounters. For instance, on four occasions during experiment 1, young birds seeking territories approached the cages of captive territory holders. A comparison of the number of songs and song types used during these events with those occurring during the preceding hour demonstrated an increased use of repertoires under such conditions (Table II). In some but not all cases, the overall number of songs increased. In all cases, the number of song types increased.

In experiment 3, I moved two pairs of wrens from the centres of their territories to two locations closer together and finally to their territorial boundaries, to simulate boundary disputes. While wrens did not use more songs in such close-range encounters, they used their songs in a very different

way than when they counter-sang at long range (140 m). At close range they used more song types and switched more frequently between song types.

At 0 m, the results are more difficult to interpret. There are several possible explanations for the cessation or near-cessation of singing by the wrens at this distance. First, I conducted all trials at 0 m in time period 3, when there was a significant decline in the number of songs used during the control period. However, this cannot fully explain the reduction in the amount of singing by the birds at 0 m. A second possibility is that I inadvertently moved some of the birds outside their territorial boundaries. Birds that are moved outside their territories become silent and less active, seemingly aware of being in the 'wrong' location. In spite of my precautions, it is possible that I misjudged the territorial boundaries of the pairs in experiment 3. Finally, as previously mentioned, a component of the normal response of Carolina wrens to intruders or playbacks inside their territories is silence. This is an effective way to surprise an intruder if the bird's objective is to attack or chase it. Silence at 0 m might indicate an attack response. Although few songs were given at 0 m, many close-range calls were given under these circumstances by both males and females. Such calls may coordinate pairs in territorial encounters.

### Use of Repertoires

Although Carolina wrens do not use their 25–43 song types with equal frequency (Simpson 1982), I found no evidence that they use particular classes of song types in certain situations. Birds responded no differently to one played-back song type than to another in experiment 2, and in previous playback experiments to wild birds (Simpson 1984). I categorized song types in several ways: (1) by syllable length, (2) by frequency of use (rare or common), and (3) by audible differences (direction of frequency sweeps). There were no differences in the use of these categories of songs at the centre or edge of the territory (experiment 1), in response to near or far playbacks (experiment 2), or when birds were moved closer to neighbours at territorial boundaries (experiment 3). Owing to the large number of song types used by Carolina wrens, I did not test each song type in each context.

On the one hand, these results provide no evidence that Carolina wrens use song types differently in different situations. On the other hand, the

categories I chose are arbitrary and may have no biological relevance to the birds. Previous reports have demonstrated the association of different classes of song types with different agonistic circumstances, which normally differ with location (Morse 1970; Lein 1978; Payne 1979; Schroeder & Wiley 1983b). The subjects of such studies sing repertoires smaller than those of wrens, however. There is no evidence for associations of song types with context in any species in which individuals sing large numbers of songs, as do Carolina wrens.

A comparison of experiments 1 and 3 can separate the effects on song of the social interactions in encounters at a common boundary from any effect of the location (Table IV). In experiment 1, I individually moved each of five caged birds from the centre of its territory to the edge, 70 m distant. The neighbours of these subjects were not caged; there was no attempt to simulate territorial encounters. In experiment 3, birds were moved the same distance, but this time a territorial neighbour was simultaneously moved nearby.

In experiment 1, birds sang more in the centre of their territory than at the edge, but birds did not differ in the number of song types or transitions between song types at each site. Although experiment 1 was conducted in summer and experiment 3

**Table IV.** Comparison of numbers of songs given by subjects in experiment 1, in which each bird was moved alone to the edge of its territory, and experiment 3, in which two neighbours were simultaneously moved to their common boundary at the edge of their territories

Bird no.	No. of songs		No. of song types		No. of song types 100 songs	
	Experiment		Experiment		Experiment	
	1	3	1	3	1	3
1	167	1	4	1	2	100
2	135	8	6	3	4	38
3	96	1	4	1	4	100
4	96	31	4	7	4	23
5	96	19	3	1	3	16
<i>P</i> †	0.004		0.075		0.004	

\* All data were collected at the same time of day. All values are rounded to the nearest song. Values for experiment 3 are the means of two trials per bird plus 25% to adjust for the difference in the length of the trials in the two experiments. Bird NC, which did not sing at 0 m during experiment 3, is omitted from the analysis.

† Mann-Whitney *U*-tests,  $N_1 = N_2 = 5$ , one-tailed.

was conducted in fall, the numbers of songs delivered from the centre in both experiments did not differ (Mann-Whitney  $U=9$ ;  $N_1=5$ ,  $N_2=6$ ;  $p=0.230$ , two-tailed). Birds sang significantly fewer songs at the edge in experiment 3 than in experiment 1. Although they did not use more song types overall, they used more song types per 100 songs than those in experiment 1 (Table IV). Consequently, use of song is affected by location within the territory as well as by social interactions at boundaries. Repertoire use appears to be most strongly affected by social interactions.

Thus, the way birds use their songs at near and far distances from neighbours is quite different. In far-range interactions (140 m), birds tend to sing for long periods by repeating one song type many times. In near-range interactions (0 m, 20 m), birds sing fewer songs and tend to switch rapidly from one song type to another. Visual displays and calls are used with high frequency in such near-range interactions. Although the total number of song types did not increase at near distances, the number of song types per 100 songs did increase.

There are a number of reasons why Carolina wrens might use different patterns of singing in close-range encounters compared to far-range interactions. Playbacks have shown that repertoires are more effective than single songs in preventing the reoccupation of empty territories (for great tits, *Parus major*, Krebs et al. 1978; red-winged blackbirds, *Agelaius phoeniceus*, Yasukawa 1981). It should be emphasized, however, that in close-range interactions, Carolina wrens did not use a greater absolute number of song types, but instead used proportionately more of their repertoires.

The proportional number of transitions between song types also increased inversely with the distance between wrens. Frequent switching between song types in close-range encounters has been reported in other species, including cardinals (Lemon 1968), plain titmice (*Parus inornatus*, Dixon 1969), and tufted titmice (*Parus bicolor*, Schroeder & Wiley 1983b). Such behaviour might provide directional and motivational information (Morton 1982; Kramer & Lemon 1983).

Neighbours more frequently matched songs as the distance between them decreased. Matching might demonstrate membership in a local population (Krebs et al. 1978; Payne 1982; Schroeder & Wiley 1983a), kinship (Treisman 1978), or subordination (Kroodsma 1979). Matching might provide distance cues (Falls et al. 1982; Morton 1982;

McGregor et al. 1983), or indicate strength of response and probability of attack (Krebs et al. 1981). Most striking was the tendency for adjacent wrens to sing the same song type at the same time—for one bird to overlay its song temporally on that of its neighbour. Overlapping matched songs could be used as a vocal threat (Todt 1981). Matching could also signify attentiveness, permitting neighbours to 'communicate directly to one another' (Lemon 1968; Bremond, cited in Armstrong 1973).

In conclusion, these studies for the first time separate the effect of location in the territory from the effect of distance from a neighbour on the use of song repertoires. At least in Carolina wrens, the location in the territory affects how much an individual sings but does not affect how it uses its song repertoire. In contrast, the distance from a neighbour affects strikingly the way that an individual uses its repertoire. The results show the influence of social spacing on singing and indirectly support the view that the use of repertoires is important in species with high male/male encounter rates (Kroodsma 1977, 1983).

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