EFFECTS OF FOOD SUPPLEMENTATION, SONG PLAYBACK, AND TEMPERATURE ON VOCAL TERRITORIAL BEHAVIOR OF CAROLINA WRENS

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ABSTRACT.—We found both the song rate and the rate of song-type change of male Carolina Wrens (*Thryothorus ludovicianus*) in winter were positively correlated with ambient temperature. When the effect of temperature was controlled statistically, food supplementation significantly increased both the song rate and the rate of song-type change. Song playback did not significantly increase either song rate or rate of song-type change, however. Because foraging and singing are mutually exclusive behaviors in Carolina Wrens, the increase in vocal territorial behavior associated with warmer temperatures and food supplementation may reflect a decrease in the time required for foraging. The rate of vocal territorial behavior in winter may be more dependent on the amount of food available to wrens than on the presence of intruders. *Received 23 December 1986, accepted 14 July 1987.*

THE establishment and maintenance of territories requires significant investments of time and energy (Wittenberger 1981, Davies and Houston 1984). Because this cost of territoriality may reduce the amount of time individuals have to devote to foraging and breeding, a variety of ecological factors may influence the amount of time individuals devote to territory maintenance (e.g. Ydenberg 1984, Tamm 1985, Ydenberg and Houston 1986). We attempted to evaluate the effects of three ecological factors, food availability, intruder pressure, and temperature, on the amount of time male Carolina Wrens (*Thryothorus ludovicianus*) devote to vocal advertisement and defense of their territories during the winter.

Increased food availability has been shown to enhance territorial behavior in many birds, including the Great Tit (*Parus major*; Ydenberg 1984), the Red-winged Blackbird (*Agelaius phoeniceus*; Searcy 1979), and the Calliope Hummingbird (*Stellula calliope*; Tamm 1985). Searcy (1979) proposed that the increase in display rates observed in food-supplemented Red-winged Blackbirds was due to food supplementation and not to intruder pressure, because he measured no increase in intrusion rate. In wintering Sanderlings (*Calidris alba*) territory size was inversely related to intruder pressure, which was in turn positively correlated with food abundance (Myers et al. 1979). When intruder pressure declined and food abundance remained the same, territory size increased, indicating that intruder pressure and not food abundance directly influenced territory size. Norton et al. (1982) manipulated intruder pressure on the territories of Black-chinned Hummingbirds (*Archilochus alexandri*) while food availability was held constant and found that territory size decreased as intruder pressure increased. Few studies are reported in which food availability and intruder pressure were manipulated simultaneously (for an exception see Tamm 1985).

Because Carolina Wrens in North America are permanently monogamous and permanently territorial (Morton 1982, Simpson 1985), they are ideal subjects for a study of the effects of food availability and intruder pressure on territorial behavior. During winters when preferred foraging microhabitats are covered by deep snow, winter mortality can exceed 90% (Morton 1982). Therefore, the ability of the male to establish and maintain a territory on which sufficient food is available during the winter often determines which pairs survive. Male Carolina Wrens defend territories primarily by singing, and they sing vigorously throughout the year. Because males form pair bonds when they are too young to sing a fully developed song, song seems to be more important in territory maintenance and defense than in mate attraction (Morton 1982). By conducting the

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study in winter, we avoided the possibility of any confounding effects of mate attraction or other breeding behavior.

The study was conducted at Memphis State University's Meeman Biological Field Station, 20 km north of Memphis in Shelby Co., Tennessee. In late October and early November 1985, playbacks of male and female songs and calls were used to attract Carolina Wrens into mist nets. Eighteen birds were banded with unique color combinations and released. From this population of color-banded wrens we chose 8 pairs for intensive study. The male and female were banded in 5 of the pairs, and only the male was banded in the other 3 pairs.

The 8 study pairs were observed extensively in late November and early December 1985. During these observations sex was determined on the basis of vocal behavior (Morton 1982), and the territories were mapped. Territory size ranged from 2.1 to 8.1 ha ($\bar{x}$ = 4.1 ha). To avoid habituation, the study pairs were not subjected to playbacks during territory mapping.

Food availability and intruder pressure were manipulated to determine if either variable had a significant positive effect on vocal behavior. Food availability was manipulated by food supplementation, and increased intruder pressure was simulated by the use of playbacks of recorded Carolina Wren vocalizations. Each of the 8 study pairs was subjected to each of four possible treatments: (1) food supplementation with playbacks, (2) food supplementation without playbacks, (3) no food supplementation with playbacks, and (4) no food supplementation without playbacks (Table 1). This produced 32 separate observation periods. The study pairs were divided randomly into two groups: those that received food supplementation during the first block of observations (10 December 1985 to 6 January 1986) and those that received food during the second block of observations (12–23 January 1986).

Four days before the beginning of each block of observations, two feeding stations were established on each appropriate territory. Feeding stations consisted of cans measuring 17 × 15 cm and open on one end. The cans were placed on their sides and partially filled with dirt to hold them in place and provide a natural surface for foraging birds. A 14 × 18 × 2.5 cm board was placed in front of the opening to the feeding station and partially covered with leaf litter. Feeding stations were placed in vine tangles and tree falls to take advantage of the Carolina Wren's preference for feeding in concealed areas. Each day throughout the observation period 100 mealworms (larvae of *Tenebrio* sp.), approximately 11 g total, were added to each feeding station. The mealworms were placed primarily inside the cans, with a few scattered on the board to attract birds to the feeding stations.

We observed Carolina Wrens near the feeding stations on 7 of the 8 experimental territories and saw birds enter the cans on 4 territories.

During the observation periods the first playback began 30 min after observations began, with additional playbacks hourly for a total of four playbacks. For each playback the tape player was placed on the ground near the center of the territory. Each playback lasted 2 min and began with 30 s of silence, during which the observer retreated approximately 5 m and made himself as inconspicuous as possible. The remainder of the playback consisted of 30 s containing 8 songs by a male from the local population followed by 1 min of 15 male songs and 6 female chatters (see Morton 1982 for a description of chatters) from a population of Carolina Wrens in North Carolina (see Simpson 1985 for North Carolina localities). Vocalizations from local and distant populations were used to avoid any possible difference in singing response to familiar and unfamiliar songs (Shy and Morton 1986). The same tape was played at the same volume for all playbacks.

Although all male and female vocalizations were noted, male vocalizations used in long-distance territory maintenance and defense (song, song-type change, and "cheer" calls) were of particular interest. Individual male Carolina Wrens have song repertoires of 27–41 different song types (Morton 1982), each consisting of a single component repeated several times (Kroodsma 1977). Switching song types is often a response to intruders on or near the territory (Simpson 1985). Because song-type change was noted only when detected aurally, our observed rate of song-type change probably underestimates the true rate. It is, however, suitable for the comparative purposes of this study. In addition to song and song-type change, we noted the number of "cheer" calls. "Cheer" is the onomatopoeic name for a middle- to long-range male vocalization used in territory defense and maintenance (Morton 1982).

Daily observations began approximately 30 min before sunrise and continued for 4 h. Observations were made on 2 territories simultaneously, with one observer on each territory. Temperature was recorded at the beginning of and hourly throughout the observation period. Efforts were made to keep the resident Carolina Wrens in sight throughout the observation period, although this was not always possible. Behavior, type and number of vocalizations produced, microhabitat, height, and location within the territory were recorded for each wren at 2-min intervals.

All songs and other vocalizations produced in response to the playbacks were noted. In addition, response to playbacks was measured as time to the first song in response to playbacks and as the resident male's closest approach to the source of the playback.

We used matched-pairs analysis to analyze the effects of food supplementation and playback. A

TABLE 1. Vocal behavior of male Carolina Wrens exposed to the four experimental treatments. Values are $\bar{x} \pm$ SE.

	Food	No food	Total
Playbacks			
Songs/h	89.4 ± 15.0	68.9 ± 22.7	79.2 ± 13.4
Song-type change/h	1.0 ± 0.4	0.9 ± 0.2	0.9 ± 0.2
"Cheers"/h	16.4 ± 6.4	13.3 ± 5.4	14.8 ± 4.1
n	8	8	16
No playbacks			
Songs/h	57.2 ± 20.5	51.2 ± 20.2	54.2 ± 13.9
Song-type change/h	1.3 ± 0.7	0.7 ± 0.3	1.0 ± 0.4
"Cheers"/h	30.2 ± 18.2	26.1 ± 15.1	28.1 ± 11.5
n	8	8	16
Total			
Songs/h	73.3 ± 12.9	60.1 ± 13.8	
Song-type change/h	1.1 ± 0.4	0.8 ± 0.2	
"Cheers"/h	23.3 ± 9.5	19.7 ± 7.9	
n	16	16	

matched pair comprised two observation periods, performed on the same territory, that differed in only one of the experimental treatments (food or playback). For example, when analyzing the effects of food supplementation, two matched pairs of observation periods were available for each territory: the "food and playback" treatment matched with the "no food and playback" treatment for the same territory, and the "food and no playback" treatment matched with the "no food and no playback" treatment for the same territory. One-tailed sign tests were used in cases in which specific hypotheses concerning the treatment effect were tested (Siegel 1956).

RESULTS

Male Carolina Wrens sang significantly more songs per hour when presented with playbacks than when playbacks were absent ($n = 16$ paired comparisons, one-tailed sign test, $P < 0.05$; Table 1). There was no significant increase, however, in the rate of song-type change ($P > 0.05$) or in the "cheer" rate ($P > 0.05$) when playbacks were used (Table 1). Males given food supplementation had higher rates of song, "cheer," and song-type change (Table 1), but the differences were not statistically significant ($n = 16$ paired comparisons, each $P > 0.05$).

There were wide, uncontrolled variations in ambient temperature during the study ($-10°C$ to $18°C$). Because we found no significant differences among the eight males in song rate (Kruskal-Wallis $\chi^2 = 5.19$, df $= 7$, $P > 0.25$), rate of song-type change (Kruskal-Wallis $\chi^2 = 10.57$,

df $= 7, P > 0.10$), or "cheer" rate (Kruskal-Wallis $\chi^2 = 5.13$, df $= 7$, $P > 0.25$), we analyzed the effect of temperature by treating each of the 32 observation periods (4 from each male) as independent samples. Ambient temperature was positively correlated with both song rate (Spearman rank correlation coefficient $r_s = 0.42$, $n = 32, P < 0.02$) and rate of song-type change ($r_s = 0.59$, $n = 32$, $P < 0.001$; Fig. 1). "Cheer" rate, however, did not correlate significantly with ambient temperature ($r_s = 0.18$, $n = 32$, $P > 0.1$).

We attempted to control for the confounding effect of temperature by calculating an expected song rate for each observation period based on the mean ambient temperature during the observation period and on the least-squares regression of song rate on temperature (Fig. 1A). This expected song rate was then subtracted from the observed song rate to obtain the adjusted song rate (the song rate due to the experimental treatment with the effects of temperature statistically removed). An adjusted rate of song-type change was obtained in a similar manner.

Once the confounding effect of temperature was removed, playback had no significant positive effect on song rate (one-tailed sign test, $P > 0.05$; Fig. 2A) or the rate of song-type change ($P > 0.05$, Fig. 2B). Food supplementation, however, had a positive effect on both the adjusted song rate ($P < 0.05$, Fig. 2A) and the adjusted rate of song-type change ($P < 0.05$, Fig. 2B).
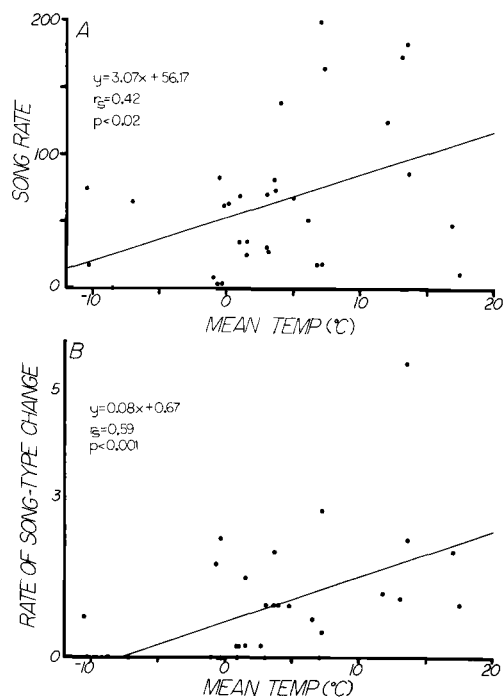
Fig. 1. Regression analyses of mean ambient temperature (average hourly temperature during the 4-h observation period) and (A) song rate (songs/h) and (B) rate of song-type change (song-type changes/h).
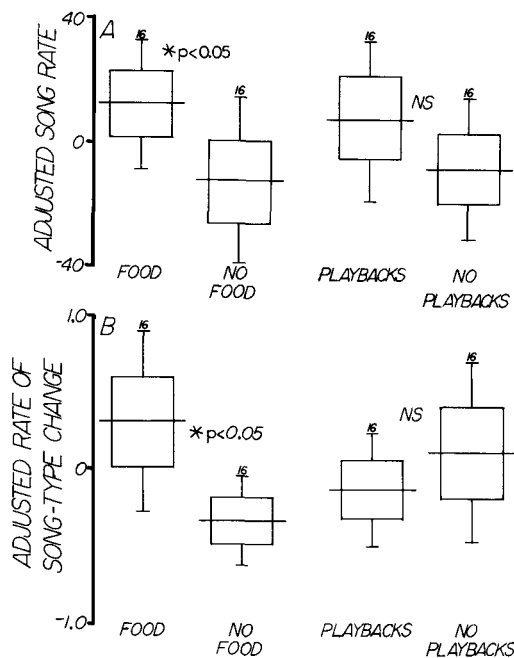

Fig. 2. Effect of food supplementation and intruder pressure on (A) song rate and (B) rate of song-type change when temperature is statistically controlled. Mean, standard error of the mean, and 95% confidence interval around the mean are indicated.

Although playback did not have a significant effect on the overall song rate once the temperature effect was eliminated, male Carolina Wrens presented with song playbacks sang significantly more songs in the first 10 min following the playbacks than did control males ($P < 0.05$, Fig. 3A). Food supplementation did not have a significant effect on vocal response by song to playback (Fig. 3B).

When presented with playbacks, food-supplemented males approached to within 20 m of the playback source in 7 of 32 trials. Unsupplemented control males approached to within 20 m in 10 of 32 trials. Therefore, food supplementation did not significantly increase the frequency with which the resident male approached the source of the playback ($\chi^2 = 0.72$, df = 1, $P > 0.25$). Food supplementation did not result in males responding to playbacks more rapidly. Food-supplemented males sang within 1 min of playbacks in 15 of 32 trials, compared with 12 of 32 trials for control males ($\chi^2 = 0.58$, df = 1, $P > 0.1$).

DISCUSSION

Temperature effects.—The positive relationship between temperature and the singing behavior of male Carolina Wrens verified the effects of temperature on singing behavior (McCabe 1951, Curio 1959, Slagsvold 1973, Garson and Hunter 1979). Garson and Hunter (1979) found that overnight temperature had the largest independent effect on the amount of time spent singing by Great Tits and Winter Wrens (*Troglodytes troglodytes*). They proposed that the birds forage more after a cold night and would sing less. Temperature could also influence song rate in insectivorous birds through its effect on foraging efficiency (Avery and Krebs 1984).

Carolina Wrens may have to spend more time foraging when ambient temperature is lower, because of either reduced foraging efficiency or higher energy requirements. Our data indicate that foraging and singing are to a considerable extent mutually exclusive activities. Males forage primarily at or near ground level (Fig. 4), in leaf litter, and among tree falls, vine tangles, and exposed roots (Morton 1982). Singing, how-
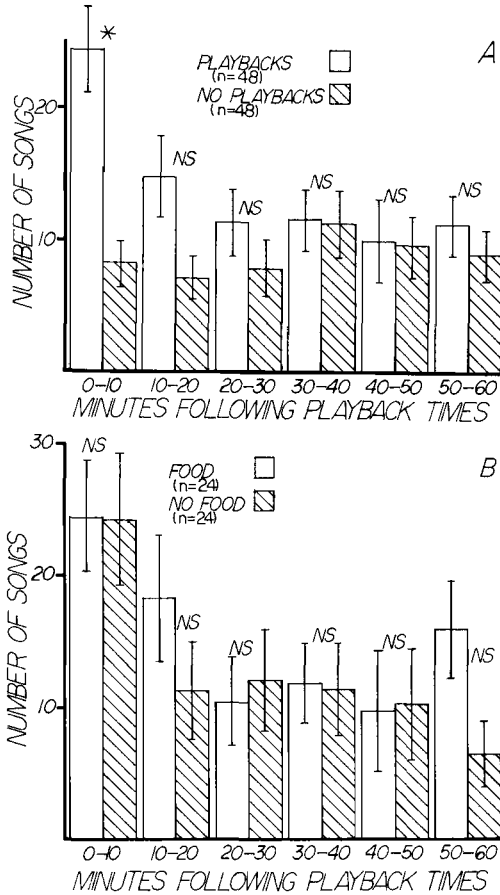
Fig. 3. Number of songs produced in the hour following playback times (A) with and without playbacks and (B) with and without food supplementation. The hour is divided into 10-min intervals. Only the first 3 playbacks in 16 (A) or 8 (B) paired comparisons could be used in these analyses. Asterisk denotes statistical significance ($P < 0.05$) by one-tailed sign test.

Fig. 4. Heights at which males were observed foraging and singing. Sample sizes for the 8 focal males were 2, 2, 15, 17, 45, 57, 67, and 94.

ever, is generally performed well above ground level (Fig. 4), presumably to enhance sound propagation. Male Carolina Wrens may have to compromise between the time they devote to singing and foraging during the winter (Ydenberg and Houston 1986). Thus, the positive relationship between singing behavior and temperature may actually reflect a negative relationship between ambient temperature and the amount of time the birds must spend foraging. We could not keep the birds in sight at all times, however, and we are unable to cor-
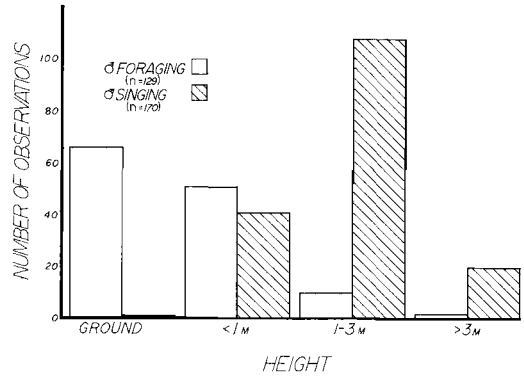
relate time spent foraging with average daily temperature.

Effect of food supplementation and song playback on song rate.—We found a relationship among food availability, intruder pressure, and song rates of male Carolina Wrens similar to that in male Calliope Hummingbirds (Tamm 1985). When the confounding effects of temperature were controlled, food supplementation had a significant positive effect on the amount of time male Carolina Wrens devoted to territory maintenance and defense by singing. Great Tits, when given access to extra food, also increase the intensity of territory defense (Ydenberg 1984). Ydenberg (1984) suggested that the excess food allowed the birds to spend less time foraging and devote more time to territory defense. Because Carolina Wrens appear to forage and sing at different heights (Fig. 4), the amount of time males devote to singing may be determined by the amount of time they must devote to foraging. Increased food availability would allow the birds to spend less time foraging and free more time for other activities, including singing (Davies and Lundberg 1984).

The increase in song rate seen immediately following playbacks reflects the male Carolina Wren's tendency to sing in response to another male singing nearby (Morton 1982). The use of playbacks did not, however, lead to a significant overall increase in song rate when the effects of temperature were statistically controlled.

Effect of food supplementation and song playback on rate of song-type change.—Simpson (1985) found that male Carolina Wrens use more song types when responding to the songs of intrud-

ers on their territories than when responding to the songs of neighbors on adjacent territories. Although our playback experiments were conducted near the center of each territory, we did not find a significant positive relationship between the use of playbacks and the rate of song-type change (Fig. 2B). A possible explanation for the different results of these two studies is that Simpson used live caged birds to simulate the presence of an intruder while we used song playbacks. In our study we found that food availability has a greater effect on the rate of song and song-type change than does song playback.

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