

REPRODUCTIVE BEHAVIOR BY A FEMALE SONGBIRD: DIFFERENTIAL STIMULATION BY NATAL AND ALIEN SONG DIALECTS

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ABSTRACT.—The responsiveness of female White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) to male songs in their natal dialect (Clear) or in an alien dialect (Buzzy) was evaluated by measuring string-gathering and paper-shredding in a laboratory experiment. Females hearing Clear dialect songs gathered more strings than did females hearing Buzzy dialect songs. More females hearing Buzzy songs shredded paper than females hearing Clear songs. Both groups placed more strings than paper shreds into nest cups, indicating that strings were regarded as a more suitable nesting material. Taken together, these results suggest that females are reproductively more responsive to the song of males in their natal dialect than to songs in an alien dialect.

Female songbirds' responsiveness to male song has been measured in various ways, including the amount of nest-building, number of eggs laid, and extent of copulatory posturing. Kroodsma (1976) found that female Canaries (*Serinus canaria*) exposed to playback of large (normal) song repertoires of male Canaries gathered more strings (an index of nest-building activity) and laid more eggs than did females hearing playback of artificially produced small repertoires of male Canaries. Nest-building, or string-gathering, was first used as an assay by Follett et al. (1973) to determine the effect of changing photoperiod on nest-building activities. In a comparison between species, Hinde and Steel (1978) found that female Canaries responded with increased nest-building activity when hearing male Canary song but not when hearing male Budgerigar (*Melopsittacus undulatus*) songs.

Male White-crowned Sparrows (*Zonotrichia leucophrys*) of a particular geographical region usually sing a stereotyped song that differs in syllabic content from songs of males in other regions. These differing song populations are called "dialects" (Marler and Tamura 1962). It has been hypothesized (Marler and Tamura 1962) that song dialects in some avian species might induce birds to breed in their natal area because the birds would be attracted to their familiar natal dialect. One behavioral mechanism that might be involved in such an attraction is for the female to select a mate who sings the dialect of her natal area (Konishi 1965).

Copulatory posturing of female White-crowned Sparrows has been measured to determine their responsiveness to songs of males

from their natal dialect region and to songs of males from alien dialect regions (Baker et al. 1981). Another method of analyzing the female response to male songs from different dialects is to study the hormone-induced song of a mated female (Baptista and Morton 1982) and determine if the song is similar or dissimilar to that sung by her mate. A different approach to considering female responsiveness to dialects is to ask whether or not a female hearing a natal dialect is physiologically more stimulated than one hearing a non-natal dialect.

To broaden the base of empirical evidence on female responsiveness to natal and alien dialects, we conducted a simple laboratory experiment to measure the nest-building activities of females exposed to playback of male songs from either their natal or an alien dialect region.

METHODS

Twenty female White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) were captured in Marin Co., California, in June 1981 at age 28 ± 3 (SD) days. These fledglings were exposed to songs of wild males while in the nest and until their time of capture. This tutoring was continued in the lab using tape-recorded songs from the natal dialect (Clear) twice daily for 45 min each session until 1 September (birds approximately 90 days of age). From 3 August until 28 September the photoperiod was gradually reduced to 8L:16D and maintained to 1 December. On 1 December the photoperiod was increased to 16L:8D.

On 30 December, the birds were implanted with an 8-mm piece of silastic tubing (Dow

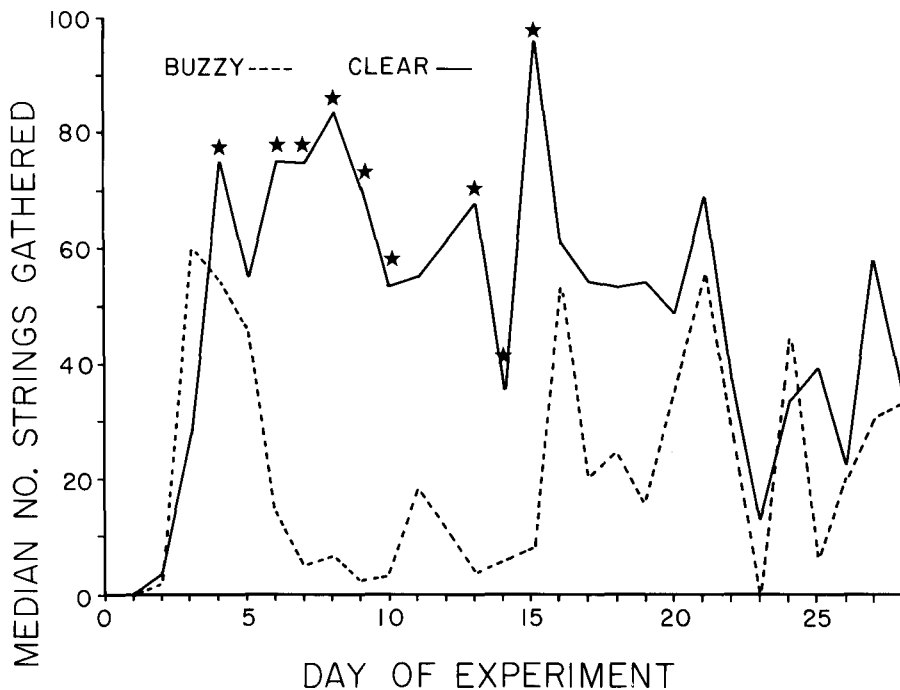


FIGURE 1. Median number of strings gathered by female White-crowned Sparrows hearing Clear (natal) dialect songs and Buzzy (alien) dialect songs for a 28-day period. Asterisks indicate days on which the groups differed significantly by Mann-Whitney U -test.

Chemical) filled with estradiol-17 β (Sigma). This treatment induced defeathering of the brood patch, copulation displays in response to male song, and paper-shredding. From 5 to 16 January, these females were used in an experiment on copulatory display reactions to Clear and alien dialects (Baker 1983). During those tests, each bird heard 72 Clear and 72 Buzzy dialect songs.

For the experiment reported here, the females were assigned to two groups and housed in individual cages. The more active displayers were assigned equally to each group. On 18 January, all birds were provided with string bundles and nest cups, and the groups were placed in two different rooms in auditory isolation. Lengths (10 cm) of wrapping twine were arranged in a paper sleeve, which was rolled and fastened with a rubber band to form a string bundle. This bundle was inserted between the bars of the bird's cage near a perch within her reach. A felt-lined plastic nest cup was hung inside each cage.

Beginning on 19 January, and continuing throughout the 28-day test period, the birds were exposed to playback of male song for 2 h in the morning and 2 h in the late afternoon. One group of 10 birds heard the Clear (natal) dialect. The other group of 10 females heard the Buzzy (alien) dialect. A 2-h session consisted of three different songs repeated at

15-s intervals, which approximated the natural singing rate of a male. Although a male sings only one song, the use of three different songs is a better representation of the dialect diversity caused by slight individual variations among the males.

Birds were cared for and data were collected at midday to avoid disturbing birds during the test periods. Each day for 28 days the number of strings pulled from the bundle was recorded for each bird. The number of birds shredding paper was also recorded. A new bundle was provided one hour before the afternoon playback session.

RESULTS

Females responded in two quantifiable ways to playback of male song. *String-gathering* occurred when a female stood on the cage floor or perch and pulled individual strings from the bundle. The bundles were constructed so as to release only the one string being pulled by the bird. Upon obtaining a string, a female would mandibulate it and fray the ends. Most strings were eventually dropped to the cage floor but some were placed in the elevated nest cup.

Paper-shredding was accomplished by a female's pecking, pulling, and tearing pieces from the paper lining the floor of the cage. Paper shreds varied in size from long thin strips to tiny pieces. We did not attempt to count the

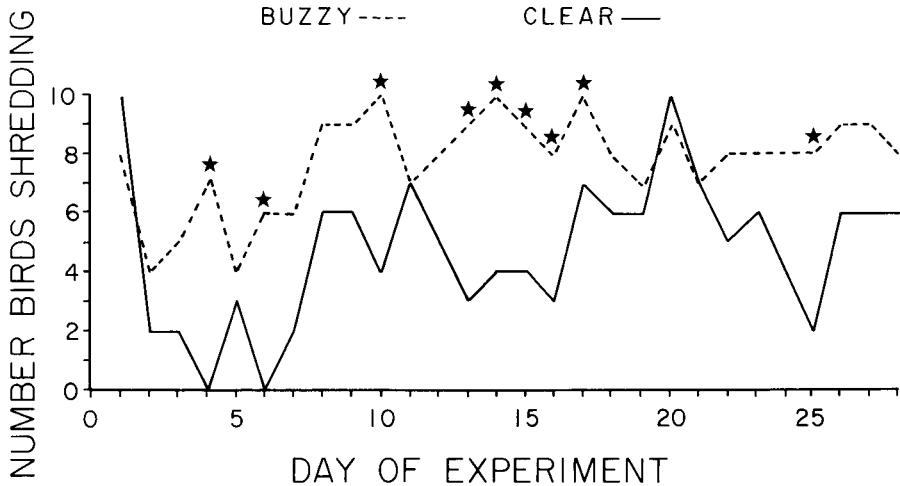


FIGURE 2. Number of females in the group hearing Clear and in the group hearing Buzzy that shredded paper during each day of the experiment. Asterisks indicate days on which the groups differed significantly by the G -test.

number of paper shreds but instead merely recorded whether or not each female shredded any paper.

For statistical analysis, we compared the number of strings gathered by females hearing the Clear stimulus to the numbers gathered by females hearing the Buzzy stimulus on 27 of the 28 days of the experiment (Fig. 1). On one day of the experiment (day 12), no data were collected. Females hearing the Clear dialect gathered more strings than those hearing the Buzzy dialect throughout most of the experiment and the groups were statistically different on nine days (Mann-Whitney U -test, two-tailed, all P 's < 0.05). The days when groups differed significantly were clustered in the first half of the experimental period. In the last half of the experimental period, birds hearing Buzzy songs tended to increase their gathering activity while those hearing Clear songs diminished their rate of gathering, although these trends were obscured by large fluctuations.

Examination of paper-shredding revealed a different pattern. More of the females hearing Buzzy songs shredded paper than those hearing Clear songs, and this trend occurred over most of the experimental period (Fig. 2). On nine days, most of which occurred in the middle part of the experiment, the differences in paper-shredding between the two groups were statistically significant (G -test, all P 's < 0.05).

To explore further the relationship between string-gathering and paper-shredding, we plotted for each bird the number of days on which papers were shredded against the mean number of strings gathered per day (Fig. 3). For birds hearing the Clear dialect, paper-shredding was positively correlated with string-gathering (Pearson $r = 0.68$, $P < 0.05$) but this was

not so for females hearing the Buzzy dialect ($r = 0.01$, NS).

DISCUSSION

Results on string-gathering indicate that females who heard Clear (natal) dialect songs were more stimulated than were females who heard the Buzzy (alien) dialect songs. If we assume, as was found to be the case with Canaries (Hinde and Steel 1978), that string-gathering is a behavioral reflection of physiological readiness for breeding, then our results suggest that reproductive activity of females in the natural population would ensue more rapidly or more completely if stimulated by male song of the natal dialect than if stimulated by an

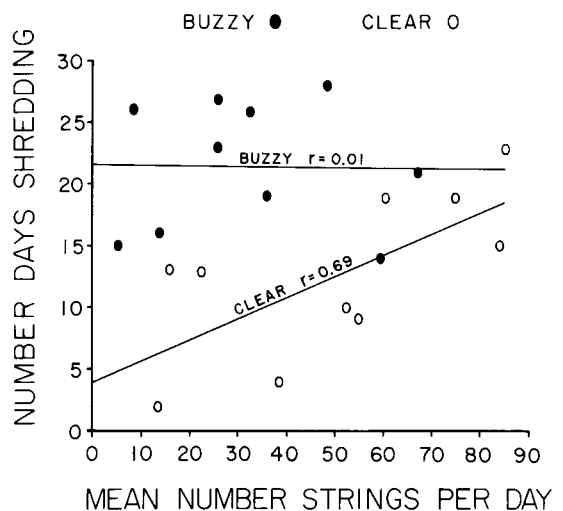


FIGURE 3. Correlations between the number of days on which an individual shredded paper and the mean number of strings it gathered for females hearing Clear or Buzzy songs.

alien dialect. A similar interpretation was made by Kroodsma (1976) about Canaries hearing complex versus simple song repertoires.

This inference from an experimental group to a natural population can be made in light of the findings that the average young White-crowned Sparrow completes at least the first 50 days of life in its natal area (Baker et al. 1982). Our approach attempted to approximate this song-learning environment. It should be noted that the first 50 days of life correspond to the sensitive period for song learning by these sparrows (Marler 1970). Experimental evidence indicates that hand-raised nestlings usually learn the dialect they were exposed to during this sensitive period, as compared to a different dialect provided from 50 to 90 days of age (Cunningham and Baker, in press).

Our experiment was designed to evaluate string-gathering behavior and, therefore, we provided all the birds with string bundles and nest cups at the time of stimulation by songs. That the groups diverged significantly for a substantial portion of the experiment is a conclusive result. Confounding this result, however, is the opposing finding that more females hearing the Buzzy dialect shredded paper than those hearing the Clear. Unfortunately, we cannot interpret this unambiguously because we failed to obtain baseline data on paper-shredding before the experiment. Thus, it is possible that the females who frequently shredded paper did so before the experimental period. Lacking this information, we can offer only an indirect argument that string-gathering is a more important reflection of reproductive motivation than is paper-shredding. First, string-gathering and paper-shredding behavior patterns were not coupled in both groups; this was true only for the females who heard the Clear dialect. It seems possible, therefore, that string-gathering and paper-shredding reflect differing underlying motivational systems. Supporting this idea are data from our experiment on the numbers of strings and paper shreds placed in the nest cups. Although both kinds of material were taken, significantly more strings than shreds were placed by birds in both groups (Clear females $P = 0.033$, Buzzy females $P = 0.045$, Binomial test, two-tailed). This result indicates that the females regarded strings as more suitable nesting material than

paper shreds. We therefore interpret string-gathering as the more reliable index of the degree of reproductive stimulation caused by songs of different dialects.

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