

The Response of Female Mountain White-Crowned Sparrows to Songs from Their Natal Dialect and an Alien Dialect

Myron Charles Baker, Kimberly J. Spittler-Nabors, and Dana C. Bradley

Department of Zoology and Entomology, Colorado State University, Fort Collins, Colorado 80523, USA

Received September 30, 1981/Accepted January 7, 1982

Summary. Female Mountain White-crowned Sparrows from Colorado were tested in a laboratory playback experiment to determine their response to male songs from their own natal dialect and to those from an alien dialect of the same subspecies, *Zonotrichia leucophrys oriantha* (Fig. 1). Observations were made on locomotor activity and copulation postures produced during each experimental test session.

The subjects gave copulation displays almost exclusively when hearing their natal dialect and few or no displays when hearing the alien dialect (Fig. 2). The birds also exhibited significantly greater locomotor activity when hearing the natal dialect than they did when hearing the alien dialect (Fig. 3).

We conclude that females are sensitized by their early song learning experience to be responsive to songs from their natal dialect and virtually sexually unresponsive to songs from an alien dialect. We speculate that the copulation posture given in the experiment implies that females in natural populations would preferably only mate assortatively with males from their natal dialect region.

Introduction

The Mountain White-crowned Sparrow, *Zonotrichia leucophrys oriantha*, is a migratory subspecies breeding in high montane meadows in Colorado. Populations exhibit dialects in male song; certain syllables in the song are common to all males in a local area but differ from the syllables characteristic of other populations. Other syllables in the same song are variable among individuals. Females seldom sing. Dialect populations often occupy entire drainage systems with individuals residing primarily in the willow habitat near streams. The typical mating system is monogamous pairs and territorial defense by males.

The biological significance of song dialects has been a matter of considerable speculation and some debate (Nottebohm 1969; Baptista 1975; Payne 1973; Petrinovich et al. 1981; Baker 1975; Baker and Mewaldt 1978, 1981). The important question was posed some years ago (Marler and Tamura 1962; Nottebohm 1969): whether females might preferentially select as mates males who sing the dialect on which the females had been imprinted during their early sensitive period for song learning. This assortative mating process would be one possible prediction from the theory that dialect populations are adapted to local environmental conditions. Such local adaptation would suggest that cross-dialect matings would be selected against. A great deal of important information has been accumulated on the general problem of geographic variation and dialects in song (see Krebs and Kroodsma 1980; Baker 1982; for reviews) but only recently has the assortative mating hypothesis been tested.

Konishi (1965) showed that some female White-crowned Sparrows (*Z. l. nuttalli*) can produce a reasonably accurate male-type song when implanted with testosterone and that these females sang the song dialect of the local area in which they were captured. Building on the small sample of this early study, Baptista and Morton (1980) determined the extent to which the song dialect of females induced with testosterone was similar to that of their male mates in Mountain White-crowned Sparrows in a single population in the Sierra Nevada of California (see also Petrinovich et al. 1981). Although the important details and sonographic data of these studies have not been published, the general conclusion of Baptista and Morton's study in the Sierras and that of Petrinovich et al. on Nuttall's White-crowned Sparrow in San Francisco, was that most of the females sang an alien dialect, not the dialect characteristic of their mates. This could be regarded as evidence against

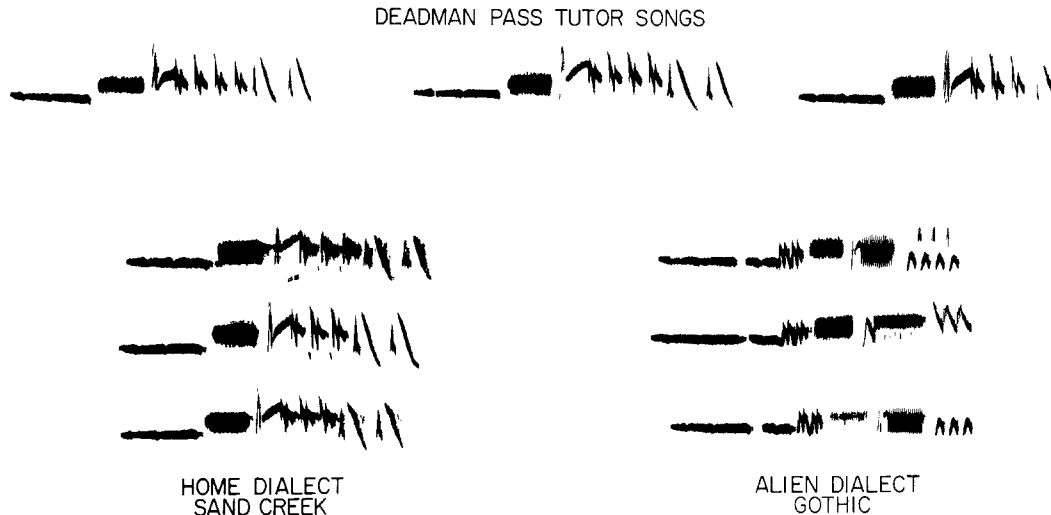


Fig. 1. Spectrograms of tutor songs and those of stimulus songs recorded in the natal (Deadman Pass and Sand Creek) and alien (Gothic) dialects of Mountain White-crowned Sparrows

the assortative mating hypothesis. Surprisingly, quite different results have been obtained in a more recent attempt to repeat these two studies in a different population (Tomback and Baker, in preparation). After treatment with testosterone in silastic implants, females from three different dialects in the Point Reyes area of coastal California sang songs containing the dialect syllables of the local male population. In contrast to the results of Baptista and Morton and of Petrinovich et al., these results provided evidence that supported the assortative mating hypothesis.

In the study we present here, we have adopted a different approach to the question of assortative mating. We tested female Mountain White-crowned Sparrows for their response to their natal dialect and to an alien dialect presented in a laboratory experiment.

Materials and Methods

We captured fledgling (20–25 days old) and adult females in a montane meadow in Colorado between 24 July and 4 August, maintained them in the laboratory in individual cages in the same room on natural photoperiod, and tutored them for 1.5 h twice each day. The sensitive period for song learning in White-crowned Sparrows ends at about 50 days of age (Marler 1970). The tutor songs were recorded from three different males, two from the neighborhood where the birds had been captured and one from a male three km away but in the same dialect (Fig. 1). Tutoring was by recorded tape played at a rate of four songs per minute to approximate the natural singing rate of a male.

After post-juvinal molt was completed by the young females, about 15 September, tutoring was ended and the group was placed on an 8L:16D photoperiod for about 6 weeks. The photoperiod was then changed to 16L:8D and on 14–17 November the birds were implanted with small sections of silastic tubing containing 17-B estradiol (Sigma Chemical Co.) plugged at both ends with silastic adhesive. Testing of the females began on 24 November.

Tests were conducted in an enclosed chamber with a single bird in its home cage near a loudspeaker. Each test consisted of 3 min of silence followed by three repeated segments each composed of 3 min of test song and 3 min of silence. During each 3 min block of test songs, a subject heard four repetitions of 3 different songs for a total of 36 songs in each 21 min test. Stimulus songs representing the home dialect were recorded from three males located 9 km from the site of juvenile and adult female capture. Thus, these songs were different from those used as tutoring songs, although all were the same dialect. Stimulus songs representing an alien dialect were recorded at Gothic, near Crested Butte, Colorado, about 275 km from the Deadman Pass area (Fig. 1), referred to as the home or natal dialect.

We conducted three series of tests on the females, each consisting of a presentation of the alien dialect on the first day and the natal dialect on the second. It would probably be preferable to randomize the order of presentation but for logistical reasons this was not convenient. The order we did employ would most likely bias results toward a stronger response to the alien dialect if such a bias had occurred. That no order effects emerged over the three series of tests suggests that randomization of stimuli would have made no difference in the results observed. A further potential improvement in experimental design would be to obtain reciprocal results using a group of females from the alien dialect but tested with the same stimulus songs. The ordering of testing sessions through the day was altered for each series so that each individual was tested in morning, mid-day, and afternoon. Afterward, an additional experiment was conducted to try to switch the response of two juvenile females who exhibited a preference for the natal dialect during the three series of regular testing. These 2 females were placed in a chamber and exposed to the alien dialect test songs 3 h per day for two days. Then they were re-tested on the alien vs natal dialect stimuli in the manner outlined previously.

We observed the birds during all test sessions and quantified activity level and displays. Activity level was measured by counting perch hopping. Female display behavior was most commonly a combination of trilling vocalization and copulation posture, although occasionally the trill was given without pronounced posturing or rarely the posture was given without the trill. We grouped these events for analysis. The posture given by the females seemed to vary in intensity; the essential components of the complete

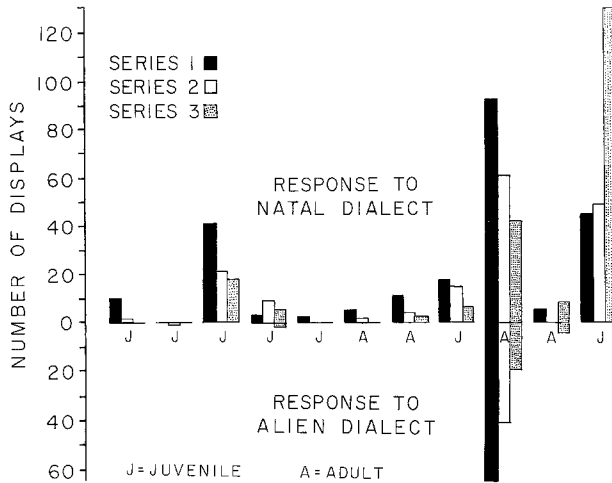


Fig. 2. Number of displays given by each female White-crowned Sparrow to natal and alien dialect stimuli during each of the three series of tests. Two birds who did not respond in any test are not illustrated

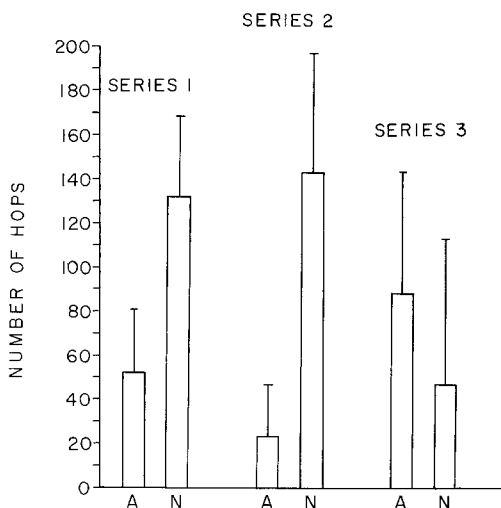


Fig. 3. Increase in number of hops above baseline number (pre-stimulus). Group means plus one standard error of hopping activity during stimulation by alien (A) Gothic dialect and by natal (N) Sand Creek dialect are represented by the histogram bars

display were a slight crouch, wings fluttering, the head tilted upward, and tail raised. The female displays resulting from our experimental procedures were no different from those observed during copulation sequences of free-living females interacting with their mates.

Results

The 13 females, 8 juveniles and 5 adults at time of capture, all developed fully defeathered brood patches by the time of testing. While still in the holding room prior to testing, 2 adult females occasionally sang. Exposure of the group to these female songs occurred well after the critical period for song learning.

In the first experimental series, juvenile females displayed exclusively to the stimulus songs representing their natal dialect and adult females gave similar but not identical results. Using each bird as its own control, the Wilcoxon matched-pairs signed-ranks test showed that the difference between stimuli was significant ($P < 0.01$, two-tailed, Fig. 2). In the second and third series of experiments (Fig. 2), the females also responded significantly more to the natal dialect than to the alien dialect (Wilcoxon test, series no. 2: $P < 0.01$, series No. 3: $P < 0.02$, both two-tailed). No displays were given during the pre-stimulus 3 min components of the testing sessions.

To analyze changes in activity level attributable to the stimuli, we assumed that the amount of hopping performed during the pre-stimulus segment of the test session was the baseline level over the remaining 18 min of testing (Fig. 3). The change in amount of hopping was determined for each bird on each stimulus and tested with the Wilcoxon test. In series no. 1 and no. 2, the birds hopped significantly more in response to the natal dialect ($\bar{x} \pm S.E.$ series no. 1 = 132 ± 36 , series no. 2 = 144 ± 54) than to the alien dialect ($\bar{x} \pm S.E.$ series no. 1 = 52 ± 29 , series no. 2 = 23 ± 24 , $P < 0.01$, $P < 0.02$, respectively, two-tailed). There was no significant activity difference between stimuli in series no. 3 ($\bar{x} \pm S.E.$ natal = 47 ± 65 , alien = 88 ± 54 , $P > 0.05$).

Following these three series of tests, we provided 2 juvenile females extra exposure to the alien dialect to see if they would switch preferences. Neither of the 2 females changed their response; both displayed to the natal dialect almost exclusively (15:0, 48:2). Although these data are preliminary, it does not appear that increased adult exposure to an alien dialect causes substantial change of female response.

The estradiol implants were replaced with testosterone implants in the adult females to determine what dialect they learned in early life. This was important to do because they were adults at the time of capture and we could not be certain of their geographic origin. Of the 5 adult females implanted with testosterone, three sang accurate copies of the home (Deadman Pass) dialect (Fig. 4) and two did not sing.

Discussion

The major conclusion we make from our results is that female White-crowned Sparrows are sensitized by an early song learning experience to be more responsive to male song of their natal dialect and virtually sexually unresponsive to song from an alien dialect. We interpret the female response as an indication of sexual arousal since the primary context of the display, used here as a bioassay, in natural popula-

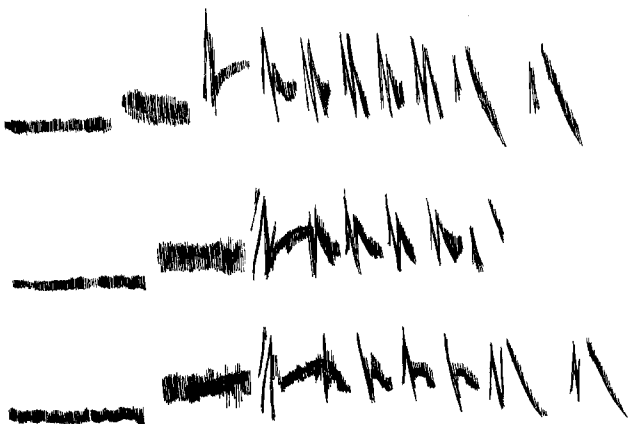


Fig. 4. Spectrograms of songs of three adult female White-crowned Sparrows induced to sing with testosterone implants. To eliminate echo noise from the songs, ink tracings were prepared from spectrograms

tions is copulation solicitation. This function of the display, was reported by Blanchard (1941) who described coition: "The female follows her mate about and trills persistently, fluttering her wings and raising her tail. Suddenly she flies straight away from her mate, and lands either on the ground or in a tree some yards distant. Her mate follows and lands near her. He hops toward her, crown raised and tail lowered and spread, flutters above her a few seconds [copulation], then flies to a nearby perch and sings." The copulation sequence and display behavior of female White-crowned Sparrows is similar to that observed in Song Sparrows (*Zonotrichia melodia*) and reported by Nice (1941): "The female postures by spreadings her wings and quivering them, and raising her head and tail; the male mounts, balancing himself with his wings, the act is consummated in about a second, after which he usually flies a short distance away." These early descriptions are similar to observations we have made in the field as well.

The copulatory posture, common in small passerines, has proved to be a sensitive female bioassay of male song. Female Brown-headed Cowbirds distinguish between their own and an alien subspecies song by responding differentially with copulation postures (King et al. 1980, West et al. 1981 for review). Searcy and Marler (1981) have shown that female Song Sparrows respond less to an abnormal temporal pattern of male song, in comparison to natural song programs.

Since the female display indicates sexual readiness, the response pattern exhibited by females in the present study has interesting inferential implications for the population biology of White-crowned Sparrows. For example, a male who obtains a territory in an

alien dialect population would be considerably less effective in attracting a female mate than would a male singing the common local dialect. The unmated male might give up and explore elsewhere under these circumstances. The net effect would be distinct dialect populations rather than a heterogeneous assemblage of song types. A female who strays into an alien dialect may also form a less effective pair-bond, or perhaps not mate at all and simply wander more widely until contacting her natal dialect. These views of male and female behavior are the most clear possibilities, and they require a positive correlation between copulatory posturing and mate choice.

It is also possible, although we did not achieve it in our laboratory manipulations, to imagine a way that females could mate in non-natal dialects as was the case in the studies of Baptista and Morton (1980) and of Petrinovich et al. (1981). If we assume that there is an excess of males in the population, as is common for many passerine species (Brown 1969), and such bachelor males court and advertise persistently, then a period of prolonged exposure might overcome a tendency of a female to be unresponsive to the alien dialect. Thus, a skewed sex ratio in favor of excess males might influence the mating system in a way that rather distinct and pure dialect populations of males are maintained but females show less fidelity to their natal areas and constitute the major agents of gene flow among populations.

Acknowledgements. We thank J.S. Augustine, A.E.M. Baker, L.C. Deutsch, M.A. Cunningham, P. Greco, W.A. Searcy, G.L. Sherman, and D.F. Tomback for assistance and advice. Research was supported by NSF grant DEB-78-22657 to MCB.

References

- Baker MC (1975) Song dialects and genetic differences in white-crowned sparrows (*Zonotrichia leucophrys*). *Evolution* 29:226-241
- Baker MC (1982) Genetic population structure and vocal dialects in *Zonotrichia* (Emberizidae). In: Kroodsma DE, Miller EH (eds) *Evolutionary and ecological aspects of acoustic communication in birds*. Academic Press, New York (in press)
- Baker MC, Mewaldt LR (1978) Song dialects as barriers to dispersal in white-crowned sparrows, *Zonotrichia leucophrys nuttalli*. *Evolution* 32:712-722
- Baker MC, Mewaldt LR (1981) Response to "Song dialects as barriers to dispersal: A re-evaluation." *Evolution* 35:189-190
- Baptista LF (1975) Song dialects and demes in sedentary populations of the white-crowned sparrows (*Zonotrichia leucophrys nuttalli*). *Univ Calif Publ Zool* 105:1-52
- Baptista LF, Morton ML (1980) Song dialects and mate selection in montane White-crowned Sparrows. *Am Ornithol Union (Abstr 4, Annual Meeting)*

- Blanchard BD (1941) The White-crowned Sparrow (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. Univ Calif Publ Zool 56:1-135
- Brown JL (1969) Territorial behavior and population regulation in birds. Wilson Bull 81:293-329
- King AP, West MJ, Eastzer DH (1980) Song structure and song development as potential contributors to reproductive isolation in Cowbirds (*Molothrus ater*). J Comp Physiol Psychol 94:1028-1036
- Konishi M (1965) The role of auditory feedback in the control of vocalizations in the White-crowned Sparrow. Z Tierpsychol 22:770-783
- Krebs JR, Kroodsma DE (1980) Repertoires and geographical variation in bird song. Adv Study Behav 11:143-177
- Marler P (1970) A comparative approach to vocal learning: song development in White-crowned Sparrows. J Comp Physiol Psychol 71:1-25
- Marler P, Tamura M (1962) Song "dialects" in three populations of White-crowned Sparrows. Condor 64:368-377
- Nice MM (1941) Studies in the life history of the Song Sparrow, vol II. Dover, New York
- Nottebohm F (1969) The song of the chingolo, *Zonotrichia capensis*, in Argentina: Description and evaluation of a system of dialects. Condor 71:299-315
- Payne RB (1973) Behavior, mimetic songs and song dialects, and relationships of the parasitic indigo birds (*Vidua*) of Africa. Ornithol Monogr 11
- Petrinovich L, Patterson T, Baptista LF (1981) Song dialects as barriers to dispersal: A re-evaluation. Evolution 35:180-188
- Searcy WA, Marler P (1981) A test for responsiveness to song structure and programming in female sparrows. Science 213:926-928
- West MJ, King AP, Eastzer DH (1981) The cowbird: Reflections on development from an unlikely source. Am Sci 69:56-66