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## APPENDIX

## GEOMETRIC DISTRIBUTION

Given that animals move a certain number of blocks ( $N$ ) before settling to breed (here blocks can equal the width of a territory, an arbitrary distance such as 100 m, etc.), the mean distance moved is  $E(N) = 1/p$ , where  $p$  is the probability of settling (Larsen and Marx 1986). Variance in the number of blocks moved is  $\text{Var}(N) = (1 - p)/p^2$ . When comparing the mean dispersal distances between two groups with individual dispersal distances  $X_1, X_2, \dots, X_m$  and  $Y_1, Y_2, \dots, Y_n$  distrib-

uted geometrically, the null hypothesis is  $H_0: p_1 = p_2$ . The  $Z$ -test is  $Z_g = \bar{X} - \bar{Y} / \sqrt{\text{Var}(\bar{X} - \bar{Y})}$ . The pooled variance is

$$\text{Var}(\bar{X} - \bar{Y}) = \frac{1}{m} \frac{1 - p_1}{p_1^2} + \frac{1}{n} \frac{1 - p_2}{p_2^2},$$

and under  $H_0$ ,  $p_1 = p_2$ , so A1 becomes

$$\text{Var}(\bar{X} - \bar{Y}) = \left( \frac{1}{m} + \frac{1}{n} \right) \left( \frac{1 - \hat{p}}{\hat{p}^2} \right).$$

The square root of this value is the denominator in the calculation of  $Z_g$  in text, with  $\hat{p}$  an estimator of  $p$ . The maximum-likelihood of  $\hat{p}_i = 1/(1 + \bar{X}_i) = m/(m + \Sigma X_i)$  (cf. Larsen and Marx 1986, when  $x$  can equal 0; see text); for the pooled sample,  $\hat{p}_1 + \hat{p}_2$  can be calculated as

$$\hat{p} = \frac{m + n}{m + n + \Sigma X_i + \Sigma Y_j}.$$

Note that  $\Sigma X_i$  = the total number of units traveled by the individuals in group one.

## POISSON DISTRIBUTION

When comparing the mean dispersal distances between two groups with individual dispersal distances  $X_1, X_2, \dots, X_m$  and  $Y_1, Y_2, \dots, Y_n$  Poisson distributed, the null hypothesis is  $H_0: \lambda_1 = \lambda_2$ . Pooled variance,  $\text{Var}(\bar{X} - \bar{Y})$ , is  $(1/m)\lambda_1 + (1/n)\lambda_2$ ; under  $H_0$ , the pooled variance is  $(1/m + 1/n)\lambda$ . For the Poisson distribution, the maximum-likelihood estimator of  $\lambda$  is  $\bar{X}$  (Larsen and Marx 1986). Given  $\bar{X} = \Sigma X_i$ , substituting into the pooled variance equation, and taking the square root, gives the denominator for the calculation of  $Z_p$  in text.

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SOCIAL TUTORING OF ADULT MALE WHITE-CROWNED SPARROWS<sup>1</sup>

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*Key words:* White-crowned Sparrow; *Zonotrichia leucophrys*; social tutoring; song learning; song dialects.

Song learning in White-crowned Sparrows (*Zonotrichia leucophrys*) has been studied extensively (for reviews see Kroodsma 1981, Baker and Cunningham 1985). The focus of attention usually has been restrict-

ed to juveniles during the first few months of life. These studies have included tape-tutoring and social tutoring of males and females in the laboratory and observations of singing behavior during territorial interactions between yearlings and adults (Cunningham and Baker 1983, Petrinovich and Baptista 1984, Baptista and Petrinovich 1984, Baptista and Morton 1988, DeWolfe et al. 1989).

In contrast to studies on young birds, song modification in older adults—those in their second breeding season or later—has received little attention. Observations of adult songs have been mostly anecdotal or ancillary to studies on juvenile song development and apparently no systematic treatment of the subject is

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available. To address the issue of song modification in older adults, we present laboratory evidence that suggests that adult male White-crowned Sparrows (i.e., birds in their second breeding season or older) from one dialect do not modify their songs through social interaction with adult males of another dialect.

## METHODS

Twenty adult male White-Crowned Sparrows (*Z. l. nuttalli*) were captured in Point Reyes National Seashore, Point Reyes, California, between 1–3 June 1984 and 20–29 May 1985. Ten adults were captured from the Drake dialect and ten adults from the Limantour dialect (Baker and Thompson 1985). At the time of capture all adults were at least yearlings (i.e., in their first breeding season) or older. The adults were kept individually in wire cages (L = 46 cm, W = 23 cm, H = 26 cm; Prevue Metal Products, Inc., Model #DB). They were fed an ad libitum diet of wild birdseed, turkey starter and grit, and supplied daily with fresh water. (Four individuals died before the end of the experiment and thus were eliminated from the results.)

Pre-tutor songs of Drake adults were recorded on 13 August 1984 and 1–10 May 1985 and pre-tutor songs of Limantour adults were recorded on 15 July 1985. Recordings were made with a Uher reel-to-reel tape recorder. Audiospectrograms were generated on a Kay Elemetrics Sonagraph with a frequency range of 0–8 kHz and wide band-pass (300 Hz) mode. Recordings were made in two anechoic chambers (L = 0.8 m, W = 0.4 m, H = 0.4 m; L = 1.2 m, W = 0.7 m, H = 0.7 m) constructed of cardboard and fiberglass insulation or plywood, soundproof batting, and felt (Casey 1988).

On 13 September 1985, all adults were moved into a single room. The cages were placed in double columns on a five-tier wooden shelf. Drake adults occupied the left-hand cages and Limantour adults occupied adjacent right-hand cages. Each pair could see each other only but could hear all birds in the room. Social interaction between pairs of adult males consisted of 16 hrs of daily visual and auditory contact. Direct physical contact was not permitted because of high levels of aggression and possible mortality. Abundant countersinging and visual displays of aggression between pairs were observed throughout the tutoring period.

The adults were placed on a "short-day" photoperiod of 8L:16D (09:00–17:00) from 13 September 1985 until 15 January 1986 and then on a "long-day" photoperiod of 16L:8D (04:00–20:00) from 15 January 1986 until 16 March 1986. Therefore, the adults first passed through a 125 day "winter" season and then through a 60 day "breeding" season. The males acquired full song approximately 7–10 days after the switch to the "long-day" photoperiod.

Post-tutor songs of Drake and Limantour adults were recorded between 25 January and 16 March 1986. Comparisons were made of song patterns from several recording sessions to ensure that all the song variation of an adult was sampled. Each adult sang only one song pattern, thus, we believe we obtained a complete sample of songs.

The songs were divided into four parts—introductory notes, complex syllables, simple syllables, and ter-

minal notes. Twenty-seven song characteristics were measured from sonagrams including: number of introductory, complex, simple, and terminal notes; the maximum and minimum frequencies of introductory, complex, simple, and terminal notes; the frequency range of introductory, complex, simple, and terminal notes; the mean frequencies of introductory, complex, simple, and terminal notes; and the internote intervals between introductory, introductory-complex, complex-complex-simple, simple, simple-terminal, and terminal notes.

Sample means and standard deviations were obtained for the 27 variables. The equalities of sample means for each song variable were tested with one-way analysis of variance (ANOVA) (SYSTAT, Wilkinson 1989). Normality and homogeneity of variance of song variables were tested with normal probability plots and Bartlett's chi-square test for homogeneity of group variances, respectively.

Linear discriminant function analysis was used to see if pre-tutor and post-tutor songs could be assigned to separate groups (SYSTAT, Wilkinson 1989). For example, an attempt was made to discriminate between pre- and post-tutor songs of Drake adults based upon the number of notes in each of the four song partitions. Similar tests were made for frequency range of notes, maximum frequencies, minimum frequencies, mean frequencies, and internote intervals. This resulted in six separate functions for each dialect. Because of the small number of observations relative to the number of song variables, it was not possible to build a single function based upon all song measurements simultaneously, which could lead to spuriously high multiple correlation coefficients (Kachigan 1991). Non-normal variables were transformed to approximate normality before generating the discriminant functions.

Hierarchical cluster analysis was used to test whether pre-tutor songs of specific adults could be classified with their own post-tutor songs or with the pre-tutor songs of their respective social tutors (SYSTAT, Wilkinson 1989). The single linkage method and Pearson product-moment correlation matrices were employed in cluster analyses. Because of widely disparate measurement scales, raw song variables were converted to standardized z-scores to equalize the means and variances across variables.

The song elements and patterns of each adult were compared by visual inspection to those of its social tutor. If an adult significantly modified the detailed structure of notes in its own song in an attempt to match corresponding notes in its tutor's song, then a positive score for song learning was recorded. In some adults one or several notes were absent in their post-tutor songs that were present in their pre-tutor songs. A negative score for song learning was recorded in these adults because they had simply dropped song elements from one year to the next. In other adults one or several notes were present in their post-tutor songs that were absent in their pre-tutor songs. If the additional notes were merely copies of other notes in their own song, then song learning was scored as negative; however, if the additional notes were present in the social tutor's song (neighbor's song), then song learning was scored as positive.



FIGURE 1. Pre- and post-tutor songs of adult male White-Crowned Sparrows (D) = Drake adult; (L) = Limantour adult.

## RESULTS

Figure 1 shows sonagrams of adult Drake and Limantour songs before and after social tutoring with tutor pairs boxed together. Results from one-way ANOVAs indicated that for all 27 song variables none of the pre- and post-tutor sample means were significantly different from one another ( $P > 0.05$ ) in either of the Drake or Limantour adults. In the linear discriminant function analyses, if social tutoring influenced adult song structure, then one would expect that pre- and post-tutor songs would be classified into separate groups. Although attempts were made to generate six different discriminant functions, none of the functions classified pre-tutor songs into separate groups from post-tutor songs (Wilk's Lambda  $> 0.80$ ;  $P \gg 0.05$ ). Therefore, results from ANOVAs and discriminant function analyses both suggest that the *general* structure of adult songs was unchanged by social tutoring, although both tests could miss fine details in the songs of specific individuals.

Figure 2 shows the results of cluster analysis of song variables. In all but three adults pre-tutor songs were highly similar to post-tutor songs. For example, the pre- and post-tutor songs of Drake adult WMB clustered together indicating a high degree of similarity and, by implication, an absence of song learning from its respective tutor, Limantour adult BRG. Likewise, the pre- and post-tutor songs of Limantour adult BRG clustered together indicating that they were similar to one another and not to the tutor, Drake adult WMB. Similar clusterings can be seen in tutor pairs WBM-BGM, WYB-BGW, WBR-BRM, WGR-BRK, and WRR-BRY. Hence, from cluster analysis one can conclude that social tutoring had no influence on song learning for the adults in these six pairs.

The remaining two pairs, WMM-BGY and WYK-BRW, showed some interesting variations. In both pairs the songs of Limantour adults BGY and BRW were similar before and after tutoring, whereas the songs of Drake adults WMM and WYK were not. These Drake adults seemed to cluster in a complex way with several other Drake adults, but not with their Limantour tutors. The cluster patterns in pre- and post-tutor songs of WMM and WYK indicate song modification. However, as discussed below, this was apparently a result of individual variation or low motivation levels for singing and not a result of learning from their social tutors.

Careful visual inspection of pre- and post-tutor songs yielded the following observations. WBM-BGM, WYB-BGW, WRR-BRY: The pre- and post-tutor songs of these six adults were identical and hence were scored as negative for song learning. WMB-BRG: The pre- and post-tutor songs of WMB were almost identical, except that it had acquired an additional simple syllable after tutoring. The new simple syllable appeared to be a duplication of other simple syllables in its song and did not resemble the simple syllables of its social tutor BRG. The pre- and post-tutor songs of BRG were identical. Thus, WMB and BRG were scored as negative for song learning. WMM-BGY: The post-tutor song of WMM had changed substantially from its pre-tutor song. There was considerable frequency degradation in its simple syllables, it dropped one simple

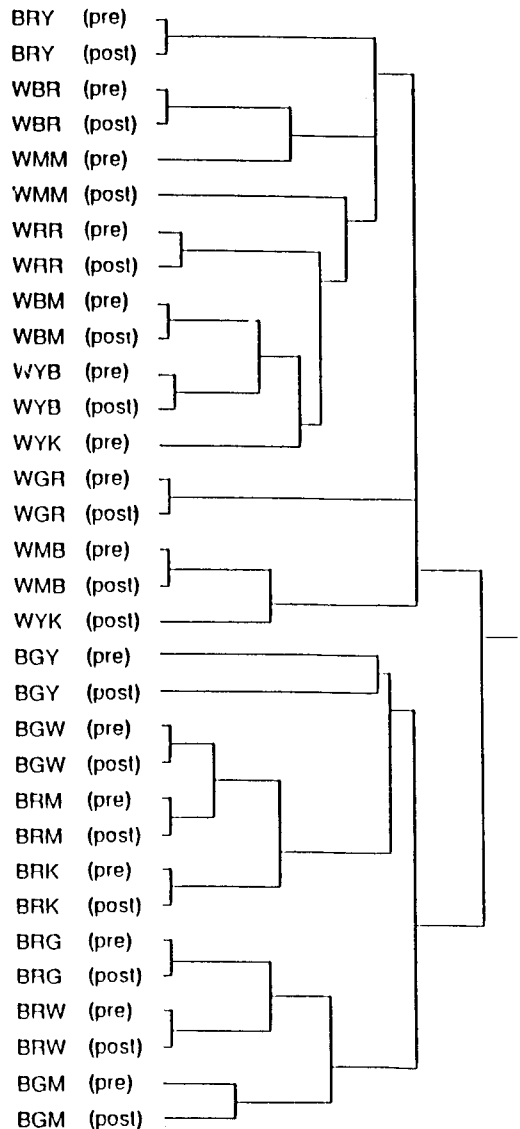


FIGURE 2. Cluster analysis of pre- and post-tutor songs.

syllable, and dropped its terminal syllables. The differences seen here seem to have been due to low motivation for singing, rather than vocal convergence with BGY. We observed that WMM sang very little and during song bouts did not show the vigorous energy normally observed when adults sing. The remaining notes in WMM's post-tutor song appear identical to those in its pre-tutor song. BGY dropped one simple syllable from its song, but all other notes appeared identical before and after social tutoring. Since the changes in song structure of both adults were unrelated to those of the tutor, both were scored as negative for

song learning. WBR-BRM: The pre- and post-tutor songs of WBR were identical. BRM dropped one simple syllable in its post-tutor song, but all other notes were unchanged. Therefore, WBR and BRM were both scored as negative for song learning. WYK-BRW: WYK appended terminal syllables to its post-tutor song. Terminal syllables were not present in the song of tutor BRW, hence WYK could not have learned this song element from its social tutor. The pre- and post-tutor songs of BRW were identical. WYK and BRW were both scored as negative for song learning. WGR-BRK: WGR decreased the number of simple syllables in its song from five to two but all other notes remained unchanged. BRK's pre- and post-tutor songs were identical. Since no vocal convergence was evident, WGR and BRK were both scored as negative for song learning.

To summarize, both univariate (ANOVA) and multivariate tests (discriminate function analysis and cluster analysis), as well as careful visual inspection and comparisons of sonagrams, revealed no evidence of song learning in 16 adult male White-crowned Sparrows. Alterations in song structure were observed in a few adults but are attributed to individual variation or low motivation for singing. Vocal convergence between tutor pairs in which specific structural changes in individual notes of one bird match those of a tutor was not observed.

## DISCUSSION

We found a high degree of song integrity in socially tutored adult male White-crowned Sparrows. When eight pairs of adult males from the Drake and Limantour dialects tutored one another in a social context, the pre-tutor songs of adults were identical or similar to post-tutor songs. All the adults were two years old or older during social tutoring and therefore in their second breeding season or later. Although the songs of some adults had changed after social tutoring, the differences were most likely due to individual variation or to the level of motivation for singing, and in no case was any change in the direction of the alternative dialect. If social interaction between tutor pairs stimulated song learning, one would expect to find some level of convergence in the detailed structure of one or several notes between the songs of tutor pairs, i.e., the sharing or exchange of song elements after completion of social tutoring, or the modification of song elements by one bird to match those of its social tutor. We did not observe such behavior.

Petrinovich (1988) studied song stability in wild adult male White-crowned Sparrows in the Presidio and Twin Peaks dialects of San Francisco, California. In the Presidio dialect he recorded the songs of 11 adults for two consecutive years, seven adults for three consecutive years, and three adults for four consecutive years. In the Twin Peaks dialect he recorded the songs of 18 adults for two consecutive years, six adults for three consecutive years, three adults for four consecutive years, and one adult for five consecutive years. Hence, these birds represented a comparable age group to the ones in our study. He measured the stability of four song components: the vibrato, complex syllables, simple syllables, and the vibrato-complex syllable sequence. Stability was determined by "how many birds

sang the same element for all years they were recorded" and by "how many birds sang the same element on any two successive years." In the Presidio area, depending on the method used, he found that 86%–91% of adults sang the same vibrato and complex syllables, 94% sang the same simple syllables, and 76% sang the same vibrato-complex syllable sequence. In the Twin Peaks area, again depending on the method used, he found that 76%–78% sang the same vibrato, 82%–91% sang the same complex syllables, and 70%–71% sang the same vibrato-complex syllable sequence. From these results Petrinovich concluded that "these individuals exhibited considerable stability of song across years." Petrinovich also commented that observed changes in some songs tended to be relatively minor. Our laboratory results generally confirm the field results of Petrinovich. In both the field and laboratory environments adult males of this species tend to retain the same song type from year to year, although there appears to be somewhat more variability in wild birds than in our laboratory population.

In a study of song dialects in montane White-crowned Sparrows from the Sierra Nevada, California, Baptista and Morton (1988) documented a single yearling male that sang predominantly the Tioga Pass dialect and only rarely the Mammoth Lakes dialect. This yearling increased the number of Mammoth Lakes dialect songs it sang in response to taped playback of Mammoth Lake songs. When the taped songs were stopped this individual reverted to singing the Tioga Pass dialect. In the following year Baptista and Morton located this individual again and repeated the tape playback experiment. Now in its second breeding season, this adult male did not respond to taped songs of the Mammoth Lakes dialect and only sang the Tioga Pass dialect. Hence, it appears that the second year adult had "fixed" its song in much the same way as the older adults in our laboratory experiments.

In our study, the stability of songs between years was fairly impressive, especially when one considers the extreme aggression that tutor birds displayed towards one another. In the field, adults have episodes of aggressive and vocal interactions with occasional "time-out" periods, where either or both adults can withdraw at any time. Although discrepancies between laboratory and field results are well known (Kroodsma 1981, DeWolfe et al. 1989), we suggest that our males experienced an exaggerated level of vocal and behavioral exposure to one another than do those in the field. Thus, it is all the more remarkable that songs were unchanged. The observations of Petrinovich (1988) and Baptista and Morton (1988) also suggest a relatively high degree of permanency of song patterns in older adult males. It has also been proposed that "the production of crystallized song is under different physiological controls than the earlier stages of motor development" (Marler 1991). Are these apparent age-specific differences in learning capacity physiologically based? In song development research perhaps greater attention could be placed on the transition period from yearlings to mature adults and older adults.

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AGGRESSION AND SONG DEVELOPMENT IN WHITE-CROWNED SPARROWS<sup>1</sup>

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The importance of social tutoring for proper song development in White-crowned Sparrows (*Zonotrichia leucophrys*) has been documented in both laboratory and field experiments (Cunningham and Baker 1983, Baker and Cunningham 1985, Petrinovich 1985, Baptista and Petrinovich 1986, Petrinovich and Baptista 1987, DeWolfe et al. 1989). Experiments in social tutoring that have been carried out in the laboratory generally involve one or more singing adult males in visual and/or auditory contact with one or several juveniles. Results from these experiments suggest that

the social stimulus of a live adult is a more potent stimulus during song development than is the presentation of songs through loudspeakers alone.

We explored the social tutoring paradigm by permitting direct physical contact between adult males and juveniles during the early phases of song development. When the experiment was conducted, we were uncertain how adults and juveniles would react to one another, and what effect, if any, such direct contact would have on song development. Although the main goal of the experiment was to assess the effect of physical interaction on development of dialects, we discovered instead that extremely aggressive behavior of adults towards juveniles affects song development adversely. Aggression exhibited by adult tutors may have caused arrested song development in juveniles, i.e., they either sang songs that resembled simplified versions of adult songs or sang highly aberrant songs. The relationship between aggression and song development has not been treated systematically in the past, although territorial interactions between adults and juveniles have been commented upon in many reports

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