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SONG DIALECT RECOGNITION BY MALE WHITE-CROWNED SPARROWS: EFFECTS OF MANIPULATED SONG COMPONENTS¹

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Abstract. Previous studies have shown that male White-crowned Sparrows (*Zonotrichia leucophrys*) discriminate among song dialects in the context of territorial behavior. We studied male response to song stimuli that differed systematically from the subjects' local dialect. We created four "hybrid" songs composed of elements from two adjacent dialects and monitored the responses of males from one dialect population to these four stimuli and to two unaltered dialect control songs. The most potent stimulus was the song from the dialect of the subjects, and the least stimulating song was that of the neighboring dialect. When we substituted the local dialect introductory components for those of the neighboring dialect, the response was as great as that given to the local dialect. Substitutions in other portions of the song caused decreased response in the subjects. Our results suggest that the vocal information controlling the territorial behavior of males in this particular dialect population is encoded in acoustic features located in the first part of the song.

Key words: *Song; dialects; recognition; Zonotrichia leucophrys; White-crowned Sparrow.*

INTRODUCTION

Geographic variation in the song of the Nuttall's White-crowned Sparrow, *Zonotrichia leucophrys nuttalli*, has been investigated by a number of workers. Marler and Tamura (1962) showed that: (1) a male typically sings a single, stereotyped song consisting of four major components (Fig. 1: introduction, complex syllables, simple syllables, ending), (2) the song structure of different males is relatively homogeneous within a local population (see also Trainer 1983) but differs distinctly between populations, and (3) the structure of songs within a local population remains stable from year to year. Thus, this subspecies exhibits a pattern of microgeographic variation described in a number of species of songbirds as dialect variation (Mundinger 1982). A system of dialects in the Nuttall subspecies in the San Francisco Bay Area has been described by Baptista (1975). A second system of dialects was described in the Point Reyes National Seashore (Baker and Thompson 1985), where the present study took place. Both of these studies confirmed in detail the findings of Marler and Tamura of a remarkable degree of song similarity within a

dialect population and distinct differences between dialect populations.

The biological significance of dialect variation has been explored by monitoring the responses of males in the field to playback of recordings of different song dialects (Milligan and Verner 1971) and by monitoring female responses to song dialects in laboratory experiments (Baker et al. 1987). Playbacks to males typically demonstrated that they responded more intensely to songs representing the local dialect than to those representing an alien dialect (Petrinovich and Patterson 1981, Tomback et al. 1983, Baker et al. 1984, see Baker et al. 1981 for an exception).

The present study addressed the following question. Do males within a dialect population attach more significance to some components of the song of an intruder than to other components during the process of recognition and response? This question was addressed through playback studies on individual territorial males in a single dialect population.

METHODS

Stimulus songs were created at the Rockefeller University Field Research Center, Millbrook, New York, using a computer and software system developed for the analysis and manipulation of animal sounds (Zoloth et al. 1980, Clark et al. 1983). From our collection of recorded White-crowned Sparrow songs, we randomly selected

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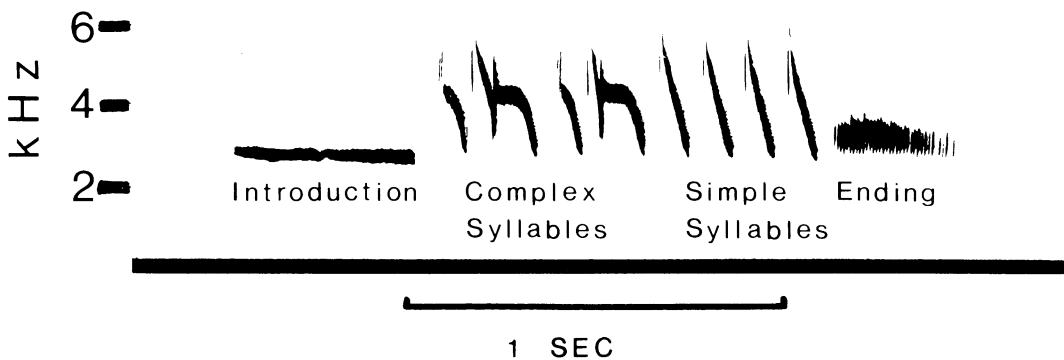


FIGURE 1. Four components (introduction, complex syllables, simple syllables, ending) of White-crowned Sparrow song, which were evaluated for their relative contributions to dialect recognition.

one song representative of the local Drake dialect and another representative of the neighboring Limantour dialect (Baker and Thompson 1985) to serve as source material for the synthesis of four “hybrid” stimulus songs (Fig. 2).

Songs of the Limantour population differ from those of the Drake in the first three of the four components of the song (Fig. 2). Limantour songs have a two-note introduction whereas Drake songs have a one-note introduction. Limantour songs have complex syllables that are relatively simple frequency sweeps whereas Drake complex syllables rapidly decrease then increase and finally decrease more gradually in frequency, producing an h-shaped appearance in the sonagram. Limantour simple syllables have a two-part structure with a brief note following the downsweeping note, producing a “fish hook” appearance on the sonagram. Drake simple syllables are usually simple downsweeping notes lacking the fish hook appearance. Both Limantour and Drake songs share similar ending components consisting of a buzzy sounding vibrato of variable duration. No consistent population differences in the ending component were found. Songs of five different males from the Drake and from the Limantour dialect reveal the consistent differences in the first three components of the songs (Fig. 3). Because of the high degree of homogeneity among songs within dialects and the clear differences between dialects, we chose to use single exemplars to represent a dialect. In addition, with the number of stimuli employed (6) and the number of subjects we could test in an experiment lasting two seasons, the creation and use of multiple stimuli were not practical. Searcy (1989) and Kroodsma (1989) debated the

design of playback experiments. It is possible that the use of a single song as stimulus limits the generality of the results (McGregor et al. 1992). Although this may be a problem in some cases, recent results (Baker 1991, Baker unpubl. data) suggest that the importance of the “limited generality” criticism was overestimated.

One hybrid stimulus song that we constructed was composed of a Drake (D) introduction, Limantour (L) complex syllables, and Limantour (L) simple syllables together with the shared ending (X). For shorthand notation, this song is described as DLLX. The three additional hybrid song stimuli were LDLX, LLDX, and LDDX. To create control stimuli, the Drake (DDDX) and Limantour (LLLX) source songs underwent analog to digital and digital to analog conversions but were otherwise unaltered. All stimulus songs were filtered with a Krohn-Hite model 3700 band-pass filter (low cutoff 1.5 kHz, high cutoff 20 kHz) and recorded with a Tandberg PM-27 open-reel recorder on Scotch Dynarange tape at 9.5 cm/s.

The playback experiments were conducted in the Point Reyes National Seashore, Marin County, California, during the breeding seasons of 1984 and 1985. We conducted 223 trials on males that had established territories in the Drake dialect region. Because birds were not banded, an unknown number of individuals tested in 1984 were also tested in 1985. It is unlikely that there are year-to-year residual effects, however (Milligan and Verner 1971, Petrinovich and Peeke 1973). All subjects sang the local Drake dialect, which to our ears were within the range of variation indicated in Figure 3. From 18–29 May 1984, 31 males were exposed to DDDX (the Drake

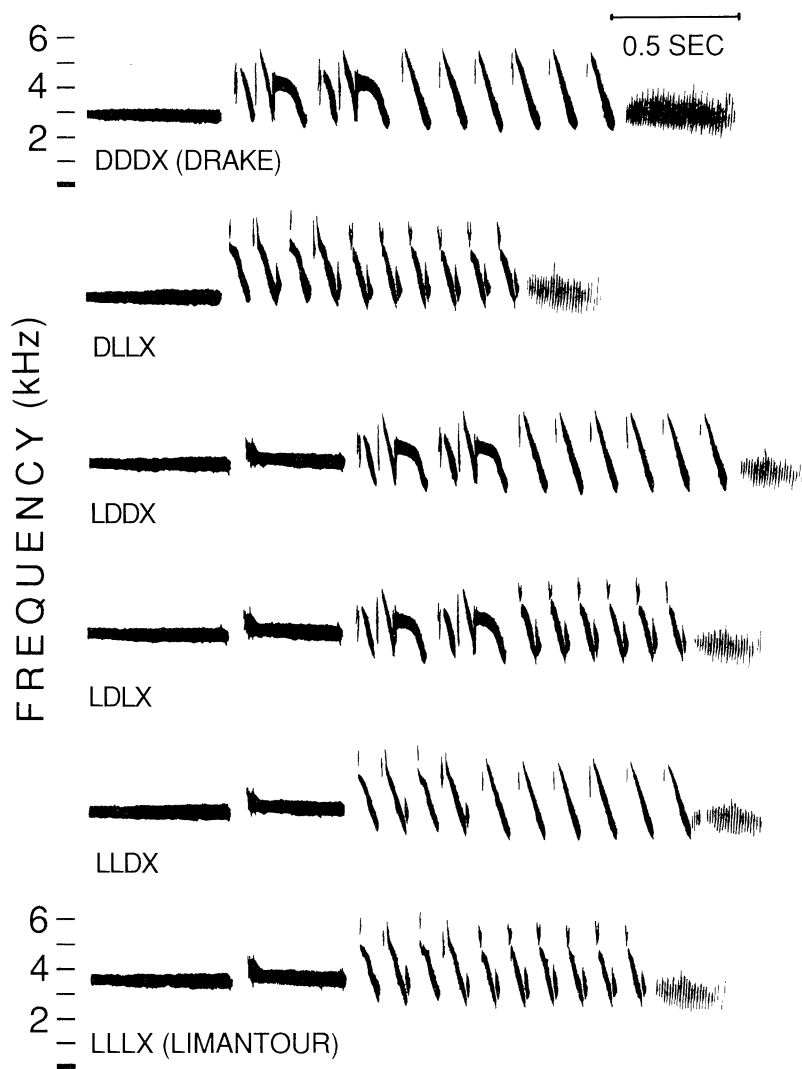


FIGURE 2. Six stimulus songs including pure Drake (DDDX) and Limantour (LLLX) dialects together with four computer-altered hybrid songs formed by substitutions of three of the components.

control song), 30 males to DLLX, and 31 males to LDLX. From 21 May to 5 June 1985, 32 males were exposed to DDDX, 34 to LLLX, 32 to LLDX, and 33 to LDDX. Tests were conducted from 07:30–16:30 hr. Time-of-day effects were minimized by randomizing the order of presentation of the stimulus songs and by conducting approximately equal numbers of playback tests in the morning and afternoon.

Playback procedures followed those of Tomback et al. (1983) and Baker et al. (1984). Prior to testing, a subject was observed for several minutes to identify the location of singing perches.

A playback loudspeaker (Perma-Power model S-610) was placed about one meter from a centrally-located singing perch. Usually, the subject was approximately 10 m or less from the speaker at the initiation of the test. Following placement of the speaker, the experimenter retreated 10–15 m and activated a tape recorder (Uher 4200 Report Stereo IC), which delivered a stimulus song at the rate of four songs per minute, approximating the normal singing rate of a territorial male. Each trial lasted 15 min and consisted of 5 min of stimulus songs (20 songs delivered) followed by 10 min of silence. Hereafter, we refer

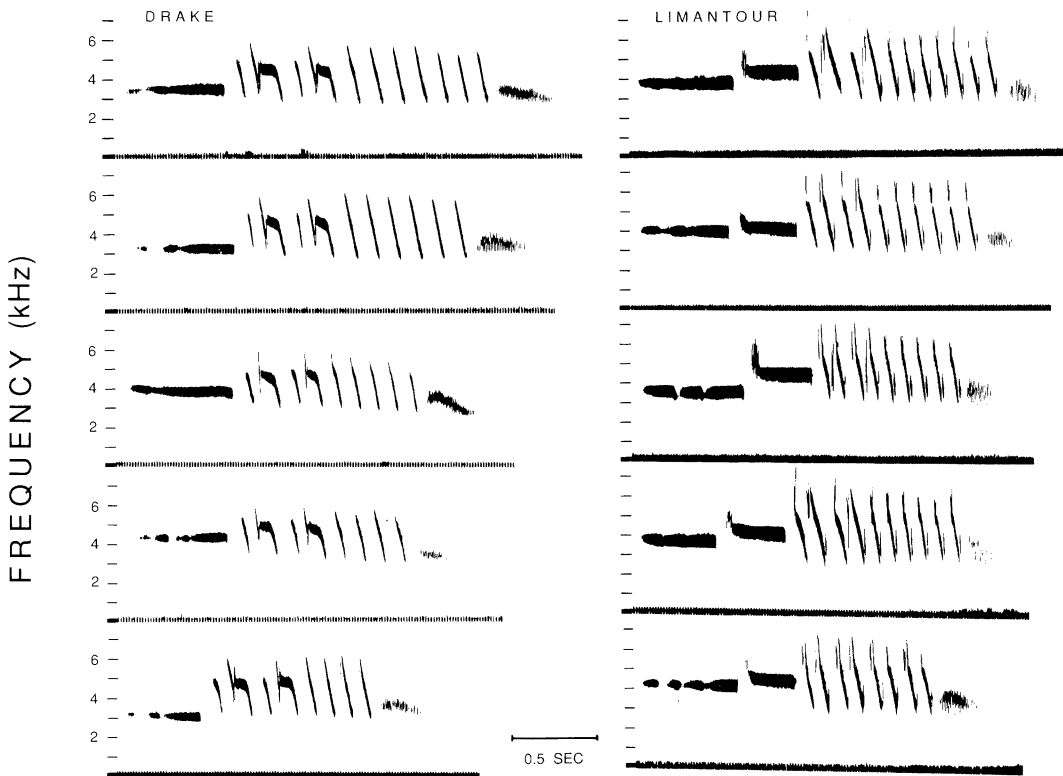


FIGURE 3. Songs of five males from the Drake dialect and five from the Limantour dialect.

to the former as the playback period and the latter as the postplay period. Playback volume was adjusted by ear to a level equivalent to that of a naturally singing male, and thereafter kept constant through all tests.

Because the stage of the nesting cycle may influence male responses (Petrinovich and Patterson 1979), all stimulus songs were rotated in sequence throughout the course of the study. Thus, subjects at differing stages of the reproductive cycle were equally represented in all treatments. Each male experienced only one trial per field season. Responses of the subject were recorded on a cassette recorder and later transcribed onto data sheets. All behavioral responses were tallied in one-min time blocks. The numbers of full songs, partial songs, flights, trills, and wing flutters were counted each minute. Hilly terrain sometimes precluded estimation of the average distance of the subject to the playback speaker during a trial. Therefore, we recorded only the closest approach to the speaker during the trial as an additional variable. For close approaches

to the speaker, estimates of distance, by eye, were accurate to within a meter. Longer distance estimates were probably less accurate but were aided through pacing by the observer.

Songs delivered at a distance from the playback speaker were sometimes difficult to categorize as full or partial because of environmental noise. When categories were initially established, we also considered that full and partial songs could be functionally different displays. To try to take these factors into account, we analyzed full songs, partial songs, and their summation, songs initiated (total songs), as a derived variable. A second derived variable was the summation of trills and flutters. These two events were often intermingled and produced in rapid succession. We expressed the responses of subjects both as totals for the playback period only and as totals for the combined playback and postplay periods, following procedures established in other studies (Baker et al. 1981, Tomback et al. 1983). This yielded a total of 15 response variables (7 playback period, 8 from

TABLE 1. Mean responses (after square-root transformation) to the Drake (DDDX) control song by male Nuttall's White-crowned Sparrows from the Drake dialect region for six variables that differed between 1984 and 1985 field seasons.

Variable	Mean response to Drake	
	1984	1985
Full songs during playback period	4.44	3.66
Partial songs during playback period	2.30	3.34
Trills during playback period	0.44	1.59
Partial songs during trial	3.10	4.71
Trills during trial	0.44	1.64
Closest approach during trial	1.17	1.86

combined playback and postplay periods including closest approach) for analysis. Responses obtained during the two field seasons were adjusted so they could be combined in a single analysis. Each variable was first screened for between-year differences in response to the Drake control song (DDDX) with parametric *t*-tests. If a significant difference was detected, the difference between the average Drake-elicited responses was added to the responses of individuals from the year representing the smaller average. The ranking of treatment effects was thereby preserved and other sample characteristics were unchanged. Six variables were adjusted in this manner (Table 1).

We employed stepwise discriminant function analysis (DFA) using the 15 response variables to construct a multivariate measure that maximized the difference in response to the Drake and Limantour control songs. We took this novel approach because our goal was to substitute Limantour components for Drake components in the Drake song and determine the loss of information to the Drake subjects as judged from the response. Responses to the four hybrid songs were then ranked according to this canonical scale. Differences in response to the six stimulus songs were determined by least significant differences (LSDs, Sokal and Rohlf 1981). This provided a means of assessing the relative importance of the introduction, complex syllables and simple syllables as dialect recognition cues. All analyses were performed using BMDP (Dixon et al. 1981). Significance of difference was accepted at *P* < 0.05, two tailed.

RESULTS

The mean responses of males to the Drake (DDDX) control song differed between years for

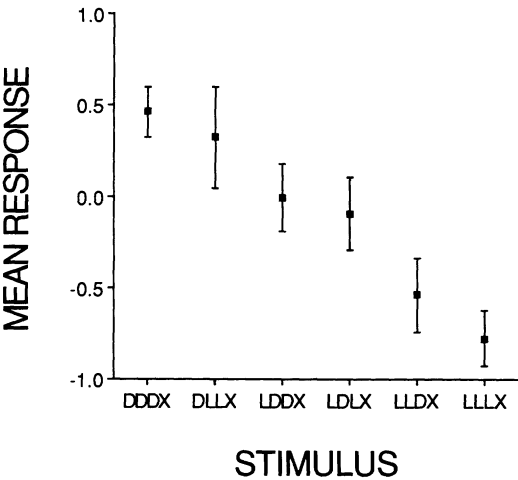


FIGURE 4. Mean composite responses (± 1 SEM) of male White-crowned Sparrows from the Drake dialect population to the six stimulus songs.

six variables (Table 1). Although the mean responses were greater in 1985 than in 1984 for five of the six variables, this pattern was not significant (*t* = 2, *P* > 0.05; Wilcoxon signed-ranks test, Siegel 1956).

The multivariate discriminant function analysis resulted in a composite response variable (*M*), which was expressed as follows:

$$M = 0.57 X + 0.48 Y + 0.38 Z - 4.49$$

- X* = total flights in playback + postplay periods
- Y* = total flutters in playback + postplay periods
- Z* = total songs in playback period

M accounted for only 14% of the total variation in the responses of the males to stimulus songs, but there was a highly significant treatment effect (1-way ANOVA; *F* = 6.96, *P* < 0.0001). The maximum response was to the Drake (DDDX) control song and the minimum response to the Limantour (LLLX) song, as generated by the discriminant function. The four hybrid songs caused intermediate responses (Fig. 4). LSDs revealed that responses to the Drake and DLLX songs were significantly greater than responses to the LLDX and Limantour songs. No other paired comparisons differed significantly. The regular decrease in mean response from that elicited by the Drake stimulus to that elicited by the Limantour stimulus (Fig. 4) suggests the relative significance of the several component substitutions in conveying dialect recognition information.

DISCUSSION

Drake males exhibited stronger responses to a local Drake song than to a song from the adjacent Limantour population. Similar results were obtained in other song populations in the Point Reyes dialect system (e.g., Limantour dialect, Tomback et al. 1983; Limantour and Buzzy dialects, Baker et al. 1984) as well as in other dialect systems (e.g., Berkeley and Sunset Beach dialects, Milligan and Verner 1971; San Francisco and Presidio dialects, Petrinovich and Patterson 1981). In addition, our study also represents a reciprocal of the Limantour/Drake playbacks of Tomback et al. (1983), in which Limantour males were tested with Drake and Limantour songs and responded most strongly to the local Limantour song.

The differences in song structure between the Drake and Limantour songs used as source material for creating the hybrid songs are in the first three of four song components. Thus, we emphasize the effects of substitutions of these components on male response as revealed by the composite response variable. If male responses to the Drake control song are the normal level of aggressive response to other Drake dialect males, then substitution of the Drake introduction into an otherwise Limantour song (DLLX) evoked responses normally reserved for local songs. There seemed to be no loss of signal function even though the song contained two Limantour components. There is a tendency that substitutions of Drake for Limantour complex syllables (LDLX) or complex and simple syllables (LDDX) evoked responses that were weaker than those elicited by the Drake song but stronger than those elicited by the Limantour song. Thus, substitutions of Drake complex syllables in an otherwise Limantour song enhanced the stimulating ability of that song but did not make it as potent as stimulus as the local song. We infer that the complex syllables convey some information but are not as important to the recognition process as the introduction. The simple syllables appear relatively less important to the control of male response; they did not increase the potency of LDDX over that of LDLX and the substitution of Drake simple syllables into an otherwise Limantour song (LLDX) elicited the weak response normally given to the pure Limantour song.

More information about the importance of the introductory elements in dialect recognition could

be obtained by playback of stimuli consisting of only the introductions or the introductions followed by a set of syllables from some other species (to create a song of normal temporal properties). This experiment would be interesting because the whistle-like introductions of White-crowned Sparrows often are the elements most obvious to the human ear when heard against the background of wind and ocean noise in the coastal scrub habitats of these populations.

A consistent general pattern is that these birds respond differentially to the songs of their own and other dialects (Baker et al. 1984, Baker and Cunningham 1985, Kroodsma et al. 1985). In some cases, responses seem to vary with geographic distance between the origin of the stimulus song and the study population or with the degree of structural similarity between the local song dialect and that of the stimulus songs. Baker et al. (1984) proposed that male White-crowned Sparrows responded to songs of other males according to a unimodal discrimination function with a peak of responsiveness to a song that differed structurally from the local dialect by one of the four song components. Decreasing responsiveness was hypothesized to occur with song stimuli that differed increasingly from the local and familiar song environment. This hypothesis was generated from the results of several studies and no systematic test has been undertaken at that time.

Our results do not support the unimodal discrimination model as a proximate mechanism underlying the control of dialect recognition. The model predicts that males should not respond differently to DLLX, LDLX and LLDX songs because all contain two Limantour elements and therefore differ from the local Drake song environment to the same degree. Males responded more to DLLX than to the other two stimuli. Furthermore, the model predicts that substitution of a single Limantour component (LDDX) should elevate response above that given to the Drake song. This did not occur.

Our results are more concordant with a "feature weighting" model such as that outlined by Nelson (1988) for species recognition by Field Sparrows (*Spizella pusilla*). Although several characteristics of the song may be used in recognition, some carry higher valence than others. This is similar also to the results of one of the few other experimental studies of features used in dialect recognition. Pellerin (1982) tested Corn Buntings (*Emberiza calandra*) with computer-

altered songs and found that dialect recognition was cued more significantly by some features than by others. Balaban (1988) showed, with manipulated songs, that Swamp Sparrows (*Melospiza georgiana*) recognized dialects primarily by the ordering (syntax) of the song elements.

In an experiment analogous to ours, Baker et al. (1987) tested in the laboratory the sexual responses of female White-crowned Sparrows from the Drake dialect with an array of computer-altered songs. Some of the stimuli were the same as those used here. They discovered that all song components contribute to the ability of females to recognize dialects. Like the results with males, the substitution of the Limantour introduction and complex syllables (LLDX) was sufficient to lower female response significantly below that given to the local Drake stimulus. They also found evidence that the introduction played some role in mediating female response, but it would not alone elicit a normal response, as it did in the present study of males. Complex syllables seemed to play a significant role as well in the stimulation of female sexual display. Thus, male and female White-crowned Sparrows are not completely concordant in their use of specific song components in dialect recognition. Such sexual dimorphism has been suggested for other songbirds (Searcy et al. 1981; King and West 1983a, 1983b). Of course, in all cases the response variable measured was different for the two sexes: territorial aggression by males and copulation solicitation by females. It would be interesting if one could induce, perhaps by hormonal manipulation, males to solicit copulations or females to be territorially aggressive and then determine if the song features used in recognition remained the same.

Our results do not resolve the "dialect problem," which Mundinger (1982) views as the lack of a universal definition of "dialect." There are few data concerning the functional significance of the population song features that researchers identified as dialect markers in a number of species. In only a few experiments has it been determined if birds pay attention to the dialect differences. For White-crowned Sparrows, playback studies are adequate to indicate that the birds do indeed recognize dialect differences. Furthermore, we now have evidence for both sexes that certain features of the songs are more salient than others in triggering recognition. Of course, it is possible that other variant features could func-

tion in social contexts other than those examined thus far.

These findings indicate that song components differ in the degree to which they can trigger biologically significant behavior patterns. These results serve to reinforce the importance of questions about possible differences in the timing of learning the different vocal features and their flexibility for change during development (Balaban 1986). Discovering biological consequences of song dialects presents a considerably more complex problem when considering not only that different features of the song may encode different kinds of information depending upon sex and social circumstance, but also that the several vocal features may be developmentally uncoupled as well.

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