DIALECT DISCRIMINATION BY WHITE-CROWNED SPARROWS: REACTIONS TO NEAR AND DISTANT DIALECTS

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Abstract.—In Marin County, California, the dialect populations of *Zonotrichia leucophrys nuttalli* are contiguous, and there is little dialect mixing. The possible importance of male–male interactions in preventing dialect mixing was tested with song-playback experiments. Males of the Limantour dialect were presented the Limantour dialect, Drake or Buzzy dialects (neighboring), or Clear dialect (distant). From previous work, we predicted that Limantour males would respond with equal or more aggression to songs of immediately neighboring dialects in comparison with their own dialect but would respond at lower levels to a distant dialect. Instead, we found that Limantour males sang significantly more songs in response to the Limantour dialect than to either neighboring or distant dialects, although the response decreased with distance, as expected. These results led us to hypothesize that responses to an alien dialect may be influenced by (1) opportunity to habituate to the alien dialect, (2) recency of divergence of the two dialects, (3) recency of contact of the two dialects, and (4) sounds common in aggressive vocalizations in other contexts being also present in some song dialects but not others. *Received 16 June 1982, accepted 10 December 1982.*

Nuttall's White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) is a nonmigratory subspecies inhabiting Pacific coastal scrub habitat. Populations of this subspecies are characterized by distinct song dialects, which are stable in time and space; within a dialect population, songs of adult males are stereotyped in relation to dialect markers, which remain constant from year to year (Marler and Tamura 1962, pers. obs.). Experiments indicate that young White-crowned Sparrows learn their home dialect during an early sensitive period (Marler 1970). The dialect populations we have studied in Marin County, California, and probably those in other relatively undisturbed areas, are contiguous, with abrupt transitions and little or no dialect mixing. In contrast, dialect mixing has occurred in urban populations (Petrinovich et al. 1981).

Baker (1974, 1975) and Baker et al. (1982) have found significant genetic differences among the contiguous Marin County dialect populations, which suggest reduced gene flow. It follows that in *Z. l. nuttalli*, song dialects may somehow restrict interpopulation dispersal and thus facilitate adaptation to local environmental and/or genetic conditions, i.e. coadapted gene complexes (Baker 1975, Shields 1982, Baker and Marler 1980). That White-crowned Sparrows discriminate among song dialects, a necessary prerequisite for proposing an adaptive significance, was first shown by Milligan and Verner (1971).

Three different behavioral mechanisms, based upon dialect discrimination, have been hypothesized as possible barriers to gene flow (Baker and Mewaldt 1978): (1) *Juvenile dispersal bias.* If dispersing fledglings are biased by early auditory experience, their dispersal pattern should show deflection at dialect boundaries. By means of trap/recapture data, this hypothesis was supported by Baker and Mewaldt (1978). (2) *Female mate choice.* If females raised in one dialect preferentially mate with males singing their natal dialect, invading males with other dialects would be at a reproductive disadvantage. Support for this hypothesis has also been found (Baker et al. 1981a, Tomback and Baker MS; but see Baptista and Morton 1982). We are currently testing this hypothesis in the

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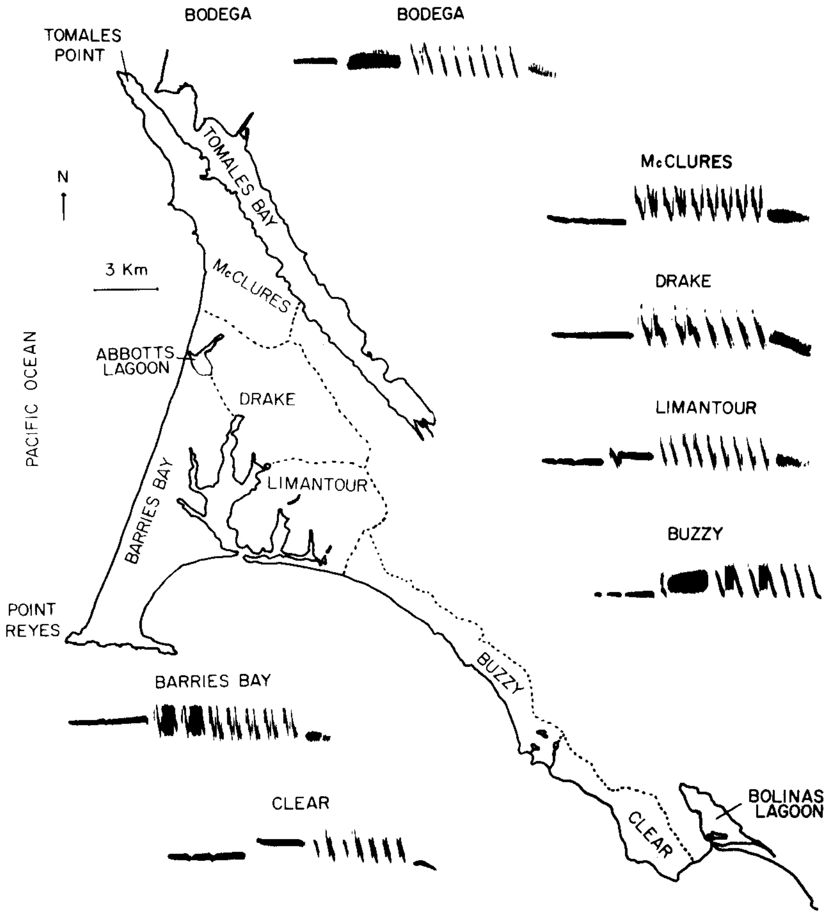

Fig. 1. Geographic relationship of *Z. l. nuttalli* dialects on the Pt. Reyes National Seashore.

laboratory. (3) *Foreign male exclusion.* If resident males are more aggressive toward invading males from a nearby or contiguous dialect population than toward males of their own dialect, then mixing should be minimized. Milligan and Verner (1971) found that the aggressive response to song playbacks, as measured by number of songs and flights, greatest toward home dialects and least toward dialects from far away, but playbacks of contiguous or nearby dialects were not included. Using the same criteria for aggressive response, Baker et al. (1981b) played songs of the contiguous Clear and Buzzy dialects and the distant Bodega dialect to Clear males. The Clear males responded least to the Bodega songs and significantly more to the Buzzy songs than to the Clear songs. Repeating this experiment, Baker et al. (in prep.) played the same Buzzy and Clear stimulus songs to both Buzzy and Clear males. The subjects sang significantly more songs in response to their neighboring dialect than to their home dialect. These results support the male exclusion hypothesis.

Working with *Z. l. nuttalli* in the San Francisco dialect population, Petrinovich and Patterson (1981) found that males and females responded least to playbacks of the distant dialect (Sunset Beach) and most to playbacks of an adjacent dialect (Presidio), as measured by trills, chinks, and fluttering. Males *sang* the most in response to the local dialect, however. Petrinovich and Patterson (1981) suggest that trills and fluttering indicate a more excited and aggressive state than do songs.

To investigate the generality of the male exclusion hypothesis, in view of the different responses by males to remote and neighboring

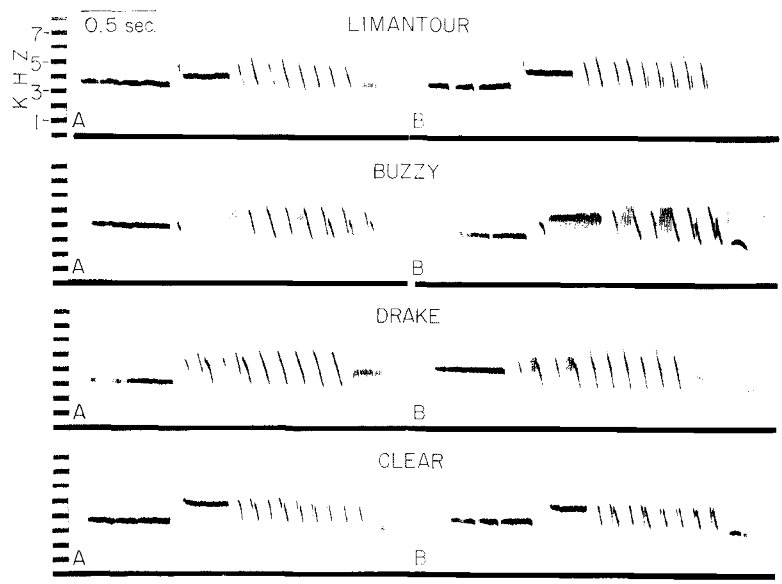

Fig. 2. A and B songs of each dialect used for the playback experiments to Limantour males.

dialects, we have undertaken a systematic series of experiments to determine how the geography of dialect populations and spectrographic differences among dialects may influence male responses. Here, we present data on responses of males of the Limantour dialect to playback stimulus songs of the Drake, Limantour, Buzzy, and Clear dialects, these four constituting a linear series from north to south.

METHODS

The dialects selected for playback experiments occur on the Pt. Reyes Peninsula within the Pt. Reyes National Seashore, Marin County, California. Study areas are described and mapped in Baker and Mewaldt (1978) and Baker et al. (1982).

Playbacks to Limantour males.—Playback experiments were conducted throughout most of the 1980 breeding season, from 29 April to 11 June. As the stage of the nesting cycle may influence *Z. l. nuttalli* male and female response to song playbacks (Petrinovich et al. 1976), all playback songs were alternated throughout the experimental period. Thus, there were similar representations of birds at different nesting stages as subjects for all playback experiments.

Experimental subjects were 141 Limantour males located throughout the dialect area. Subjects were separated by one to several territories to avoid prior exposure to playback songs. Each male was tested only once with a playback tape of either the Limantour (home) dialect, the Buzzy dialect, which is contiguous to the south, the Drake dialect, which is contiguous to the north and east of the Limantour dialect, or the Clear (distant) dialect, which is contiguous with the Buzzy dialect to the south (Fig. 1).

The distinguishing dialect characteristics are apparent in Fig. 2: the Limantour dialect has a two-note whistle introduction, clear trill, and downslurred vibrato ending (terminology from Marler and Tamura 1962); the Drake dialect has a single introductory whistle, clear trill, and downslurred vibrato ending; the Buzzy dialect has a two-note introductory whistle, followed by two, stressed vibrato, trill syllables, and a weak "phew" ending; and the Clear dialect has a two-note introductory whistle, clear trill, and a weak "phew" ending.

Two typical songs were selected from recordings of each dialect (Uher 4200 Report stereo recorded at 9.5 cm/s) and made into two playback tapes (A and B) for a total of eight tapes (Fig. 2). Each playback experiment lasted 15 min and consisted of 5 min of song playback, with 20 songs delivered at a natural singing rate of 1 song/15 s, followed by 10 min of silence. Playback sound volume was constant for all experiments and approximated that of the normal male songs.

Playback trials were conducted by one or two persons as follows: a loudspeaker (Perma-Power, model S-610) was placed next to a shrub within 4–6 m of a singing male. The power cable trailed back 10–15 m to a tape recorder (Uher 4200 Report stereo IC) where the observer stood. The playback songs and a stopwatch were started simultaneously. Male response was recorded on a data sheet in 1-min intervals. For each minute, we counted the number of full songs, partial songs, and flights and estimated the closest

TABLE 1. Responses of Limantour subjects to playbacks of Limantour, Drake, Buzzy, and Clear dialect stimuli.

Response	Stimuli			
	Limantour	Drake	Buzzy	Clear
Total songs[a]	5.6	4.5	4.2	4.3
Full songs[b]	3.7	2.9	2.4	2.2
Percentage of full songs	66.4	66.6	55.9	47.8
Flights[c]	1.0	1.0	0.7	0.9
Song latency (s)[d]	37.4	64.5	44.3	37.8
Approach to speaker (m)[e]	1.5	2.1	2.6	2.5
Number of trials female present	20	16	17	16
Number of trials male trill	22	16	9	16
Number of trials female trill	8	9	5	8
Number of experimental trials	39	33	36	33

[a] Full and partial songs combined, average number/min over 15-min trials: Limantour > Drake ($t = 15.2, P < 0.001$), Limantour > Buzzy ($t = 7.1, P < 0.001$), Limantour > Clear ($t = 9.5, P < 0.001$). All two-tailed t-tests for paired minute-by-minute comparisions, df = 14.
[b] Average number/min over 15-min trials: Limantour > Drake, Buzzy, and Clear ($t = 6.2, 8.9, 9.1$; all $Ps < 0.001$), Drake > Buzzy and Clear ($t = 2.4, 4.6$; $P = 0.031, P < 0.001$, respectively).
[c] Average number/min over 15-min trials: Limantour > Buzzy ($t = 2.8, P = 0.014$), Drake > Buzzy ($t = 2.9, P = 0.012$), Clear > Buzzy ($t = 2.6, P = 0.021$), Limantour vs. Clear or Drake not significant, Clear vs. Drake not significant.
[d] Average time from first stimulus song to first song of subjects in each group.
[e] Average nearest distance subjects in each group approached speaker.

approach to the speaker (Milligan and Verner 1971, Baker et al. (1981b). A full song consisted of introductory whistle(s), trill, and ending, whereas a partial song consisted only of introductory whistle(s) or whistles and trill but no ending. Additional information scored for each playback experiment included: response latency (seconds to first song), presence of female, fluttering and/or trilling by male, and fluttering and/or trilling by female. For each playback tape, the number of completed trials follows: Limantour A = 19, Limantour B = 20 (total = 39); Buzzy A = 15, Buzzy B = 21 (total = 36); Drake A = 17, Drake B = 16 (total = 33); Clear A = 15, Clear B = 18 (total = 33).

For song and flight data, the minute-by-minute means and standard errors were determined for all experiments with each playback tape. With the t-test method of paired comparisons (Bailey 1959), responses to the A and B playbacks of each dialect were compared and combined, and then responses among the dialects were compared (df = 14 in all minute-by-minute comparisons). Absolute t-values are reported, as the sign merely reflects comparison order. Parametric and nonparametric statistical tests used in this study are from Bailey (1959) and Siegel (1956), respectively.

RESULTS

Total songs.—A comparison of the mean number of total songs (full and partial) per minute sung in response to A versus B tapes for all dialects indicates that only the two Limantour samples differed significantly (response to Limantour A > Limantour B, $t = 2.65$, $P = 0.019$). The t-test analysis of total songs per minute sung by Limantour males in response to each playback dialect (Table 1) and the minute-by-minute means and standard errors for total songs in response to all dialects (Fig. 3) indicated that Limantour males sang the most total songs in response to the Limantour dialect and the fewest in response to the Clear dialect. In all cases, the number of total songs was significantly greater in response to the Limantour dialect (Table 1). The number of total songs did not differ significantly in comparisons among the Buzzy, Drake, and Clear dialects.

Full songs.—A comparison between A and B samples of each dialect indicates that only the two Buzzy songs yielded significantly different results (Buzzy B > Buzzy A, $t = 4.96$, $P < 0.001$). The overall mean number of full songs per minute sung by Limantour males in response to each playback dialect (Table 1) and the minute-by-minute comparison reveals that Limantour males sang the most full songs in response to the Limantour playbacks and fewest in response to the Clear playbacks (Fig. 3). In all paired comparisons, the numbers of full songs were significantly greater in response to the Limantour playbacks (Table 1). Also, the number of full songs in response to the Drake dialect was significantly greater than the number in response to the Buzzy and Clear dialects (Table 1).

Percentage of full songs.—The percentage of

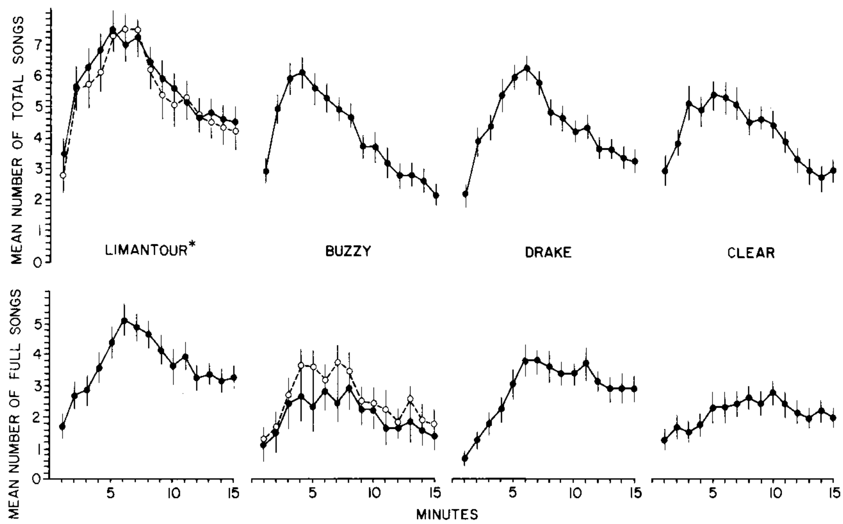

Fig. 3. The minute-by-minute means and standard errors of total and full songs sung by Limantour males (*) in response to dialect playbacks. See text for further explanation.

full songs of the total songs sung by Limantour males in response to dialect playbacks did not differ between A and B playbacks (t-test). The overall percentage of full songs indicated that two comparisons between dialects (Normal Distribution Test) were significant (Table 1). The percentage of full songs was greater in response to the Limantour playbacks than to the Clear playbacks ($d = 2.35, P = 0.02$) and greater in response to the Drake playbacks than to the Clear playbacks ($d = 2.52, P = 0.01$).

Flights.—Comparisons between A and B playbacks of each dialect indicated no significant difference in the number of flights, so all A and B data were combined. No pattern is obvious from the graphs of minute-by-minute mean numbers of flights in response to each dialect, except that flights decreased in frequency precipitously for all dialects after the stimulus portion of the playback trial ended (Fig. 4). Data analysis (Table 1) confirmed that this behavioral category did not discriminate among dialects in a consistent way. The number of flights evoked by the Buzzy dialect was significantly less than the number evoked by Limantour, Drake, or Clear, however.

Latency to first song.—The variance of the elapsed time before a male sang in response to a playback tape was compared between A and B samples for each dialect with F-tests. Only the Clear A–Clear B comparison showed a significant difference in variance (Clear B > Clear A, $F = 8.96, P = 0.01$, one-tailed). Therefore, the Clear A and Clear B sample means were compared with the Normal Distribution Test, according to the procedure suggested by Bailey (1956) for two samples of unequal variance; they did not differ significantly. The other A and B mean latencies were then compared with t-tests for means of small samples of equal variance; no significant differences were found. Finally, all A and B samples were combined, and the mean song latencies among the dialects were compared with the Normal Distribution Test; none differed significantly (Table 1).

Closest approach to speaker.—The variance in closest approach to the speaker among playback trials was compared with F-tests for A and B samples of each dialect. Only the Drake and and Drake B samples differed significantly (Drake A > Drake B, $F = 2.53, P = 0.05$, one-tailed). The other A and B samples were then compared with t-tests for means of two small samples of equal variance. The Drake A and B samples were compared with the Normal Distribution Tests procedure for two small samples of unequal variance (Bailey 1956). None of the differences between A and B samples was significant, so samples were combined. All comparisons of closest approach among dialects (Normal Distribution Tests) showed no significant differences.

Female presence.—The number of trials in which the female appeared in response to the

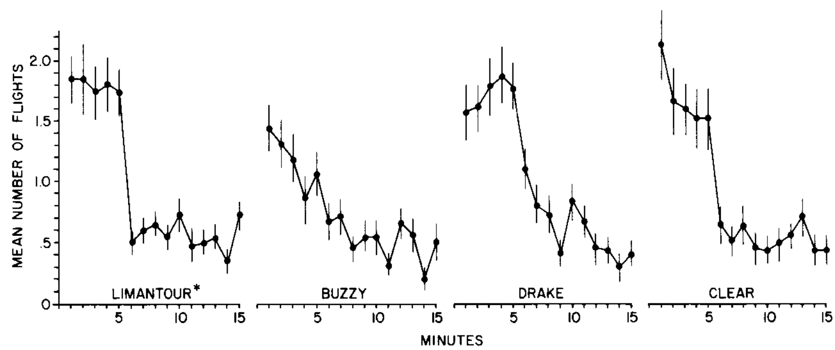

Fig. 4. The minute-by-minute means and standard errors of the number of flights by Limantour males (*) in response to dialect playbacks.

playback was compared for A and B samples of each dialect (χ^2 test for two independent samples); there were no significant differences. Similar comparisons between Limantour female presence and that of Buzzy, Drake, or Clear indicated no significant differences (Table 1).

Male trilling and fluttering.—The number of trials in which males responded to playbacks by trilling and assuming a fluttering posture, in addition to singing and flying, was compared for A and B samples of each dialect (χ^2 test for two independent samples). As there were no significant differences, the entire Limantour playback sample was compared with the Buzzy, Drake, and Clear samples, using the same statistical test. Only the number of males trilling and fluttering in response to Limantour playbacks was significantly greater than the number of males responding to the Buzzy playbacks ($\chi^2 = 6.38$, $0.02 > P > 0.01$, Table 1).

Female trilling and fluttering.—Of those playback trials in which females appeared, the number of trials in which the female trilled and fluttered was not statistically different between A and B samples of dialect playbacks (χ^2 test for two independent samples). Using the same statistical technique, we compared the occurrence of trilling and fluttering females in response to Limantour playbacks to that in response to the Buzzy, Drake, and Clear playbacks; there were no significant differences (Table 1).

Discussion

Males of the Limantour dialect sang significantly greater numbers of total and full songs in response to Limantour playbacks and fewer in response to Clear playbacks, the most geographically distant dialect. If a higher percentage of full songs relative to total songs is a correlate of aggressive response (i.e. full songs indicating stronger motivation), it is also of interest that Limantour males responded with the lowest percentage of full songs to Clear playbacks. Therefore, Limantour males were more responsive to the playbacks of their own dialect than to those of neighboring dialects and least responsive to playbacks of the most distant dialect. This latter observation is in accord with the playback responses to distant dialects described by Milligan and Verner (1971), Petrinovich and Patterson (1981), and Baker et al. (1981b).

These results differ from the Clear male playback results of Baker et al. (1981b), however, who found that subjects sang more in response to an adjacent dialect than to their own dialect. Petrinovich and Patterson (1981) found that both males and females chinked, trilled, and fluttered more in response to the neighboring dialect than to their own dialect, but males sang more full songs in response to their own dialect than to the neighboring dialect. Chinking, trilling, and fluttering are considered by Petrinovich and Patterson (1981) to be indicative of an excited and aggressive state. In contrast, there were no important differences in trilling and fluttering by Limantour females and males among the playback experiments of our study. Like the Petrinovich and Patterson (1981) results, Limantour males sang more full and partial songs in response to their own dialect than in response to neighboring dialects.

If the song rate correlates with aggressive response, then the lower level of response demonstrated by Limantour males to neighboring and distant songs suggests that intruders with these dialects may have an easier time establishing a territory in the Limantour dialect area than would Limantour males (Baker and Mewaldt 1978). Yet, misplaced males were extremely rare in the Limantour population (on the order of 1 to 2 males per 100, Tomback, unpubl. obs.). Alternatively, invading males may be disadvantaged by a lower probability of obtaining a mate, or they may not establish and hold a territory because their songs are less effective.

That male exclusion may not always prevent dialect mixing underscores the importance of juvenile dispersal bias and female mate choice as behaviors that limit gene flow. These two behavioral mechanisms alone may be adequate to maintain distinct dialect populations in *Z. l. nuttalli.*

Variation in response to A and B dialect songs.—Limantour males sang significantly more total songs in response to the Limantour A song than to the B song and significantly more full songs in response to the Buzzy B song than to the A song (Fig. 2). An explanation for this response variation is not obvious, as all songs selected were typical of their dialect and played at the same speaker volume. Songs of each dialect did vary in the strength of the ending phrase, however (see Fig. 2). Some males sang strong or weak endings, and these may elicit more or less response.

Each *Z. l. nuttalli* dialect population appears to be composed of a mosaic of small subdialects (Cunningham and Baker in prep., Tomback unpubl. obs., Baptista 1975). These subdialects vary in characters not considered to be dialect markers (e.g. breaks in introductory whistles and vibrato second introductory whistles) and similar small subdialects are dispersed throughout the dialect area. Subdialects may represent kin associations and/or facilitate social interaction as proposed in Payne's social adaptation model (Payne 1981). It is possible that a playback song might evoke a somewhat different response, depending on how similar or dissimilar it is to the subdialect of the male subject. Such similarities and dissimilarities of playback songs to subdialects, and the relative frequency of certain song subdialects among male subjects, may account for the observed differences in response to A and B songs.

Difference in response hierarchies for Marin County dialects.—Baker et al. (1981b) found that Clear males responded significantly more strongly to songs of the neighboring Buzzy dialect than to songs of the Clear dialect, whereas this study shows Limantour males respond significantly more strongly to their own dialect than to neighboring dialects. Several possible explanations for this difference in response hierarchy can be suggested.

1. The responsiveness of males with one dialect to songs of a neighboring dialect may be inversely proportional to the length of a dialect boundary and, consequently, the opportunity to habituate to the neighboring song dialect. For example, during winter months, White-crowned Sparrows may wander beyond their territory boundaries or form foraging associations with other birds, including individuals from more than one dialect area. As males begin to sing, flock members or transient individuals may be exposed to songs of both dialects. The probability and degree of habituation and the number of males habituating to songs of the neighboring dialect may be directly proportional to the boundary length between two dialects. Here, low response to geographically distant dialects may relate to the explanation proposed below in 2. The Clear-Buzzy dialect boundary is much shorter than the Buzzy-Limantour or Limantour-Drake boundary and may afford little or no exposure to neighboring song. There are problems with the habituation explanation, however, because the response of Limantour males to Drake songs was greater than their response to Buzzy songs, despite the longer Limantour-Drake boundary.

An alternative explanation to habituation might be sensitization, i.e. the greater the previous exposure of males to a dialect, the greater their response to that dialect. Sensitization would satisfactorily explain the hierarchy of dialect responses observed in this study, namely Limantour > Drake > Buzzy > Clear, but it does not explain the reciprocal Buzzy-Clear playback results.

2. The response hierarchy may reflect the origin of and relationship among neighboring dialects. If *Z. l. nuttalli* dialects arise by splitting and differentiating and/or from a founder group, some dialect pairs or groups may be more closely related than others. A comparison of similarities and differences in sound structure among the dialects used in this study (Fig. 2)

suggests that Limantour and Drake are closely related, as are Buzzy and Clear. For example, the Buzzy and Clear dialects, which differ only in one character, may have diverged recently. If so, the response hierarchy observed may be akin to that of the "neighbor-stranger effect" (Baker et al. 1981b), in which a territorial male responds more strongly to a stranger's song than to a neighbor's song. Buzzy songs may be similar enough to Clear songs that a very strong "stranger" response occurs.

If dialect affinity affects response, the low response to the Bodega song by Clear males in the Baker et al. (1981b) experiments and the lower response to the Clear and Buzzy songs by Limantour males in the present study may be the consequence of the divergence between these groups. Because these songs are dissimilar to the songs of the playback subjects, a probable consequence of the origin and relationship among these coastal dialects, the distant songs may have less biological significance to the subjects than home or neighboring dialects.

3. The level of response of males of one dialect to songs of a neighboring dialect may be inversely proportional to the length of time the dialects have been in contact. After the founding of a new dialect, or at first contact between two dialects, there may be strong selection both for males of one dialect to exclude males of a neighboring dialect and for females to mate preferentially with males of their home dialect. After enough time, when these dialects are structured into discrete populations and mixing is minimized, selection for male aggression against neighboring dialects may relax. At this point, female mate choice and juvenile dispersal bias may be adequate to maintain dialect integrity. This explanation would be plausible if the Buzzy-Clear dialect association were more recent than the Limantour-Drake or Limantour-Buzzy associations, as suggested by the relative differences among these dialects.

4. A fourth explanation involves the dialect markers of songs. Certain song characteristics or combinations of characteristics that are manifest as "harsh" sounds may elicit a higher level of aggression from males of a given dialect, regardless of dialect affinities (Morton 1977). For example, characteristics of the Limantour song may be especially stimulating to Limantour males, whereas characteristics of Buzzy songs may be more stimulating to Clear males than are Clear songs. If this explanation is correct, we might expect all *Z. l. nuttalli* males to respond similarly to certain sounds, i.e. males of all dialects should respond more to Buzzy and Limantour songs. This is not supported by the results of reciprocal playback experiments between Buzzy and Clear males (Baker et al. in prep.), which indicate that Buzzy songs are not more stimulating to Buzzy males than are Clear songs. The hypothesis that certain song characteristics may elicit a greater response in males has merit, however, and bears testing, perhaps with playback experiments using synthetic songs.

Playback experiments and interpretation: problems to consider.—One major concern about quantifying male response to playbacks relates to the validity of the bio-assays selected, i.e. songs, flights, latency, and closest approach to speaker. By watching male subjects carefully, one gains the impression that male response at either extreme of the aggression spectrum is not accurately scored. Uninterested males do no respond quickly or much. Males that appear to be extremely agitated by the playback songs, as indicated by flights, trilling, fluttering, and/or searching for the song source, may show a long latency period before singing or sing few or no songs. We anticipated a linear correlation between behavioral response to playbacks and levels of aggression, but this may not be the case. The behavioral response of a male may not reflect its actual level of aggression but rather the context of the encounter and the cost-to-benefit ratio of responding to a territorial challenge (e.g. Maynard Smith 1974, Maynard Smith and Parker 1976).

We are also uncertain about the meaning of partial songs in comparison to full songs. Do partial songs indicate a lower level of motivation than do full songs, and are they the consequence of changing hormonal levels and stage in the nesting cycle (e.g. see Petrinovich et al. 1976)? To circumvent this difficulty, total and full songs sung per minute were analyzed separately for this study. The results were similar for both analyses, but the meaning of partial songs is still unclear.

Although it is abundantly clear that *Z. l. nuttalli* discriminates among dialects, it is necessary to ask whether or not the differences in response by males to neighboring and home dialects are biologically meaningful. Differences in response that are assigned significance by statistical tests may not have any effect on male reproductive success. As an alternative to playbacks for testing the male exclusion hypothesis, field observations are needed of the time spent in territorial defense, the reproductive success, and the fate of offspring of the few male invaders with neighboring dialects and that of their home dialect neighbors, compared to similar data from sets of home dialect neighbors. Such information may allow conclusions about the relative success of invading and home dialect males.

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