

# SONG DEVELOPMENT AND TERRITORY ESTABLISHMENT IN NUTTALL'S WHITE-CROWNED SPARROWS<sup>1</sup>

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**Abstract.** Song development and territory establishment were studied in the permanently resident Nuttall's White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). Hatching-year birds (juveniles) begin subsong in July, and the first crystallized songs are heard in late September. Social interaction with territorial adults accelerates song development so that song crystallizes earlier in wild juveniles than in hand-raised laboratory birds. Some juveniles begin staking out territories in September and October. At this time individuals may sing up to four song types. As time progresses settling juveniles use only one or sometimes two song types which match those of neighbors with whom they interact. Singing is performed circumannually, even during the molt in this subspecies, reflecting its year-round territoriality.

**Key words:** *White-crowned Sparrow; song; territory establishment.*

## INTRODUCTION

Singing activity in oscines is a seasonal phenomenon in temperate regions, reaching its peak in the spring and regressing in late summer (Cox 1944, Thompson 1972, Bezzel 1988). For example, in central California, singing in Rufous-sided Towhees (*Pipilo erythrophthalmus*) and House Finches (*Carpodacus mexicanus*) begins in late January and early February and wanes in July (Davis 1958, Thompson 1960). The disappearance of singing activity appears to coincide with gonadal regression and the onset of postnuptial molt (Davis 1958).

Songs in oscines are learned from adults in the population (Slater 1983). The learning process may be divided into (1) a perceptual phase when the vocal information is received and stored, and (2) a motor phase when the stored information is vocalized (Nottebohm 1969, Marler 1987). At temperate latitudes the perceptual and motor phases are typically separated by a long period of silence coinciding with the fall and winter months (Lanyon 1960, Marler and Peters 1982a).

Nuttall's White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) is permanently resident in

the San Francisco Bay Area of California (Blanchard 1936, 1941). Breeding activity begins in early March, and fledglings appear in the population in early May to late August or early September (Mewaldt and King 1977; DeSante and Baptista, in press). Fledglings learn songs from adults during an early sensitive phase (Marler 1970, Cunningham and Baker 1983, Petrinovich 1985, Baptista and Petrinovich 1986), and laboratory studies have suggested that learned songs are stored in memory through the fall and winter months and are first vocalized in early spring when daylength increases (Konishi 1965, Marler 1970). However, there are anecdotal reports of young birds singing subsong in July and August (Blanchard 1941, Baptista 1975), and Blanchard (1941) has reported on hatching-year (juvenile) birds singing adult songs in November.

Juvenile (hatching-year) White-crowned Sparrows are easily distinguishable from adults during the fall: fledglings have spotted breasts and following the postjuvenile molt crowns are brown-and-tan in juveniles, in contrast with black-and-white in adults (Parsons and Baptista 1980). DeWolfe recorded a brown-crowned individual singing a fully crystallized adult song in Golden Gate Park, San Francisco, on 21 September 1981. A quick search through the park revealed other

<sup>1</sup> Received 18 August 1988. Final acceptance 3 January 1989.

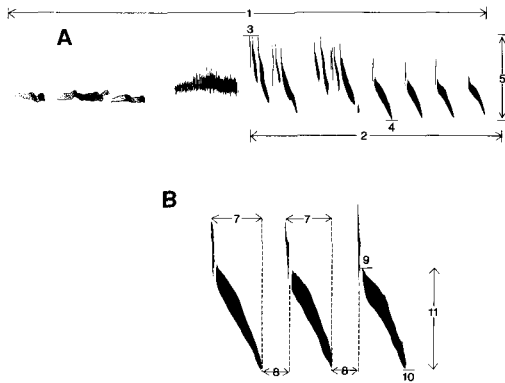


FIGURE 1. A. Variables of White-crowned Sparrow song measured in this study. B. Variables of terminal trills considered in this study. Numbers correspond to variables measured and treated statistically in Tables 1 and 2.

juveniles in song. This prompted us to seek out juveniles in the fall, color-mark them, and follow their singing behavior through the fall and winter months.

In this paper we describe development of song and document fall and winter song in free-living Nuttall's White-crowned Sparrows. We demonstrate that in many individuals subsong is not postponed until the following spring, as has been documented for other temperate latitude, migratory birds, but may occur in late summer and fall when some individuals stake out territories on which they remain to breed in spring.

## MATERIALS AND METHODS

We banded adult and juvenile *Z. l. nuttalli* at three sites in Golden Gate Park, San Francisco, California between 1981 and 1983. Color bands were added if we noted that certain individuals were delivering loud songs from exposed perches at restricted sites, indicating that they were defending those areas. Birds were usually captured by attracting them to a trap with a tape recorder placed nearby. The tape-recorded song stimulated the birds to sing, enabling us to record their song or songs before catching them for color-banding. Color-banded birds were recorded periodically through the study period. We noted that stimulation by tape recordings may influence the juvenile to switch from plastic to stereotyped song (see beyond), thus recordings subsequent to capture were spontaneous utterances that were not elicited by tape playback.

We also recorded songs of other unmarked ju-

veniles at these sites. These songs were usually sporadic and spontaneous, in contrast to songs of territorial juveniles that delivered continuous bouts of songs.

Songs were recorded on Nagra and Sony tape recorders using Sennheiser microphones and sound spectrographs were prepared using a Kay-Elementrics sound spectrograph machine Model 7029A. To compare quality of song of juvenile vs. adult birds, we made the following measurements on the spectrographs (Fig. 1): (1) Duration of song (sec). (2) Duration of trill (sec). (3) Highest frequency of song (kHz). (4) Lowest frequency of song (kHz). (5) Frequency span of song (kHz). (6) Number of syllables in the trill. (7) Duration of note in terminal trill (sec). (8) Duration of silent intervals between terminal syllables (sec). (9) Highest frequency of trill note (kHz). (10) Lowest frequency of trill note (kHz). (11) Frequency span of trill note (kHz).

The note in the terminal trill was selected for analysis because we felt that it was least susceptible to various recording artifacts. Using a random number table two notes and two intervals of silence were selected from each song for analyses. Differences in the quantitative characteristics of song of adults and juveniles were then tested with the Wilcoxon's two-sample test.

For purposes of brevity we use the term juvenile to describe all hatching-year birds including spotted fledglings and birds followed from the time of postjuvenile molt to the time of first breeding.

## RESULTS

### SONG DEVELOPMENT IN WILD BIRDS

Marler and Peters (1982b) studied song ontogeny in Swamp Sparrows (*Melospiza georgiana*) and distinguished seven different stages that grade into each other, but pointed out (p. 448) that in most cases four stages would suffice. In this study we recognize three stages:

(1) Subsong: These are the first attempts at singing by fledgling White-crowned Sparrows (Fig. 2A). These utterances usually consist of a series of whistles and chirps which vary in morphology and duration from rendition to rendition. No syllables typical of adult White-crowned Sparrow song are recognizable in these singing attempts.

(2) Plastic song (also known as "rehearsed" song by some authors): Although characterized

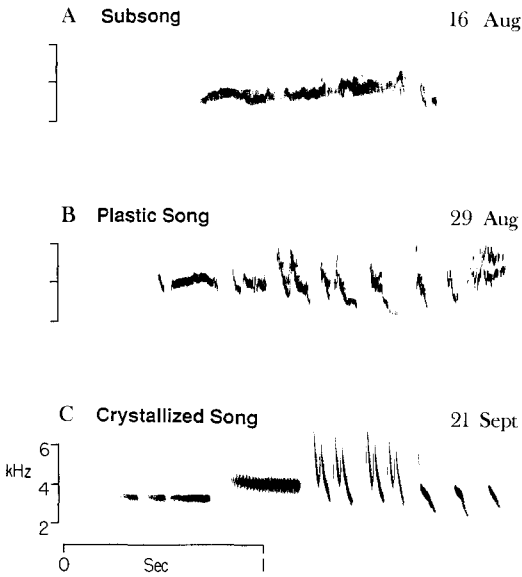


FIGURE 2. Developmental stages of White-crowned Sparrow song.

by much variation, these songs already contain elements recognizable by the trained eye as White-crowned Sparrow syllables (Fig. 2B). The songs are also divisible into the introductory whistle portion and terminal trill portion characteristic of White-crowned Sparrows of the San Francisco Bay Area (Marler and Tamura 1962, Baptista 1975).

(3) Crystallized song: This is the loud stereotyped song characteristic of breeding adults. There is little variation in syllable morphology or duration of each song element, although song du-

ration may vary between renditions by the addition or deletion of syllables in the song (Marler and Tamura 1962, Cunningham and Baker 1983; Fig. 2C).

In the laboratory, the plastic song stage gradually develops into the stereotyped, crystallized song stage in birds not subjected to song playback (Marler 1970). We found, however, that a bird singing plastic song (Figs. 3A, 3B) may immediately switch to using crystallized song (Figs. 3-A1, 3-B1) if challenged by another singing bird or if subjected to playback of taped White-crowned Sparrow song. We were therefore careful in our field studies of song development never to use playback to elicit singing.

The trained eye may also recognize two classes of stereotyped song sung by juveniles in the field. A few juveniles sang songs with slightly quavering whistles and syllables (songs A to C, Fig. 4). Others sang songs indistinguishable from those of adults (e.g., song D and E, Fig. 4). On rare occasions we also recorded adults in the fall singing songs that were quavering in quality. We believe that the quavering songs represent a motivational state rather than a developmental stage. We thus use the word crystallized throughout the text to describe both classes of stereotyped song.

Pooled data consisting of singing juveniles from 1981 and 1982 censuses are summarized in Figure 5. Most of the fledglings (80%) censused in July were in subsong. However, three individuals were already in the plastic song stage. Twenty-six of 27 individuals recorded in August were in plastic song. The first stereotyped songs were given by three of 16 birds (18.75%) recorded during

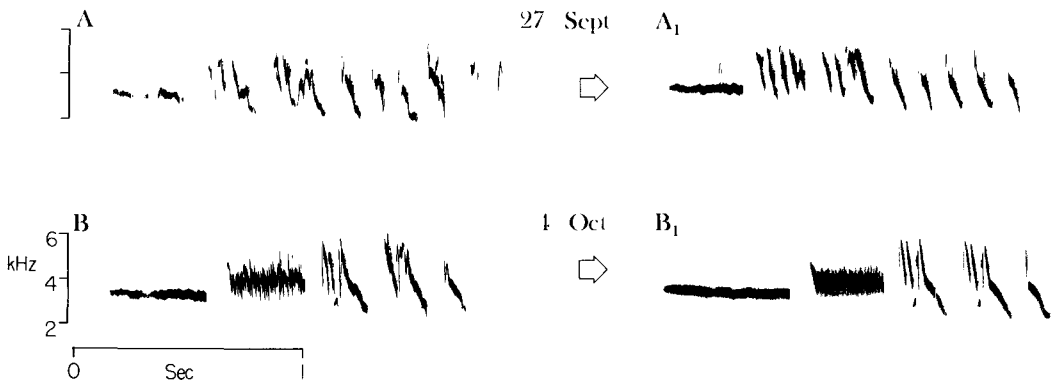


FIGURE 3. A and B. Plastic song of juvenile White-crowned Sparrows. A1 and B1. Stereotyped song of juveniles when challenged by neighboring male. Arrows from plastic song to stereotyped song of the same bird. Song A consists of variable introductory whistle and trill. Song B represents a more advanced developmental stage, and it is only the introductory vibrato that is most visibly variable.

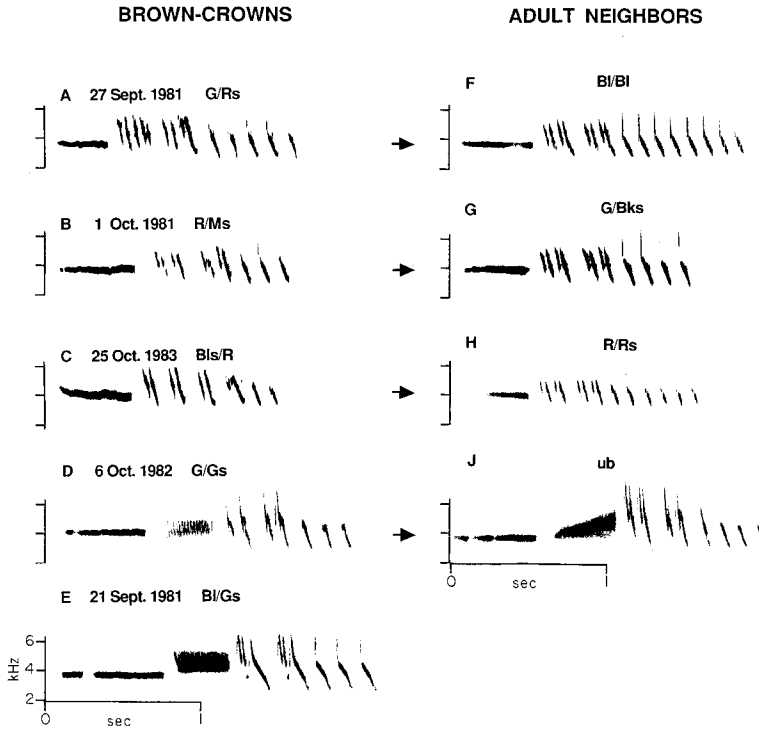


FIGURE 4. A to E. Earliest recordings of live juveniles on territory to illustrate degree of song development in juveniles and similarity of songs of adult neighbors when present. F to J. Adult songs of one immediate neighbor of each juvenile. Arrows point from songs of juveniles to those of their adult neighbors. Bird E had no immediate neighbor. Songs D and E are similar to crystallized song of adult males. Whistles and syllables in songs A to C are quavering indicating that they are not completely crystallized.

the first 2 weeks in September. By the second week of October eight individuals (42%) were singing crystallized song. This number may be an underestimate since birds singing plastic song may spontaneously change to crystallized song if challenged by another conspecific (Fig. 3).

DESCRIPTIVE STATISTICS OF ADULT VS. JUVENILE SONGS

Crystallized songs of juveniles were compared to songs of adults by measuring several characteristics as summarized in Tables 1 and 2. Songs of adults contain more syllables than songs of juveniles (9.30 vs. 5.10 syllables). Syllable number was related to both duration of the trill and of the song. Thus songs of adults are longer than those of juveniles (1.91 vs. 1.66 sec). Although highest frequencies are the same for songs of both age classes, lowest frequencies of songs of adults are higher than those for juveniles (2.88 vs. 2.53 kHz). The frequency span was significantly broader in juveniles than in adults (3.43 vs. 2.88 kHz).

There were no significant differences in duration of each trill syllable between the age classes (Table 2). Nor were there significant differences in highest frequency of each syllable between the two age classes. However, trills of juveniles were significantly slower in rhythm than those of adults as manifested in the intervals of silence between successive syllables (0.05 sec in juveniles vs. 0.04 sec in adults). This difference in most cases was

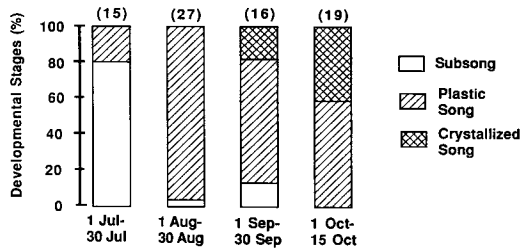


FIGURE 5. Bargrams showing percentages of juveniles singing subsonic, plastic song, and crystallized song during each month from July to mid-October. Numbers in brackets are number of birds recorded.

TABLE 1. Descriptive statistics ( $\bar{x} \pm SD$ ) of songs of adult vs. juvenile White-crowned Sparrows.

	Adult ( $n = 10$ ) <sup>1</sup>	Juvenile ( $n = 10$ ) <sup>1</sup>
Duration (sec)	1.91 $\pm$ 0.29	1.66 $\pm$ 0.32*
Trill duration (sec)	1.20 $\pm$ 0.34	0.89 $\pm$ 0.14***
High frequency (kHz)	5.75 $\pm$ 0.41	5.95 $\pm$ 0.68
Low frequency (kHz)	2.88 $\pm$ 0.18	2.53 $\pm$ 0.25***
Frequency span (kHz)	2.88 $\pm$ 0.48	3.43 $\pm$ 0.74*
Number of trill syllables	9.30 $\pm$ 2.19	5.10 $\pm$ 1.10****

<sup>1</sup> Sample sizes of syllables measured from 10 adults and 10 brown-crowned birds. Wilcoxon's: \*  $P < 0.05$  \*\*  $P < 0.01$  \*\*\*  $P < 0.005$  \*\*\*\*  $P < 0.001$ .

evident from visual inspection of spectrograms (e.g., compare song A and song F in Fig. 4). Lowest frequency of a trill syllable was significantly higher in adults than in juveniles (2.90 vs. 2.64 kHz), and the frequency span was wider in juveniles than in adults (1.89 vs. 1.65 kHz). In sum, there were small but significant differences between songs of adults as compared to those of juveniles in eight of the 11 characteristics quantified.

#### ESTABLISHMENT OF TERRITORY

The preceding indicates that young Nuttall's White-crowned Sparrows begin subsong in July and many sing crystallized song by September or October. Major dispersal movements that coincide with the postjuvinal molt in July and August have been noted (Mewaldt and Archibald 1966). The onset of singing coincided with the time of territory establishment as developed below.

Singing occurred every month of the year, even during August and September, when postnuptial and postjuvinal molt were at their peaks. Fifty-nine of 86 birds (adults and young) trapped in these months were molting, as were many other individuals seen in the field but not handled. Yet in the population as a whole singing never stopped completely either in juveniles or adults. We indexed the amount of singing by juveniles during

each month in 1981 and 1982 by looking at the percentage of field dates during which we encountered them singing (Fig. 6). Peaks of singing are evident between August and October during which singing was noted at between 64.7 and 81.8% of the days spent in the field. This dropped to 37.5% in November. Thus, amount of singing did not decrease in the population of brown-crowns in August through October despite the fact that most of the birds were in some state of molt.

Crystallized song was first recorded in nine color-banded individuals between 21 September and 15 October. Seven of these nine individuals eventually bred in the vicinity of the sites where stereotyped songs were first recorded (Fig. 7). The first date when these juveniles sang from exposed perches was also the first time we observed them manifesting all the behavior associated with territoriality. Song at this time was loud and delivered in bouts. Song quality in some juveniles was indistinguishable from the song of adults (song D and E, Fig. 4) although as we have seen earlier, others sang songs with small but consistent quantitative differences from adult songs. All juveniles responded to playback with approach, posturing, and singing.

We observed juveniles posturing and countersinging with adults or other juveniles at this time. We noted 60 countersinging bouts between 27

TABLE 2. Descriptive statistics ( $\bar{x} \pm SD$ ) of note in terminal trill of syllables of adult vs. juvenile White-crowned Sparrows.

	Adult ( $n = 20$ ) <sup>1</sup>	Juvenile ( $n = 19$ ) <sup>1</sup>
Duration of note (sec)	0.08 $\pm$ 0.02	0.08 $\pm$ 0.01
Duration of silence (sec)	0.04 $\pm$ 0.01	0.05 $\pm$ 0.02****
High frequency (kHz)	4.55 $\pm$ 0.21	4.49 $\pm$ 0.23
Low frequency (kHz)	2.90 $\pm$ 0.15	2.64 $\pm$ 0.29****
Frequency span (kHz)	1.65 $\pm$ 0.21	1.89 $\pm$ 0.24**

<sup>1</sup> Sample sizes of syllables measured from 10 adults and 10 brown-crowned birds. Wilcoxon's: \*  $P < 0.05$  \*\*  $P < 0.01$  \*\*\*  $P < 0.005$  \*\*\*\*  $P < 0.001$ .

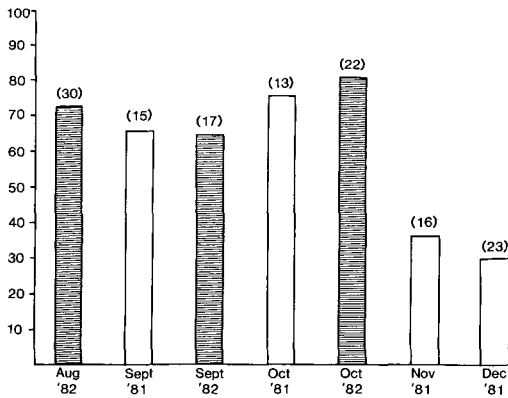


FIGURE 6. Percent of field dates when juveniles were seen or heard to sing without using playback. Numbers in brackets are numbers of days sampled in that month. Data from 1981 are represented by clear bars and data from 1982 by hatched bars.

July and 1 November of which 23 (38%) involved juveniles. On 7 October 1982 we also observed the first evidence of "patrolling" by one individual (RS/G). This juvenile sang a few songs from one perch, then changed perches and sang another bout of song, then changed perches again and sang a bout of song, etc.

There appeared to be a peak in singing activity in these juveniles from mid-September through October. The amount of singing decreased in November (Figs. 6, 7), then picked up again toward

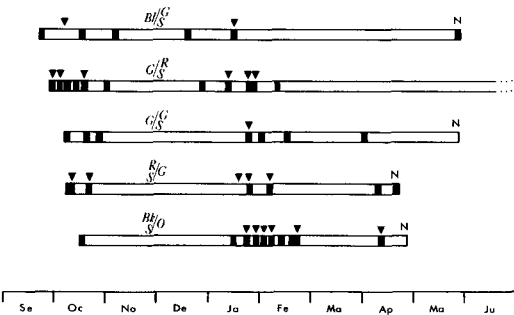


FIGURE 7. Histories of five of the seven juveniles followed from the time they were first recorded singing from exposed perches to the time their nest was found. The date when each nest was found is represented by the letter N. The nest of G/RS was not found, but the individual remained on territory. Each black bar within each horizontal clear bar represents a date when that individual was noted producing spontaneous song. Each black inverted triangle represents an observation of an interaction between that juvenile and another bird. An interaction may be a threat, a chase, a fight, or a countersinging bout with another individual.

TABLE 3. Interactions between the age classes of *Z. l. nuttalli* in 1982. Interactions include challenges, chases, and actual fights.

	August	September	October	Total
Young vs. young	13	11	6	30
Young vs. adult	1	6	1	8
Adult vs. young	0	3	2	5
Young vs. unknown age	3	0	6	9
Total	17	20	15	52

the end of December through mid-February. The first peak probably coincides with the first attempts by juveniles to establish territories. The second peak probably coincides with a second attempt by juveniles to seek territories and adults to reassert territory boundaries as noted earlier by Blanchard (1941).

These two periods are also periods of much social interaction with other adults and juveniles (Table 3 and Fig. 7). In addition to countersinging, between August and October we observed juveniles involved in 52 aggressive interactions (Table 3). Twenty-three of these were chases and six were fights. Thirteen of the interactions were between juveniles and adults. This is undoubtedly an underestimate, because for nine other interactions we could not see the crown color of the bird interacting with the juvenile.

A juvenile's song need not be fully crystallized to evoke an attack from an adult. For example, one individual was observed singing loud but not fully crystallized song in between bouts of foraging on 4 September 1982 when it was attacked by an adult. They faced each other and flew up into the air several times. Upon landing the juvenile sang again. The adult did not respond.

The fact that in eight other instances we observed juveniles challenging adults suggests that these individuals were actively attempting to stake out territories. All the above observations indicate that in *Z. l. nuttalli* territory establishment may occur in the fall months coinciding with peaks of singing in the general population and time of song crystallization.

Not all attempts at territory establishment were successful, however. For example, one individual (O/RS) was recorded and color-marked on our study area on 4 October 1981. It remained in the same vicinity for about a week and then disappeared. Joyce Dinslage found it dead on 17

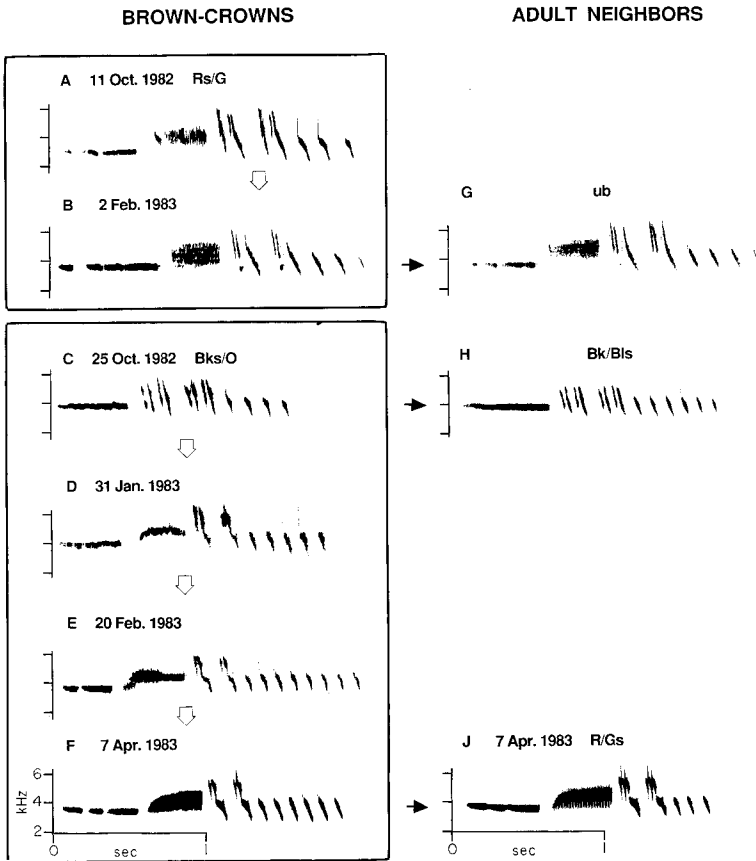


FIGURE 8. Song histories of two juveniles, RS/G and Bks/O. Note that complex syllables in song B of RS/G resemble those in adult song G. Note also whistle in song D of Bks/O gradually changing to vibrato in song F.

January 1983 at a site 3 km away and sent its number to the banding office.

#### MATCHING OF SONG TYPES WITH TERRITORIAL NEIGHBORS

Social interaction with adults may influence the choice of a song model that is imitated by oscines (Eales 1985). Six of the seven juveniles that established territories in the fall had from one (Figs. 4, 8) to as many as four (not illustrated) immediate neighbors singing song themes that matched their own. As will be seen below, the singing behavior of neighbors exerts an important influence on the type of song used by the settling juvenile.

Bird RS/G was banded 17 September 1982 near the Polo Field in Golden Gate Park. It was recorded singing on 11 October at a new site a

few hundred meters from the place of first capture. On 3 February 1983, we found that its song had changed and now matched closely that of its neighbor (Fig. 8B and G). The second subsyllable of the complex syllables in its song consisted of two notes in the song recorded on 11 October (Fig. 8A). In its new song it is the first subsyllable that consists of two notes (Fig. 8B), a close copy of its neighbor's complex syllables (Fig. 8G).

A second individual (Bks/O) was recorded singing a song with one whistle in the introduction on 25 October 1982, closely matching that of its neighbor (Fig. 8H). On 31 January 1983, it was recorded singing a second song type for the first time. This new theme had two whistles in the introduction (Fig. 8D). The second whistle gradually changed into a vibrato (Fig. 8E). On 7 April it was recorded countersinging with its

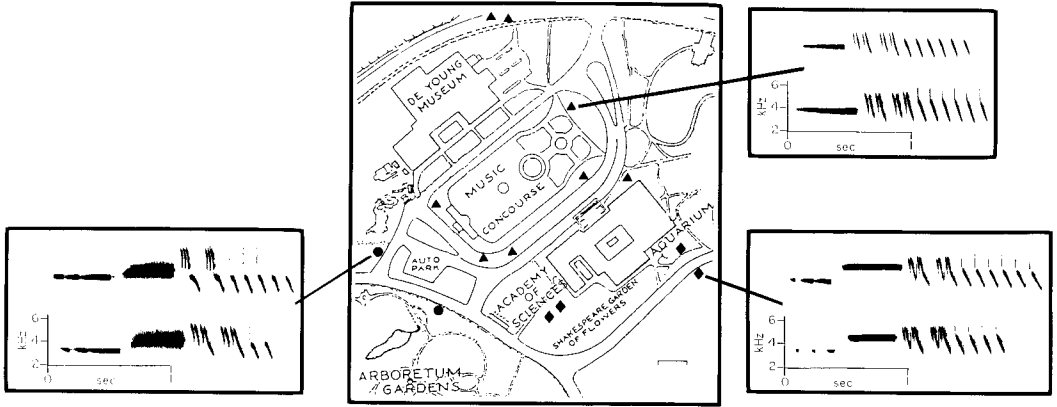


FIGURE 9. Theme sharing by neighboring White-crowned Sparrows in 1981. Each black triangle represents one individual singing a song with one introductory whistle. Each black diamond represents one individual singing a song with two introductory whistles. Each black circle represents one individual singing a song with a vibrato in the introduction. Scale on bottom right-hand corner of map represents 100 m.

neighbor, singing a theme which was an almost perfect match of the neighbor's song (Fig. 8F, J). Now the second phrase was a complete vibrato. This is the only instance we have of a White-crowned Sparrow's song changing gradually in structure to match its neighbor's song type.

A third individual (B1S/R) was first recorded singing two song types in January. In February and March it was singing only one of these, the song that matched its two nearest neighbors (not illustrated).

A fourth individual (G/GS) was recorded on the north shore of Lake Merced (see map in Baptista 1975) using both a Lake Merced and a San Francisco dialect. As time progressed its preferred song was the San Francisco song matching its neighbor's (Fig. 4J) with whom he frequently engaged in matched countersinging bouts.

In January of 1984 we recorded two birds, BkR/S and B1Bk/S, singing three and two themes, respectively. These two individuals settled next to each other, and in March both individuals sang matching songs with only one whistle in the introduction (not illustrated).

#### SHARING OF SONG TYPES WITH NEIGHBORS

Songs of neighboring White-crowned Sparrows in the San Francisco Bay Area often have more similar introductory phrases than songs of non-neighbors, giving rise to small "subdialect" groups (Baptista 1985). White-crowned Sparrows in this study also often shared similar introductory phrases with neighbors (Fig. 9). For example, in

1981 eight individuals north of the Academy of Sciences building sang songs containing only one introductory whistle. Four birds occupying territories south of the building sang songs with two introductory whistles. Two birds occupying territories west of the building sang songs with a vibrato. The number of birds singing each song type changes from year to year. In 1988, the one-whistle and two-whistle song types were still to be found in the same geographical areas.

#### DISCUSSION

At high latitudes and altitudes territory establishment by yearling White-crowned Sparrows occurs in the spring or early summer when birds return from wintering in more southerly climes (Blanchard 1941, Morton et al. 1972, DeWolfe et al. 1973, King and Mewaldt 1987). At the latitude of San Francisco (37°46') White-crowned Sparrows are permanently resident and are permanently territorial (Blanchard 1936, 1941). This study indicates that establishment of territories by juvenile (hatching-year) birds does not begin in spring as it does for the migratory races, but rather begins in the fall. During this fall period full song and skirmishes with established territorial adults occur (Fig. 7). In contrast to the migratory subspecies, *Z. l. nuttalli* may establish territories while still in juvenile plumage, prior to the prenuptial molt. Juveniles will respond in the fall to playback of recorded song by approach towards the speaker, aggressive flights, and countersinging with the recorded song, additional evidence that the territorial instinct is manifest



in juveniles in the fall in this permanently resident subspecies.

In the mild climate of coastal western North America at least two other songbirds are known to be territorial year-round and it has been documented that their young also establish territories in the fall. Erickson (1938) noted circannual song in Wrentits (*Chamaea fasciata*), associated with year-round territoriality. She noted an increase in song between August and October when young of the year were seeking territories. She also documented disputes between adults and young at this time. Circannual singing and defense of territory have also been reported for the Bewick's Wren (*Thryomanes bewickii*) by Kroodsma (1974). Fledglings may move into unoccupied areas in July and August; four fledgling males ranging from 60 to 135 days of age had already established territories and begun singing by then.

It is well-known that testosterone treatment increases the amount of singing in White-crowned Sparrows and other birds (Baptista et al. 1987). The autumn and early winter singing and aggressive behavior of juvenile Nuttall's sparrows was thus unexpected, because that time of year coincides with small testis size and presumably with low titers of plasma testosterone (Nottebohm et al. 1987). Blanchard (1941) found testis volumes of adult Nuttall's sparrows minimal from October through at least early December (p. 52 and figs. 18 and 19). Although the testes are the chief sources of testosterone, and testis cycles often track the song cycle in oscines (e.g., Davis 1958), our observations of fall and winter song suggest that correlation need not imply causation, and that factors other than testosterone level may also affect song volume. Kroodsma (1974) suggested that the late summer crystallization of song in hatching-year Bewick's Wrens is due to stimulation by singing adult males. He proposed (p. 373) that wild birds come into song earlier than those raised in isolation. Kroodsma's proposal may also apply to White-crowned Sparrows, which, when raised in isolation, learn taped songs from 10 to 50 days of age but do not begin subsong until 150 to 200 days of age (Marler 1970). A field-recorded juvenile estimated to be 90 days old (it was in a comparable stage of molt with a captive of that age) was already singing crystallized song in September. Another male banded as a nestling in San Francisco on 8 June was recorded singing crystallized song on 2 Oc-

tober when it was 123 days old. This suggests that White-crowned Sparrows in the wild may crystallize their song by 90 days of age. We suggest that for young Nuttall's sparrows the presence of a singing adult, or competition with flock mates for food and space, may constitute "supplemental information" (term used by Wingfield and Farner 1980) which stimulates early singing and aggressive behavior and early song crystallization.

Close scrutiny of spectrograms has revealed that White-crowned Sparrows occupying neighboring territories often share similar introductory phrases in their songs (Baptista 1975, 1985; Cunningham et al. 1987; this study). Using univariate and multivariate analyses Trainer (1983) sought but did not find nearest-neighbor sharing of song types. Utilizing different analytical techniques Cunningham et al. (1987) found that distribution of song variants was nonrandom near Point Reyes, California, so that nearest neighbors often shared similar songs, although song groups often overlapped in geographical space. These disparate results may reflect different analytical approaches. However, these differences may be real and may indicate that there is geographical variation in White-crowned Sparrows in dispositions to share songs as has been documented for Sage Sparrows (*Amphispiza belli*) by Wiens (1982).

Sharing of similar songs by nearest neighbors may be due to young birds learning songs directly from their fathers (Cunningham and Baker 1983) and settling near their hatching site (Cunningham et al. 1987), or due to young birds dispersing into the study area and learning the songs of neighbors at sites settled. Two detailed studies on singing behavior of White-crowned Sparrows banded as nestlings and followed into adulthood indicate that whereas some individuals may learn their songs directly from fathers, this is not the normal mode of cultural tradition (Petrinovich 1988, Baptista and Morton 1988). Most juveniles sang songs unlike those of their fathers but often closely matching those of territorial neighbors at settling sites.

In a laboratory study, naive, hand-raised *Z. l. nuttalli* were tutored with one song dialect when they were between 10 and 50 days of age. The experimentals were then moved to a different building and placed in special cages where they could see and hear a live tutor singing a second dialect that they had never heard before. At ma-

turity about 50% of the experimentals sang the song of the second tutor (Petrinovich and Baptista 1987). Large-scale dispersal movements by White-crowned Sparrows about 50 days of age have been documented for both *Z. l. nuttalli* and *Z. l. oriantha* (Baker et al. 1982, Wakamatsu 1983). Thus the above experiments may be interpreted to mean that dispersing juveniles are capable of learning new songs at sites settled. Our observations (see above) and those of previous studies indicate (Baptista 1977, Baptista and Morton 1988) that individuals tended to match songs with neighbors or playback of tape-recorded songs using similar themes and suggest that neighbors influence the song types used by juveniles attempting to establish territories. Laboratory and field studies suggest that one explanation for the sharing of similar song themes by territorial neighbors is that juveniles learn and use song of established territory holders at sites settled. This is consistent with studies on other avian taxa in which color-marked birds were followed from hatching to settling sites (Jenkins 1978, Payne et al. 1987).

We have records of juveniles using from two to as many as four themes during the plastic song stage. It is likely that fledglings of *Z. l. nuttalli* wander over the study area and learn songs from several territorial males as documented for *Z. l. oriantha* (Baptista and Morton 1988). A settling fledgling will tend to use themes matching those of his neighbors during countersinging bouts. Themes not so used may be stored in memory and used to distinguish neighbors from strangers as suggested by McGregor and Avery (1986).

In sum, field studies indicate that in the permanently resident Nuttall subspecies of the White-crowned Sparrow, song is produced circumannually, even during the molt and months characterized by minimum testis size. Many hatching-year birds develop adult songs by the fall, at which time they attempt to claim breeding territories. Male/male interaction accelerates song development in hatching-year birds and often results in sharing of similar song themes with neighbors.

#### ACKNOWLEDGMENTS

We thank James Cunningham, Kathy Golden, and Enid Leff for preparing the illustrations. Michael Cunningham, Enid Leff, Fernando Nottebohm, Peter Slater, Pepper Trail, and an anonymous reviewer read earlier

drafts of the manuscript and offered valuable suggestions for its improvement.

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