

A comparative approach to vocal learning: intraspecific variation in the learning process

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Abstract. Vocal learning in birds often results in geographically distinct 'dialects'. To examine whether genetic variation underlies intraspecific differences in vocal development, young male white-crowned sparrows from sedentary (*Zonotrichia leucophrys nuttalli*) and migratory (*Z. l. oriantha*) populations were reared in standardized conditions in the laboratory, and tutored throughout the first year of life with a changing roster of tutor songs. Male *nuttalli* acquired their tutor imitations at a later age, and over a broader range of ages, than did *oriantha* males. All males eventually crystallized a single song type, but male *oriantha* sang imitations of more tutor songs in plastic song, and persisted in plastic song twice as long as *nuttalli* males. *Nuttalli* imitations of tutor songs were fragmentary, but their imitations of specific syllables were more accurate than those of *oriantha*. These genetically based differences in vocal learning may be different strategies to achieve song matching with territory neighbours in migratory and sedentary populations. Young migratory *oriantha* face a shorter singing season during the early sensitive phase for song acquisition and greater uncertainty over where they will breed as yearlings relative to *nuttalli* males, who may occupy territories relatively closer to their birthplace, and may settle as early as their first autumn. Male *oriantha* acquire several song dialects when young, and then, through a process of selective attrition, retain the song that matches the local dialect where they settle to breed. In contrast, *nuttalli* may retain the ability to acquire an accurate song copy from a neighbour when they establish a territory.

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The task of disentangling genetic and environmental contributions to variation in behaviour is a challenging one. The pervasive effects of individual experience make it especially difficult to establish the nature and extent of genetic effects on the ontogeny of behaviour. As a consequence, there is a temptation to view genetic contributions to behavioural variation as minimally important, especially when the behaviour is learned. Learned, culturally transmitted bird songs are among the most individualistic of all types of behaviour with exceptionally high degrees of intraspecific variation. It is generally assumed that this variation is a reflection of differences in individual experiences, with genetic factors intruding only to the extent of underwriting general, species-wide rules that guide the overall process of vocal learning. In a study of the role of song in mate selection, for

example, Chilton et al. (1990) acknowledged that there could be subspecific differences in the mechanism of song learning but, 'in the absence of contradictory information, it seems simplest to assume that these basic biological features do not vary in this fashion' (page 226).

On the other hand King & West (1983) found robust subspecific differences in the development of song recognition in female brown-headed cowbirds, *Molothrus ater*. Compelling indications of genetic contributions to variation in song learning arise from the work of Kroodsma & Canady (1985) who demonstrated that subspecific differences in song repertoire sizes and patterns of song delivery in marsh wrens, *Cistothorus palustris*, persist in males brought into the laboratory in infancy and reared under identical conditions. Furthermore, these behavioural differences were correlated with some specific differences in the size of song system nuclei in the brain.

We have adopted a similar approach to Kroodsma & Canady to explore further into

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potential genetic contributions to variation in mechanisms of song acquisition and development. We have taken very young male songbirds from two populations and reared them in the laboratory to determine whether they interact similarly or differently with identical learning environments. As a subject we chose the white-crowned sparrow, *Zonotrichia leucophrys*, a species in which song development has been studied extensively, although not from the viewpoint of intraspecific variation in the learning process (Marler & Tamura 1964; Marler 1970; Baptista & Petrinovich 1984, 1986; Konishi 1985; Petrinovich 1985).

The short, 2-s song of the male white-crowned sparrow is a distinctive sequence of pure whistles, buzzes and trills, recognizable throughout the species' range. Each adult male typically has a single song type. White-crown song is marked by the existence of well-defined local dialects. Some are limited to small clusters of neighbouring males, and others encompass hundreds or thousands of individuals (Marler & Tamura 1962; Baptista 1975, 1977; Orejuela & Morton 1975; Baptista & King 1980; Baker & Thompson 1985).

Breeding habitats of the white-crowned sparrow range from the benign environment of coastal, fog-belt chaparral to the inclement conditions of the subalpine meadows of the High Sierras. Despite this climatic diversity, the degree of morphological variation throughout the range is low, and the five designated subspecies are distinguished primarily by subtle aspects of plumage and beak coloration (Blanchard 1941; Banks 1964). Such behavioural and ecological traits as food habits, breeding and flocking behaviour are generally similar. White-crowned sparrow populations do vary in one striking respect. Some of them, including the coastal *nutalli* subspecies, are year-round residents. Others, including the montaine *oriantha* subspecies, are strongly migratory, moving to southern California and Mexico in the non-breeding season.

We hypothesized that, despite the uniformity of this species in many aspects of morphology, ecology and behaviour, the neural and hormonal mechanisms underlying the process of learning to sing will have been exposed to different selection pressures, and so may have evolved differently in sedentary and migratory populations. For the migratory subspecies breeding in subalpine environments, we reasoned that the shorter breeding

season, the high degree of year-to-year variation in local breeding conditions (Morton 1978), and the uncertainty of prospects for establishing a breeding territory close to the natal site, all result in strong potential pressures impinging on the process of learning to sing that differ from those imposed on a sedentary population. If verified, the hypothesis offers promise of new insights into the degree of evolutionary lability of the physiological substrates of vocal plasticity. With this end in view we embarked on a comparative laboratory study of song acquisition and motor development in male white-crowned sparrows, some taken from coastal populations of the *nutalli* subspecies, and others taken from the montaine *oriantha* subspecies, in the Sierra Nevada, all reared and maintained under identical conditions in the laboratory.

METHODS

White-crowned Sparrow Song

White-crowned sparrow songs consist of series of notes organized into syllables, note complexes and phrases (Fig. 1). All white-crowned sparrow songs studied began with a whistle, followed usually by another whistle or a buzz. A buzz phrase consisted of either a single buzz or a short note followed by a buzz (a whistle-buzz; Baptista & King 1980). Syllables, often subdivided into complex and simple syllables, have usually been used by researchers to define different geographical 'dialects'.

Subjects

Our subjects were 26 male white-crowned sparrows (12 *Z. l. nutalli* and 14 *Z. l. oriantha*) collected in the wild as 3-9-day-old nestlings and hand-reared to independence at 3-4 weeks of age. We collected *nutalli* at the Bodega Marine Reserve, Sonoma County, California (123°E, 38°N, elevation 10m) between 25 and 28 May 1990 and *oriantha* at Tioga Pass, Mono County, California (119°E, 38°N, elevation ca 3000m) between 24 June and 2 July 1990. Sex was determined by laparotomy using Metofane as the anaesthetic. The birds were reared and tutored in a group before they were individually housed in sound isolation chambers when they first began

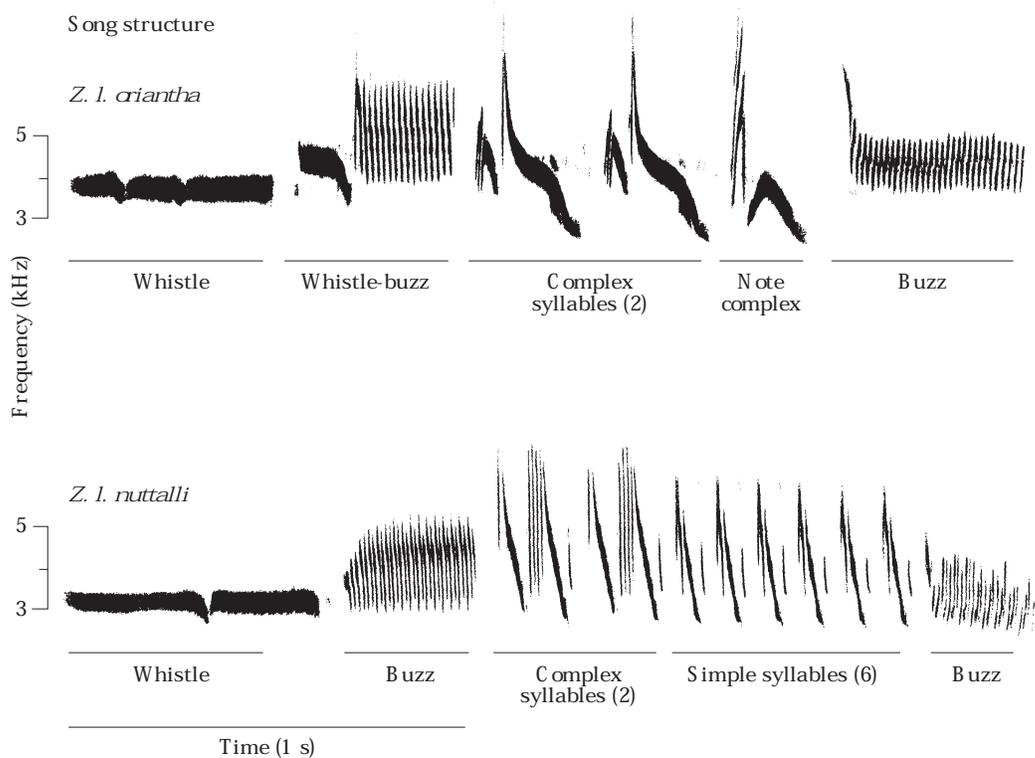


Figure 1. Examples of white-crowned sparrow song, with definitions of terms. A note was defined as a continuous tracing on an audiospectrogram, uninterrupted by silence of more than 3ms (about 1mm on a spectrogram produced with a 300-Hz analysing filter and 8-kHz bandwidth on a Kay Sonagraph). Syllables are a note or note cluster repeated in identical fashion. A note complex is an unrepeated note or series of notes. Notes and syllables are grouped into phrases: whistle, buzz or whistle-buzz, note complex, trills of complex or simple syllables, and terminal note (buzzes in the examples shown here).

subsong, at an average of 36 days old. Each chamber contained a light, fan for ventilation, loudspeaker (Radio Shack 10cm auto speaker), and microphone (Radio Shack Model PZM). Birds were kept on ambient photoperiod, controlled by digital time clocks that were changed once per week. The fan, controlled by the timer to turn off for 2h every morning during the tape-recording session, helped maintain temperature at 17°C. The cage within each chamber measured 48 × 30 × 26cm. Young birds were hand-reared with a modified Lanyon diet delivered from a 50-cc syringe. Older birds were fed dry seed and water ad libitum, along with greens, soaked seed and monkey chow, and a vitamin supplement. At the conclusion of the study, birds were given to colleagues holding the necessary permits for neurophysiological study.

Tutoring

Tape-recorded tutor songs were chosen from a library of 56 acoustically distinct geographical song dialects recorded from the two subspecies. By comparing the subjects' imitations to specific tutor models presented for short periods at known times, we could infer when memorization occurred ('pattern-type labelled tutoring'; Kroodsma 1978; Marler & Peters 1987; Hultsch 1993). Songs were assigned at random, without replacement, to 28 tutor blocks spanning the first year of life. In each block birds heard two song types (one *nuttalli*, one *oriantha*). One song type was repeated 80 times over 10min, followed by 10min of silence, and then 80 repetitions of the other type. The ordering of *nuttalli* and *oriantha* tutor types was randomized across blocks. Fifteen

10-day-long periods were used during first summer and early autumn, followed by four 20- or 30-day-long blocks in winter, and then nine 10-day-long periods extending into the birds' first spring (May). The *oriantha* were collected about 40 days after the *nuttalli*, and entered the experiment during tutor block 5. They heard blocks 5-28, followed by blocks 1-3. Tutoring thus extended throughout the first year of life, beginning the day after collection and continuing every day at approximately 0800 hours.

Sound Recording

Singing was recorded twice-monthly throughout the birds' first summer, autumn and winter, and at least weekly once plastic song began. Prior to the onset of plastic song in late winter, the birds were recorded for 60 or 90 min per day on Nakamichi cassette-recorders. Microphone outputs were amplified with Yamaha MLA7 8-channel amplifiers. Recordings were made in the morning beginning around 0800 hours, often during tutoring. Tapes were monitored later, and any subsong or plastic song was dubbed onto a monoaural edit tape for later spectrographic analysis.

Once plastic song began, the birds were recorded using a computer-controlled system that turned the tape-recorders on and off when they sang. Subsong was too quiet to trigger the control system accurately. Digital delay devices (Digitech RDS 4000 with 20-kHz bandwidth and 12-bit precision) delayed the signal fed to each tape deck for 1.9 s to allow the deck to come up to speed and to prevent truncation of the beginning of the song.

Song Analysis

Vocalizations were analysed by real-time sound spectrography (Hopkins et al. 1974). Tapes were played at one-half speed into a Princeton Applied Research real-time analyser which produced a continuous audiospectrographic trace recorded on 35-mm Kodak Linagraph film (1 cm δ). The film was compared visually to a library of tutor sonagrams prepared on the same equipment. We assigned a score to each day's recording for each bird as follows: 0 = quiet, no singing; 1 = subsong; 2 = as 1 with long whistles; 3 = presence of tutor song imitations (the onset of plastic song); 4 = syllable trills; 5 = complete songs, but note structure variable; 6 = crystallized song (songs sung with

little variation and emphasis on the frequency stability of the introductory whistles). We also counted the number of tutor songs imitated each day. Approximately 3250 h of tape recordings, and 7.7 km of real-time sonagram film were analysed in preparing this paper.

Identification of Tutors by Cross-correlation

To produce quantitative estimates of the resemblance between subjects' imitations and the tutors, and thereby identify when songs were learned, we used digital spectrogram cross-correlation (Clark et al. 1987; Nelson & Marler 1993). This technique takes two digital sound spectrograms and slides one past the other in small time steps. At each step, the level of energy is correlated in corresponding 'cells' (points in frequency-time space) of the two spectrograms. The maximal cross-correlation value was used to represent the similarity between two spectrograms. Two identical spectrograms (an autocorrelation) yield a value of 1.0.

Ten crystallized songs from each subject, sampled on 1 or 2 days, and in some cases plastic songs also, were digitized (25-kHz sampling rate, 12-bit precision) and stored as computer files using the SIGNAL sound analysis system (Engineering Design 1987). Each song was 'cut' into separate files each containing one song phrase: a whistle, buzz, syllable, or note complex (Fig. 1). We generated spectrograms using a 256-point discrete Fourier transform. Step size was defined as total spectrogram duration/200 and varied from 2.5 ms for syllables and note complexes and 30 ms for buzzes, to 625 ms for whistles. Energy below 1500 Hz and above 9000 Hz was excluded from the calculations. To eliminate differences in recording amplitude, the amplitude in each spectrogram was first normalized on a linear scale relative to the spectrogram's peak level.

Whistles were cross-correlated with the entire catalogue of whistles from the tutor songs (69 in all), buzzes with all tutor buzzes (86) and syllables or note complexes with all tutor syllables and note complexes (156). The analysis was done phrase-by-phrase rather than on complete songs because some songs were obvious 'hybrids' of two or more tutor songs, and the accuracy of the technique is diminished with long, multipartite signals. The mean cross-correlation ($N=10$) between each phrase and every relevant tutor phrase was

Table I. The age and duration in days of various phases of vocal production in the two subspecies of white-crowned sparrow reared under identical conditions in the laboratory

	<i>nutalli</i>			<i>oriantha</i>			<i>P</i>
	<i>N</i>	Median	Range	<i>N</i>	Median	Range	
Age of subsong onset	9	35	34-38	13	38	38-40	NS
Duration of subsong	9	231	71-237	13	215	190-245	NS
% Days singing during subsong	9	58%	39-61	10	85%	60-90	*
Storage interval	11	201	177-215	14	201	176-250	NS
Age of plastic song onset	12	265	110-270	14	259	229-285	NS
Duration of plastic song	12	53	39-67	12	90	68-112	*
Age at song crystallization	12	323	309-328	12	340	336-351	**

* $P < 0.05$ ** $P < 0.025$

calculated. We then tabulated the five largest cross-correlations (i.e. the five most similar tutor phrases) for each phrase in every bird's song, and used them as a basis for identifying tutors (see below). Acquisition age was taken as the bird's age at the mid-point of the tutor block with the highest cross-correlation score.

Visual Identification

In a few cases the computer identifications were ambiguous. In six of these, sonagrams of songs or partial songs were independently compared with the entire set of tutor songs by a panel of three judges. For five additional songs the judges' identifications were compared with those made by the spectrogram cross-correlation method. Sonograms were prepared on a Kay Elemetrics Model 7800 digital sonograph using a 300-Hz analysing filter and bandwidth of 8kHz.

Song Stereotypy

To provide a measure of song stability or stereotypy, spectrogram cross-correlations were also calculated within each bird. Ten syllables in the crystallized song of each subject were cross-correlated with each other and means were calculated (45 correlations possible among 10 objects). This was also done with 10 whistles from each bird. A high mean within-bird cross-correlation will result when song production is stable.

Statistical Analyses

We used non-parametric tests for all analyses because most distributions were non-normal.

Except where indicated, the sample size in every test is the number of individual birds involved in the comparison. In cases where two or more measurements on the relevant variable were made for an individual, we calculated the mean, and used that value for the individual in hypothesis testing. All analyses were performed using Systat (Wilkinson 1989). Probabilities are two-tailed.

RESULTS

Production of Subsong, Plastic Song and Crystallized Song

Subsong began at a similar age, median 36 days, in the two populations, and lasted for a similar time, median 227 days, before plastic song began (Table I). The occurrence of subsong throughout the first summer, autumn and winter was quite variable. In both populations, however, there was a tendency for subsong to be more frequent in the first 3 months, followed by a lull in winter (November and December), with another increase in frequency before it merged into plastic song in January or February of the next year. Superimposed on this overall trend was a subspecific difference in the incidence of subsong. Male *oriantha* gave subsong during 85% of our twice-monthly samplings, while a significantly lower percentage, 58%, of *nutalli* gave subsong (Mann-Whitney $U = 19$, $N = 19$, $P = 0.03$, Table I).

The storage interval, defined as the time between when songs were memorized from tutor models (see below) and when imitations of those models first appeared in plastic song, was about

200 days in both populations (Mann-Whitney $U=65.0$, $N=25$, $P=0.51$; Table I). In *nuttalli*, subsong began on average about 4 weeks before tutor songs were committed to memory, while the onset of subsong coincided with acquisition in *oriantha*. In general, the timing of early stages of vocal development was strikingly similar in the two subspecies. Differences appeared in later stages, however.

Plastic Song

The age of onset of plastic song was similar in the two subspecies, beginning at about 9 months after hatching (approximately 260 days; Table I). One *nuttalli* began plastic song in September at an age of 110 days, and sang plastic song throughout the winter. Five other birds (one *nuttalli*, four *oriantha*) sang plastic song on 1 or 2 days in their first autumn, but all then reverted to subsong for at least another 100 days before beginning consistent plastic song that progressed to crystallization. These isolated instances of plastic song were set aside in recording the time of onset of plastic song for these five birds.

Plastic song lasted significantly longer in *oriantha* ($U=25$, $N=24$, $P<0.01$), with the result that they crystallized their song significantly later ($U=9$, $N=24$, $P<0.01$; Table I). The plastic song period was almost twice as long as in birds from the non-migratory population. Two *oriantha* died in the plastic song period so the sample size for some analyses is reduced. The age of crystallization is actually an underestimate for *oriantha* because four males had not quite fully crystallized their songs when the experiment was terminated in June 1991. We estimate that it would have taken another 10–14 days for these birds to crystallize their songs.

Song Acquisition

Comparisons of plastic and crystallized songs of tutors and subjects revealed that all but one of the 26 males developed identifiable imitation of tutor songs. One *nuttalli* developed a simple song, consisting of a whistle followed by two buzzes, that could not be confidently matched to any tutor type. This was treated as an improvised song. The 25 remaining birds each produced one to three song types with components derived from up to three different tutor song types. Several of these

birds developed invented phrases along with their imitated material.

In identifying the tutor models for each bird's imitations, we placed the greatest emphasis on the structure of syllables and note complexes, as previous students of white-crowned sparrow song development have done (Marler & Tamura 1962; Baptista 1975). Whistles and buzzes for the most part were not distinctive enough to use them as a sole basis for unique identification of tutors. In most cases, however, visual identification of whistles and buzzes in a particular song were compatible with computer-based identification of the associated syllables and note complexes.

Fifteen of the 41 songs or partial songs produced were each assigned to one tutor as what we have termed 'consensus' computer identifications. In these songs, all syllables and note complexes in the song had the highest to third highest cross-correlations to one tutor, and no single other tutor had such high similarities to the subject's imitation for more than one syllable or note complex (Fig. 2). In these 'consensus' identifications, visual assignments of the whistle and buzz phrases were compatible with those made by computer (e.g. if the tutor had a low-pitched whistle followed by a long buzz, then so did the imitation). Since in most cases the three highest cross-correlations for a phrase were very similar (within 5% of one another), it was simplest to assign these imitations to a single tutor, rather than to different tutors. Seven additional one- or two-phrase-long songs were 'unanimously' assigned to single tutors by spectrogram cross-correlations.

Twelve of the 41 songs were acquired from two or more tutor models ('hybrid' songs) using cross-correlations as the basis for identification. In these cases, different syllable or note complex phrases had their highest similarities to different tutor models: no single 'consensus' model was apparent (Fig. 2). Finally, seven songs, five from early plastic song and two crystallized songs, were assigned to tutors not by cross-correlation but by the panel of judges. For these songs, the spectrogram cross-correlations were uniformly low and did not uniquely identify tutors. In summary, 83% of the 41 songs or partial song types produced were assigned to tutor models using spectrogram cross-correlation coefficients to quantify similarity. The remainder were assigned by visual comparison.

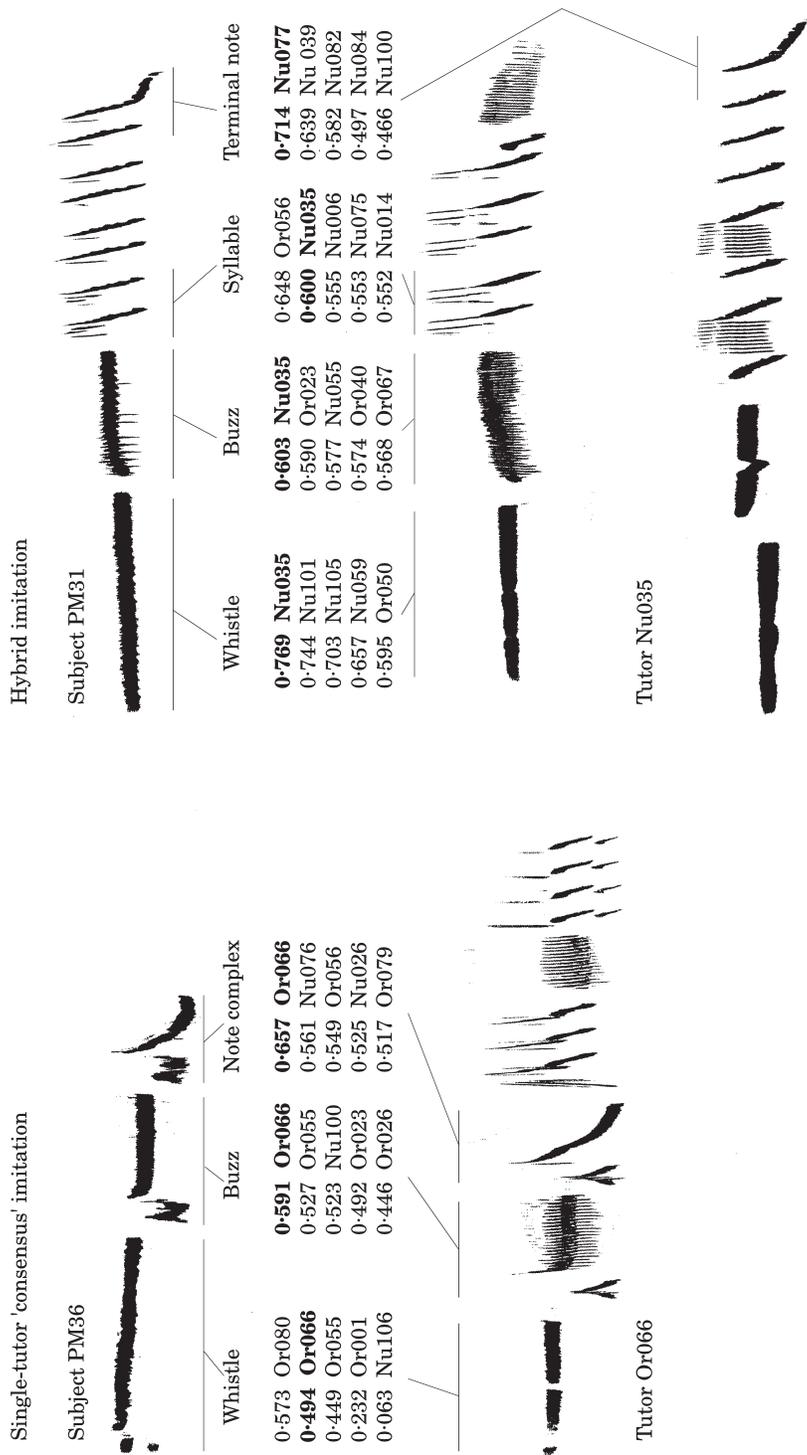


Figure 2 Examples of imitations produced by two subjects. PM36's song is a partial 'consensus' imitation of one tutor, Or066. The spectrogram cross-correlation coefficients between the imitated phrases and tutor phrases are shown. This is a consensus imitation, since Or066 (shown in bold), was the first or second most similar tutor for all three phrases. PM31's song is a hybrid song derived from copying tutor Nu035's whistle, buzz and complex syllable, and the terminal note from tutor Nu077.

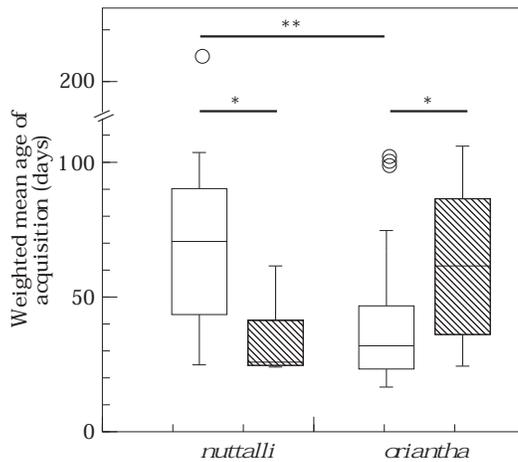


Figure 3. Box plots of the weighted mean age of acquisition of crystallized (\square) and non-crystallized (\boxtimes) song types. The lower and upper edges of the boxes represent the first and third quartiles, the median bisects each box. Outliers are individual circles. Bold horizontal lines identify statistically significant differences. (* $P < 0.05$; ** $P < 0.025$)

Sensitive Period for Acquisition

All subjects crystallized a single song type. In addition, some birds sang imitations that were present only in plastic song, which we refer to as 'non-crystallized' types. We distinguish between these two classes of song in much of what follows. We expressed age-related variation in song acquisition in two ways. The weighted mean age of acquisition was calculated as the sum of the products between acquisition age and number of phrases acquired at that age, divided by the total number of phrases acquired. For example, if a bird acquired three phrases at 30 days and one at 70, his weighted mean age of acquisition was $((3 \times 30) + 70) / 4 = 40$ days. On this measure, *nuttalli* males memorized their crystallized songs significantly later (median = 71 days) than did *oriantha* males (median = 31 days; $U = 121.5$, $N = 25$, $P = 0.02$; Fig. 3). In *nuttalli*, the weighted mean age of acquisition of non-crystallized types were significantly earlier than for their crystallized types ($U = 47.5$, $N = 16$, $P = 0.02$; Fig. 3). In *oriantha*, the opposite relationship held ($U = 32.5$, $N = 23$, $P = 0.05$; Fig. 3).

The weighted mean age of acquisition has the virtue of not pooling acquisition dates within males and thus inflating the sample size. This

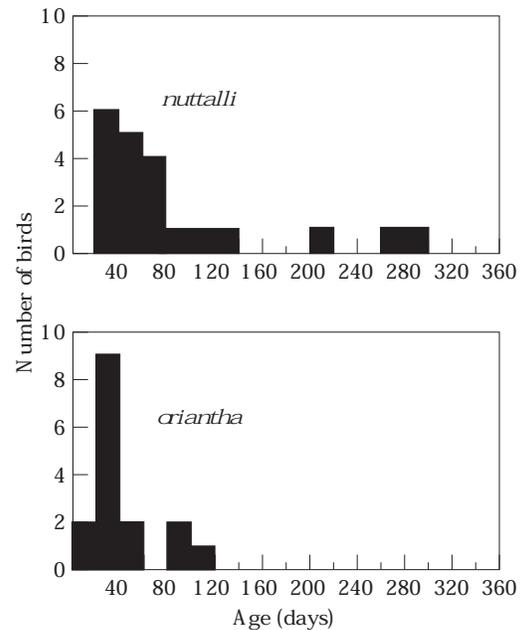


Figure 4. Ages when one or more phrases incorporated into crystallized song were acquired.

procedure, however, obscures the real data, namely when individual song phrases were actually acquired. Figure 4 shows how many birds acquired one or more phrases as a function of age. The number of phrases acquired at any given age is not included here. *Nuttalli* males learned the material incorporated into their crystallized songs significantly later (*nuttalli* median = 52 days, *oriantha* median = 33 days; $U = 237$, $N = 37$, $P = 0.03$), and over a significantly broader range of ages (Levene's test: Mann-Whitney $U = 249$, $N = 37$, $P = 0.01$). Two *oriantha* males learned song phrases between the ages of 11 and 21 days, while six *nuttalli* learned between 20 and 30 days. Birds were tape-tutored an average of 28 days as nestlings. There was no evidence of learning either then, in the laboratory, or in the wild prior to collection.

In summary, the timing of song acquisition in the sedentary (*nuttalli*) and migratory (*oriantha*) populations differed significantly in a number of respects. The sedentary birds acquired songs later than the migratory birds, and over a greater range of ages. There were also differences in the time of acquisition of crystallized song themes, on the one hand, and of overproduced and discarded songs

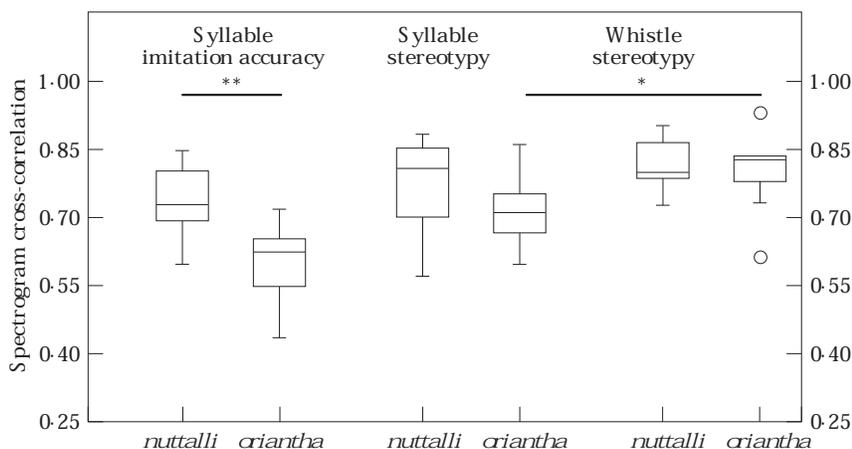


Figure 5. Box plots showing variation in syllable imitation accuracy, and stereotypy of production of syllables and whistles. Imitation accuracy is the highest mean spectrogram cross-correlation between a subject's syllable and the imitated tutor's syllable. Stereotypy is the average cross-correlation of all pair-wise comparisons between syllables (or whistles) sampled from 10 songs by each subject. Boxes defined as in Fig. 3 (* $P < 0.05$, ** $P < 0.025$)

(i.e. non-crystallized songs), on the other. In the migratory birds, with their compressed sensitive period, crystallized songs were acquired earlier than those that were produced in plastic song and then discarded. The resident birds, with their extended sensitive period, acquired their crystallized songs later than their non-crystallized songs.

Imitation Accuracy

In addition to providing the basis of tutor identification, the spectrogram cross-correlation coefficients were also used as a quantitative index of how faithful the imitations were to specific tutor songs. We took the maximal cross-correlation coefficient for each syllable and note complex in a bird's crystallized song and calculated the average per bird. This procedure was used for all except the two birds whose tutors were identified by the panel of judges; for them we took the coefficient(s) associated with the tutor the judges identified. Only syllables and note complexes were used because they provided the most reliable information about tutor identity. The data show the *nuttalli* males imitated their tutors' syllables significantly more accurately than did *oriantha* males ($U = 117$, $P < 0.01$; Fig. 5).

Song Stereotypy

Spectrogram cross-correlations also provided a measure of performance stereotypy in the

subjects' crystallized song production. We calculated all possible pair-wise cross-correlations among the 10 whistles ($N = 45$ comparisons per bird) and 10 syllables sampled for each bird. Consistent reproduction from song to song would be reflected in a high mean within-bird cross-correlation. There were no differences between the two subspecies in the stereotypy of whistle or syllable production (Fig. 5). Therefore, the difference in syllable imitation accuracy is not a consequence of more variable syllable production in *oriantha*, at least in crystallized song. It is possible that plastic song production was more variable in *oriantha*, because imitations were more likely to be modified by improvisation than in *nuttalli*, but we were unable to address this question quantitatively. Within subspecies, *nuttalli* whistles and syllables were equally stereotyped (Wilcoxon matched-pairs signed-ranks test: $z = 1.07$, $P = 0.29$); but *oriantha* performed their whistles more consistently than their syllables ($z = 1.99$, $P = 0.05$; Fig. 5).

The within-bird cross-correlation values also provided a benchmark against which the imitation accuracy values, which were calculated between tutor and subject, were compared. A perfect spectrogram cross-correlation between two signals of 1.0 will rarely occur in practice because of subtle changes in amplitude and frequency modulation that vary from moment to moment. Some birds approached this value: seven *nuttalli* had

cross-correlations of 0.95 or greater between two or more of their own syllables, while only two *oriantha* did so. The median syllable stereotypy value of 0.82 for *nutalli* did not differ significantly from their median syllable imitation value of 0.74 ($U=79$, $N=11$ birds, $P=0.22$; Fig. 5). This indicates that their accuracy in imitating syllables from another source was as high as their precision in reproducing syllables. In contrast, *oriantha*, reproduced their syllables with greater precision (median=0.72) than they imitated them (median imitation value=0.64; $U=95$, $P<0.01$).

Selective Acquisition

Since all birds were presented with equal numbers of both subspecies' songs, we were able to examine the data for evidence of learning preferences. Neither the resident nor the migratory birds showed a preference for acquiring tutor models from one subspecies or the other. Seven of 11 *nutalli* acquired a higher percentage of phrases from *nutalli* tutors than were present in the complete set of tutor songs (Wilcoxon matched-pairs signed-ranks test; $z=-0.98$, $P=0.33$), while four of 14 *oriantha* males favoured *oriantha* tutors ($z=-1.73$, $P=0.08$).

Song Repertoire Size

In addition to each male's single crystallized song theme, five of 12 *nutalli* and nine of 14 *oriantha* males sang partial or complete imitations of tutor songs in plastic song that did not survive into crystallized song ('non-crystallized' song types). One additional *oriantha* male sang an invented non-crystallized type, which could not be assigned to a specific tutor.

We distinguished two aspects of plastic song repertoire size: one describes the number of distinct song patterns produced in plastic song, and the other reflects the number of tutors from whom they were acquired. *Oriantha* males produced significantly more distinct song patterns (song types) than did *nutalli* males (Fig. 6). Seventy-one per cent of *oriantha* males and only 25% of *nutalli* males (three of 12) sang two or more imitated song types in plastic song ($U=43.5$, $N=26$, $P=0.02$). A song type was considered distinct if it differed from other songs in at least one phrase, and was produced for at least 2 weeks. Two other *nutalli* males produced single-phrase

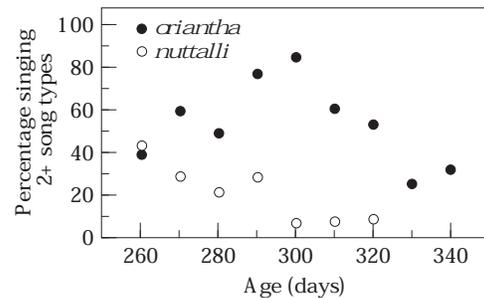


Figure 6. Percentage of birds that sang two or more song types within 10-day-long intervals in plastic song. One *nutalli* and two *oriantha* sang two song types when the experiment was terminated, and so were not fully crystallized.

non-crystallized imitations, but on only 1 day, early in plastic song.

In addition to the difference in the number of plastic song types produced per male there was a difference in how the song types were constructed. The crystallized song types of *nutalli* were significantly more likely to be 'hybrids' created from two or more tutor songs than were *oriantha* crystallized types ($U=124$, $N=25$, $P<0.01$). As noted above, non-crystallized *nutalli* imitations were more fragmentary than their crystallized types. In *oriantha*, crystallized and non-crystallized types did not differ either in the number of phrases imitated (median=3 phrases in each type, $U=74$, $N=23$, $P=0.47$), or in the number of tutors imitated in each type (median=1 tutor in each type, $U=64$, $N=23$, $P=0.91$). In addition to this imitated material, one male of each subspecies improvised or invented one phrase of crystallized song, and one male of each subspecies included two improvised or invented phrases in crystallized song. In summary, *oriantha* tended to acquire more complete imitations from a few tutors which persisted in plastic song as two or more discrete types for several weeks; *nutalli* tended to incorporate partial imitations of several tutors into their songs, some of which were quickly discarded.

DISCUSSION

In this study we asked whether song learning is a highly conservative trait, represented in the same fashion in all species members, or whether there is significant variation within a species in the

mechanisms underlying the process of learning to sing. We anticipated that the answer would throw new light, both on the relative degree of evolutionary plasticity of the physiological underpinnings of the vocal learning process, and on the selective forces that impinge on mechanisms of song development.

Timing of Song Production

A comparison of the patterns of song production in the two subspecies has revealed several aspects in common. Both develop crystallized repertoires consisting of a single, learned song type. There is no difference between the two populations in the interval for which learned songs are stored before rehearsal begins, when subsong begins, how long subsong lasts, nor in the age of plastic song onset. Some striking differences do emerge later, as noted below.

Timing of Song Acquisition

White-crowned sparrows rear their young on an insectivorous diet, and perhaps the greatest contrast between the two habitats under study is the time when insects are available, thus determining the duration of the potential breeding season. Mountain white-crowned sparrows breed in sub-alpine meadows while Nuttall's white-crowned sparrows inhabit the benign coastal chaparral. In the montane environment this period is strongly curtailed by the seasonal temperature cycle. Coastal *nuttalli* frequently rear two, and sometimes three broods in a single season (Blanchard 1941; Mewaldt & King 1977), whereas the montane *oriantha* rear one and only rarely two broods (Morton et al. 1972). Correspondingly, males of the two subspecies differ in the timing of song acquisition. This contrast in the timing of song acquisition, displayed under standardized conditions in the laboratory, must reflect genetic differences between the populations. Using sequential tape-tutoring as an experimental paradigm, we have shown that the readiness of *oriantha* to acquire song peaks at the remarkably early age of 30-40 days, more than a month earlier than in *nuttalli* who may sporadically acquire song when 9 months of age or more (Fig. 4). This contrast in the time of song acquisition makes sense in light of the behavioural differences displayed by these two populations during the

annual cycle. Beginning at about 2 months of age, varying with the timing and severity of the alpine weather in late summer and autumn, *oriantha* begin to migrate south to warmer climates (Morton 1992); *nuttalli*, on the other hand, remain indefinitely in the general neighbourhood of the birthplace, and are under no such compulsion to learn quickly or to terminate the sensitive period for song acquisition at an early date. Also, adult *nuttalli* males have a longer singing season than *oriantha* males, so that tutors are available for a longer time, making it possible for song acquisition to occur later in the season than in *oriantha*. Indeed, DeWolfe et al. (1989) have shown that *nuttalli* may establish territories and sing in their first autumn, a time when *oriantha* are migrating south.

This difference in the timing of song acquisition in different populations appears to be an adaptation to the different climatic conditions under which breeding takes place in the two subspecies, and is maintained endogenously under standardized laboratory conditions. In natural circumstances, the pattern of song acquisition will vary more, both from year to year and from individual to individual within a given year. Our laboratory experiments were not designed to permit precise extrapolation to the timing of song learning in the field. What they do show is that resident and migratory populations approach their natural learning environments with a contrasting set of genetically based predispositions to acquire song at different stages of development.

Variation in Imitation Accuracy

The subspecies differed in several aspects of the accuracy with which tutor models were imitated. The match between syllables and their models was less precise in *oriantha* than in *nuttalli* males. The results of within-bird cross-correlation analyses show that the contrast is not a result of less precise song control in *oriantha*. Individuals of both subspecies reproduce their own song type with an equal degree of precision.

Another aspect of the accuracy of imitations is their completeness. The two subspecies also differed in this respect. *Oriantha* imitations were more complete renditions of their models and persisted for several weeks before overproduced songs were lost. In contrast, *nuttalli* songs were more often incomplete renditions, either

Table II. Natal dispersal distances in white-crowned sparrows

		N	Median (m)	Range (m)
<i>Z. l. oriantha</i>	(Morton 1992)	25*	755	150-3430
<i>Z. l. nuttalli</i>	(Blanchard 1941)	4	—	183-480
<i>Z. l. nuttalli</i>	(Blanchard 1941)†	8	—	108-433
<i>Z. l. nuttalli</i>	(Petrinovich & Patterson 1982)	55	110	0-586
<i>Z. l. nuttalli</i>	(Baker & Mewaldt 1978)†	198*	300	0-2550

Note that estimates of dispersal distances are affected by many factors, including sample size and size of the sampling area. The estimates for *nuttalli* were derived from small samples, urban study areas, or birds first encountered as fledglings (see Kroodsma et al. 1984 for a critique).

*Males only. Other studies include males and females.

†Birds were first captured after fledging, so hatch sites were not known. In the other studies nestlings were banded.

fragmented, or combining phrases from more than one model and also incorporating inventions. The few *nuttalli* that did overproduce sang fragments that were quickly discarded.

There is perhaps a correlation here with the longer period of plastic song in *oriantha* males, which may allow them to achieve more complete plastic song renditions than is possible in *nuttalli*. Also, *nuttalli* males retain their ability to acquire new songs until a later age than *oriantha* males, and those songs that *nuttalli* males crystallize tend to be acquired later in the sensitive period than those that are discarded from plastic song. It is not the case that the ability to memorize whole songs improves as the male grows older, and as the long *nuttalli* sensitive period progresses. In both subspecies birds tended to learn most material from the heart of the sensitive period.

The data suggest that the two subspecies are adapted to different learning strategies, one memorizing fragments of several tutor types well, the other memorizing larger 'chunks', from fewer tutors, but doing so more superficially. Our results agree with those on other species, reviewed by Ewert & Kroodsma (1994), in which males in resident populations are more likely to share songs with neighbours than are those from migratory populations.

Different Song Matching Strategies

The phenomenon of 'matched countersinging', in which neighbouring males exchange similar songs is widespread in songbirds. Marler (1960) suggested that this might be a mechanism by which local song dialects come about, and

other authors have demonstrated a tendency for territorial males to use similar song types during countersinging in several species (e.g. Baptista 1975; Falls et al. 1982; Weary et al. 1990; Stoddard et al. 1992).

Until now it has been assumed that for a male to match songs with a territory rival, he must either: (1) acquire his song(s) and then settle to breed nearby, or (2) disperse somewhere and then acquire song(s). In a separate study we have shown that a different process is at work. Post-dispersal song matching during the plastic song phase is achieved, not by the acquisition of new songs to match those of rivals, but rather by a selective attrition process, in which yearling males overproduce, and then selectively retain the one song type in their plastic song repertoire that provides the closest match with the song types of their rivals (Nelson & Marler 1994). There is evidence that this occurs in several sparrows (Marler & Peters 1982; De Wolfe et al. 1989; Nelson 1992a, b).

Viewed in this light, the two-fold increase in song overproduction in migratory *oriantha* relative to the sedentary *nuttalli* makes sense (Fig. 6). There appears to be an order of magnitude difference between the two subspecies in breeding dispersal distance, with the Sierra birds moving much greater distances (Table II). This contrast in dispersal distance is attributable to several factors, including the heterogeneous structure of montane habitats, year-to-year variation in snow cover conditions at different elevations in the Sierras, and perhaps most fundamentally, to the migratory habits of *oriantha*. All of these factors introduce an element of uncertainty about the

place where yearling *oriantha* males will set up their first territories: they may settle several dialects away from their birthplace, especially if we take account of the smaller areas encompassed by each dialect in montane environments (DeWolfe & DeWolfe 1962; Banks 1964; Baker 1975; Orejuela & Morton 1975). In contrast, *nutalli* males, with their short dispersal distances and large dialect areas, will often be able to settle within the natal dialect or an adjacent one. Given that the ability to acquire songs is limited to early in life (Figs 3 and 4), then an *oriantha* male must learn his repertoire in his first summer and autumn if he is to match song types with his territorial rivals.

We can thus begin to discern selection pressures that would favour a greater variety of plastic songs in *oriantha*, increasing the probability that one of the overproduced song types will match those of rivals in the settlement area. Young *oriantha* males are known to wander widely at the time when songs are being memorized (Morton et al. 1991; Morton 1992) and are likely to learn from several tutors. Baptista & Morton (1988) reared wild-tutored fledglings in the laboratory, and found that two of four males overproduced. Baptista has also described several cases of overproduction in wild *oriantha*, and has suggested that song matching in this subspecies is achieved by a process of selective attrition (Baptista & King 1980; Baptista & Morton 1982, 1988).

Another contrast in the pattern of motor development that may function to achieve song matching with territorial rivals is the greater precision of syllable imitations in *nutalli* than in *oriantha* males. If this is true in nature, it will make for a greater degree of within-dialect song variation in *oriantha*, which may also increase a yearling male's prospects of achieving at least an approximate match with the song patterns in a new area.

We thus argue that the greater degree of overproduction in the migratory birds facilitates song matching with rivals at a site remote from their birthplace. The sedentary habit of *nutalli*, combined with the more homogeneous nature of the chaparral habitat, and the larger area occupied by a given dialect, favours accurate memorization of a smaller repertoire, as well as the ability to acquire a song when a territory opening occurs.

In conclusion, we have demonstrated that genetic variation underlies variation in several

aspects of the development of vocal behaviour in the white-crowned sparrow. This is significant, because with a learned behaviour, such as oscine birdsong, there is a tendency to dismiss the contribution of genetic variation to developmental plasticity. While it is clear that interspecific differences in singing behaviour are based on genetic differences, these results provide only the second case in which intraspecific variation in song learning by males is genetically based (Kroodsma & Canady 1985). Since song functions in inter-sexual communication, it will also be necessary to study the development of female preferences (King & West 1983, 1987). If early experience of song proves to influence female mate choice, and this is a contentious issue (e.g. Chilton et al. 1990), it will then be necessary to study the dynamics of female song learning, and to explore the likelihood that in females, as we have shown in males, there may be adaptive differences in females of the two populations in the ways in which their song preferences are acquired.

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