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# Ecological influences on vocal development in the white-crowned sparrow

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Gambel's white-crowned sparrow, *Zonotrichia leucophrys gambelii*, is a long-distance migrant that, in contrast to other subspecies of white-crowned sparrow, does not form vocal dialects. I studied the process of vocal development in the field and laboratory to determine how it differed from the process in three other subspecies previously studied. Four common song types existed in a random spatial pattern in my 2.6-km$^2$ study area. Of 106 males studied in 2 years, all arrived at the beginning of the breeding season singing their adult repertoire and no male changed his song during the season. In the laboratory, hand-reared males overproduced as much as other migratory subspecies of white-crowned sparrow. They learned their songs during the shortest sensitive phase of any white-crowned sparrow yet studied. In contrast to other subspecies that form vocal dialects, male *gambelii* chose their final adult song at random from their overproduced repertoire. I suggest the absence of vocal dialects in Gambel's sparrow results from the short, delayed breeding season on their sub-Arctic breeding grounds. The short breeding season has favoured a narrow sensitive phase in hatching-year birds, and prevents the extended vocal interactions among adults that lead to vocal dialects in populations breeding at temperate latitudes.

Songbird males typically learn their songs by imitating the songs of adult males. A common consequence of song learning is the formation of vocal dialects in which neighbouring males sing similar songs that differ from those of males at more distant locations (Marler & Tamura 1962; Mundinger 1982). Most experimental investigations of the song learning process have focused on taxa that form vocal dialects. Vocal dialects result when males learn their song(s) in the same area in which they breed (Lemon 1975; Kroodsma 1982). In species in which natal dispersal distances are large relative to the size of dialect areas, males have usually been assumed to retain the ability to imitate adult models, their breeding territory neighbours, at least into their first breeding season (Thompson 1970; Cunningham et al. 1987).

Recent studies, however, have suggested that vocal dialects may result even if the ability to imitate is restricted to the first few months of life and males disperse long distances. A phase of 'overproduction' in early spring in which the full variety of songs memorized previously is produced, is followed by a stage of selective attrition in which males retain the local song dialect by countersinging matching songs with their territory neighbours, and discard the extra, nonmatching songs they memorized earlier. This process, termed 'action-based learning' (Marler 1990) or 'selective attrition' (Marler & Peters 1982a), has been documented in field and laboratory studies (DeWolfe et al. 1989; Nelson 1992; Nelson & Marler 1994).

Vocal dialects are not universally present in songbirds, however, even in species in which learning is known to play a role in vocal development. Dispersal between the site of song imitation and the site of breeding, and/or improvisation of songs, rather than imitation, could hinder the development of local song dialects. Improvisation is a conspicuous component of song development in red-winged blackbirds, *Agelaius phoeniceus* (Marler et al. 1972), sedge wrens, *Cistothorus platensis*, (Kroodsma & Verner 1978), and grey catbirds, *Dumetella carolinensis* (Kroodsma et al. 1997).

Field studies on the white-crowned sparrow, *Zonotrichia leucophrys*, have revealed subspecific variation in the tendency to form vocal dialects. Males of this species sing a single song type in their adult repertoire which they retain for their entire lives (Petrinovich 1988; Nelson 1998). Males of the sedentary *Z. l. nuttalli* and migratory *Z. l. oriantha* and *Z. l. pugetensis* races form vocal dialects

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varying greatly in size (Marler & Tamura 1962; Baptista 1975, 1977; Orejuela & Morton 1975; Baptista & King 1980; Chilton & Lein 1996). In contrast to these three subspecies, males of the Arctic and sub-Arctic *gambelii* subspecies do not form distinct vocal dialects (DeWolfe et al. 1974; Austen & Handford 1991; this study). *Zonotrichia l. gambelii* is a long-distance migrant that breeds near the tree line west of Hudson's Bay to Alaska. Males do not return to their northern breeding grounds after migration until early to late May (Blanchard & Erickson 1949; Cortopassi & Mewaldt 1965; Morton 1976; Wingfield & Farner 1978). The breeding season in the sub-Arctic is very short compared to the breeding season enjoyed by *nuttalli* and *pugetensis*, and is even shorter than in the montane *oriantha* (Morton 1976). I suggest later that this compression of the breeding schedule, especially in the initial stages following arrival on the breeding grounds, has influenced the evolution of the song learning process in *gambelii*.

The goal of the present study was to combine field observations with laboratory study to determine how the song learning process in *gambelii* differs from the subspecies of white-crowned sparrow in which vocal dialects are prominent. Previous work on *nuttalli, oriantha* and *pugetensis* employing hand-reared males raised under standardized conditions in the laboratory discovered correlations between aspects of the natural history of each subspecies and variation in the song learning process (Nelson et al. 1995, 1996a). Males typically imitate conspecific model songs accurately, although some variation in imitation accuracy exists (Marler 1970; Petrinovich 1985; Petrinovich & Baptista 1987; Nelson et al. 1995, 1996a, b). Males of the migratory forms *oriantha* and *pugetensis* overproduce songs significantly more than the sedentary *nuttalli* subspecies. This was interpreted as an adaptation that increases a migratory male's chances of being able to countersing matching songs with territory neighbours in the face of uncertainty over which dialect would hold a territory vacancy the next spring. These results formed the basis for the predictions tested in the present study on *gambelii*.

In light of these findings, I expected that the random spatial patterning of song types in *gambelii* would be maintained if: (1) males overproduce songs learned from tutors in an early sensitive phase, but then, in contrast to other subspecies, select a song at random for retention as the crystallized song; (2) males do not overproduce; or (3) males improvise their songs, rather than imitate tutors. Predictions 1 and 2 are mutually exclusive, but prediction 3 is not exclusive of the others. The findings are integrated with data on the subspecies' natural history to build an evolutionary scenario of variation in the song learning process (Kroodsma 1996).

## FIELD OBSERVATIONS

### Methods

#### Study sites

*Wintering birds.* I recorded songs from male *gambelii* wintering in Davis, California during 13–17 December 1997 and 22–27 March 1998. Birds in their first winter possess brown crowns that can be easily distinguished from the black and white crowns worn by adults. Birds were not banded, but I assumed that individuals recorded at different locations and times were different birds.

*Breeding birds.* I studied singing behaviour on the breeding grounds from 1995 to 1997 at Churchill, Manitoba (58°45′N, 94°10′W). I chose Churchill because previous studies indicated a large *gambelii* population existed there (Rees 1973; Austen & Hanford 1991), and because its relative proximity to my laboratory made transporting nestlings easier. Churchill is on the northwestern edge of a zone of intergradation between the *gambelii* and *leucophrys* subspecies of white-crowned sparrow (Banks 1964). These subspecies are most readily distinguished by the presence (*leucophrys*) or absence (*gambelii*) of black in the lores, the area between the eye and base of the beak. The amount of black can vary among individuals in the intergradation zone. I labelled a bird with any amount of black in the lores a '*leucophrys*', even though some of the individuals at Churchill were probably of mixed parentage. A few males each year were not seen clearly, and were not identified to subspecies level.

My main study area was approximately 2.6 × 1 km centred along Twin Lakes road immediately south of the Churchill Northern Studies Centre. From 1 to 15 June 1995 and 17 May through to 4 July 1996, I tape-recorded 45 and 61 males, respectively within this area. In 1995, I recorded 13 additional males at different sites within a 20-km radius of my main area. I used a Sony TC-D10 digital cassette tape recorder with a Sennheiser MKH70 'shotgun' microphone. Gabe McNett recorded 27 males between 14 June and 25 July 1997. He used a Sony TCD-5M tape recorder and Sennheiser ME67 shotgun microphone. I made audiospectrograms using Signal (Engineering Design 1996) or a Kay DSP sonagraph.

*Census.* In 1996, I walked along Twin Lakes Road south of the Churchill Northern Studies Centre at least once daily between 0500 and 1000 hours. I also walked over the tundra immediately west of the road. Every day I counted the number of males singing in different locations and plotted their position on a map. I attempted to record every male on the first day that I found him. I tried to record, or listen to, 25–50 songs from each male when first found. I captured and colour-banded six males in 1995 and 14 males in 1996 using a mist net or seed-baited 'Potter' traps. I found 26 nests in 1996 and estimated the date of clutch initiation by subtracting the number of eggs plus 12 days (average incubation period) from the date of hatching.

#### Song sharing

I mapped the position of each singing male on a tracing of an aerial photograph. I used the Mantel test (Schnell et al. 1985) to test hypotheses concerning the degree of song sharing among males. The Mantel test correlates two matrices; in this case, a matrix of between-bird acoustic dissimilarity measures and a hypothesis matrix that represents the comparison being made between the dissimilarity measures of the song pairs. To construct the acoustic dissimilarity matrix, I measured 41 variables on each song as described in Nelson (1998) using the Signal software (Engineering Design 1996). I then calculated the first five principal components derived from the original set of variables, and calculated the acoustic dissimilarity as the Euclidean distance between pairs of songs in the five-dimensional principal component space. Five principal components summarized 68 and 60% of the variation in the original 41 variables in the 1995 and 1996 data sets, respectively.

To investigate whether males learned their songs from breeding territory neighbours after arrival in the spring, I tested three hypotheses concerning spatial patterning of songs. Three hypothesis matrices: an all-neighbours matrix, a single-neighbour matrix and a map-distance matrix, represented possible influences on males' songs. The two neighbour matrices assumed males learned from one or more birds that held a common territory boundary. A cell$_{r,c}$ in the neighbour matrix contained a 1 if the bird in the $r$th row shared a territory boundary with the bird in the $c$th column. Cells formed by the intersection of non-neighbouring birds, and the diagonal, contained zeros. The single-neighbour matrix contained a 1 for the single neighbour whose song was most similar to the male's, and zeros for the other neighbours and all other birds. The single-neighbour analysis was restricted to the subset of birds that sang the most common song type each year (see Results). The map-distance matrix tested for similarity among songs over all distances within the study area. Each cell in the map-distance matrix contained the reciprocal of the straight-line map distance between the centres of the two birds' territories. I took the reciprocal to emphasize local effects (Sokal 1979). Each full matrix for the 1995 analysis was 45 (rows) × 45 (columns), and 61 × 61 in 1996. I calculated the Mantel statistic in SPSS (Norušis 1993) using the formulae in Schnell et al. (1985).

### Statistical analyses

I used nonparametric tests, and report the sample median to estimate central tendency, with the first and third quartiles to estimate dispersion throughout this paper. I made planned, pairwise comparisons using Mann–Whitney $U$ tests and used the sequential Bonferroni procedure to control the total error rate at the stated value (two-tailed) for all comparisons (Rice 1989). I used William's correction to the $G$ statistic for contingency tables with expected values less than five (Sokal & Rohlf 1981). All tests were performed using SPSS (Norušis 1993).

## Results

### Wintering birds

My purpose in studying the singing behaviour of males on their wintering grounds was to determine whether yearling males (brown-crowns) practised singing two or more song types ('overproduced'). In December 1997, when the brown-crowns were probably 5–6 months old, there was little spontaneous singing as the weather was cold and foggy. Total counts of birds in flocks revealed approximately equal numbers of adults (79) and brown-crowns (84). Six adults and one brown-crown sang spontaneously, and five adults and two brown-crowns sang in response to playback. I recorded 15 other birds whose age was not determined. Only one bird, an adult, sang more than five times, and no bird overproduced in these small samples. The birds sang songs typical of Alaskan populations of *gambelii* (DeWolfe et al. 1974; Nelson 1998).

Spontaneous singing by males in small flocks of 5–25 birds was common in late March 1998. I tape-recorded a median of eight songs (first quartile=4, third quartile=13) from 31 different individuals in March 1998. The brown-crowns were just beginning to moult into adult plumage. Birds fell unambiguously into two classes: entirely black and white crowns, or crowns with more than 80% brown and tan feathering. Song types were distinguished on the basis of the note complex after the whistle, or by the terminal trill (Fig. 1). Five of 11 (45%) yearlings sang two different song types, while two of six adults did so (Fig. 1). Of 14 birds that could not be aged (because they were up in the tops of trees), five birds sang two song types, and one bird sang three song types (43% overproduced). Overall, 13 of 31 (42%) of the birds recorded overproduced song types.

### Breeding cycle

When I arrived in Churchill on 1 June 1995 much of the available habitat appeared to be occupied, and most birds were already paired. To ensure that I observed singing behaviour beginning with territory establishment the next year, I arrived on 17 May 1996. The first males arrived on 24 May 1996, and 75% of the 31 territories on my study site were occupied by 2 June (Fig. 2). I first observed and caught females in Potter traps on 29 and 30 May. On the 11 territories where I knew the date of arrival and date of clutch initiation to within 1 day, a median of 15 days elapsed between male arrival and clutch initiation. Because females arrived 5 days after males, about 10 days elapsed between female arrival and clutch initiation. The median date of clutch initiation was 13 June ($N$=22; 1st quartile=10 June, 3rd quartile=16 June). Clutches contained a median of 5 eggs ($N$=22; quartiles=4, 5 eggs).

Individual males stopped singing during my daily censuses when they paired, and resumed singing 15 days later ($N$=21; quartiles=11, 19 days), about the time incubation started (Fig. 2). As a consequence of the early arrival of females, most males only sang for a single day immediately after arrival (median=1 day; quartiles=1, 3 days). The number of days singing prior to pairing was negatively correlated with arrival date (Spearman's $\rho = -0.67$, $N$=20, $P$<0.001). I saw several males on the plot that I never heard sing until after incubation had started.

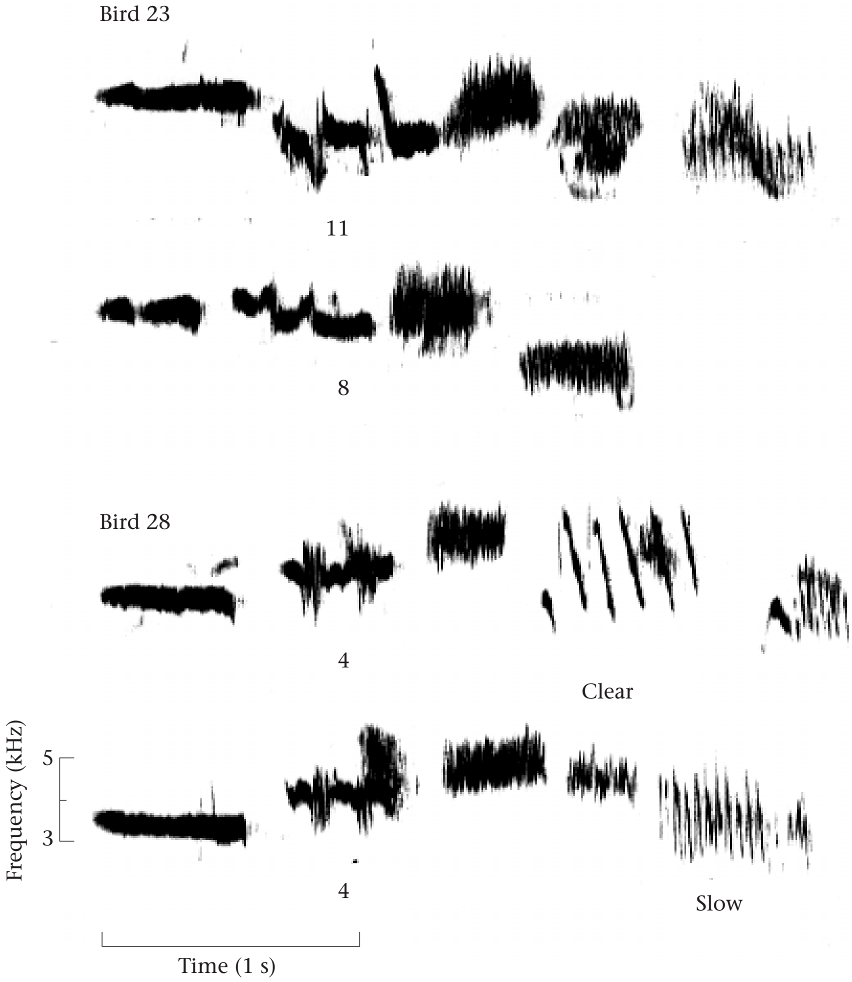

**Figure 1.** Song types produced by two yearling male *gambelii* in March 1998 on the wintering grounds. Both of these birds were in plastic song, which has a more variable structure than adult song. Bird 23's song types contained different note complexes, while bird 28's had different terminal trills. Note complexes and trills were matched to the catalog of Alaskan *gambelii* songs in Figures 4 and 6, respectively, in DeWolfe et al. (1974). Note complex type 11, and trill type 'clear' were not described by these authors, but were common on the California wintering grounds (Nelson 1998).

### *Return rates*

I made an effort to find previously banded males each year. Two of six (33%) males banded in 1995 returned to the same territory in 1996, while three of 14 (21%) males present in 1996 returned in 1997. No banded male moved his territory between years.

### *Song types*

Examination of audiospectrograms, and my aural impression in the field, suggested there were three common song types in the local Churchill population (Fig. 3). Using the structure of the note complex as the defining feature (DeWolfe et al. 1974), I termed them the 'warble', 'high' and 'low' types. A cluster analysis based on the five principal components derived from the 41 acoustic measures suggested that the 'warble' type could be further subdivided into two subtypes based on the structure of the trill syllables in phrase V (Fig. 4). Trill syllables also vary among Alaska *gambelii* songs (DeWolfe et al. 1974; Nelson 1998). The short terminal branches in the dendrogram indicate that the clusters are relatively homogeneous, that is, the songs within each cluster are very similar acoustically. In addition, three males (7%) in 1995 and six males (10%) in 1996 sang rare song types (Figs 3, 5). Some of the rare types lacked a single note present in the note complex of the more common types (cf. males 7 and 32 to the low type in Fig. 3).

In 1995, 84% of 45 males, and in 1996, 79% of 57 males identified to subspecies in the study area were *gambelii*. In 1996, both *gambelii* and '*leucophrys*' males sang the three note complex types with equal probability ($G_2$=0.18, $N$=51, NS). To avoid small cell sizes due to the scarcity of '*leucophrys*' males, only the 1996 data were analysed, and the six males singing rare types were excluded. Male '*leucophrys*' were scattered throughout the study area. Because males of the two subspecies behaved similarily, they are both referred to as *gambelii* hereafter. Rees (1973)

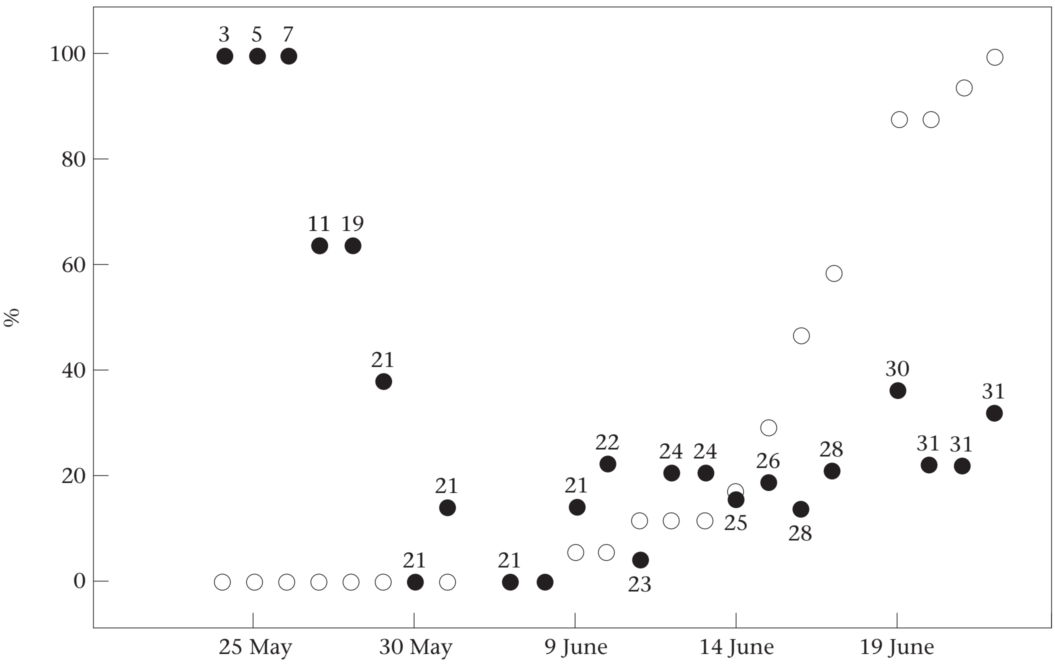

**Figure 2.** The progression of the singing and breeding seasons at Churchill in 1996. ●: Percentage of the number of males present on a given day (*N* males above each circle) that were singing during daily walks through the study site; ○: the cumulative percentage of clutches initiated on that date (*N*=17) on the study plot. Females were first observed on 29 May. Males stopped singing as they paired, and resumed singing as incubation in the population started.

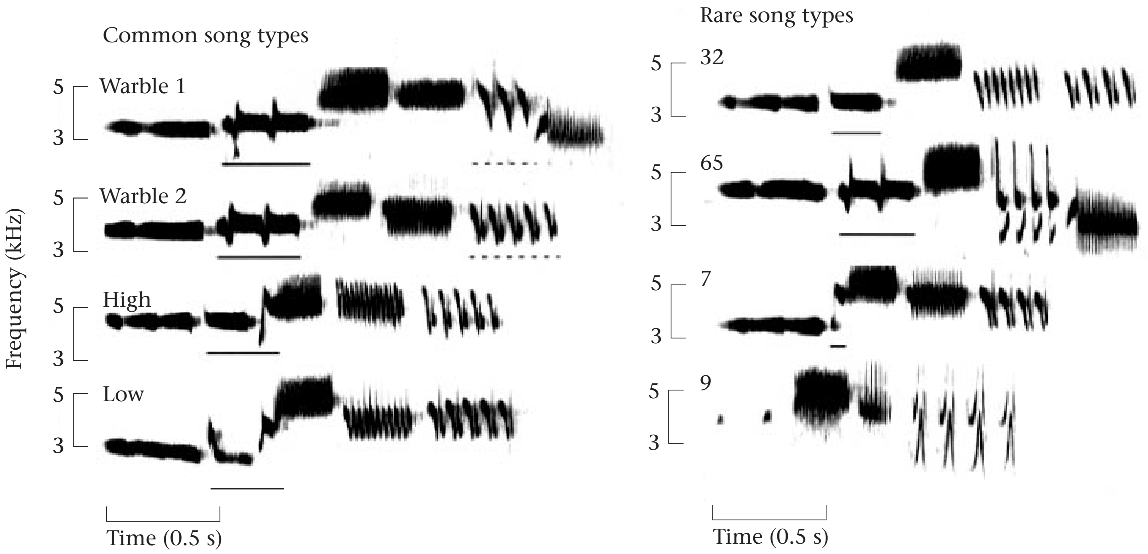

**Figure 3.** Audiospectrograms (300 Hz frequency resolution) of the four common and four rare song types present in 1996. The common song types are named after the sound of the note complex (solid underline) immediately after the introductory whistle. Warbles 1 and 2 are distinguished by the trill of repeated syllables near the end of the song (dashed underline). Notice that rare types sung by males 32 and 7 were incomplete versions of common types 'high' and 'high' or 'low', respectively. Two other rare types are shown in Fig. 5 (male M/Y, similar to male 32, and male W/W). Male 9's song resembles somewhat the song developed by birds isolated from song in the laboratory until their first spring (Whaling et al. 1998). Such males produce trills composed of conspecific call notes. Male 9 kept this song throughout the 1996 season.

also found the two subspecies to be very similar at Churchill. The relative proportions of the three note complex types on the study plot differed significantly between 1995 and 1996 ($G_2$=8.2, $N$=97, $P$<0.025). The warble type increased from 40 to 69% between years, while high and low types decreased from about 30% each to 18 and 12%, respectively. Proportions of the note complex types remained constant from 1996 to 1997, although the sample was small in 1997 ($G_2$=0.31, $N$=82, NS).

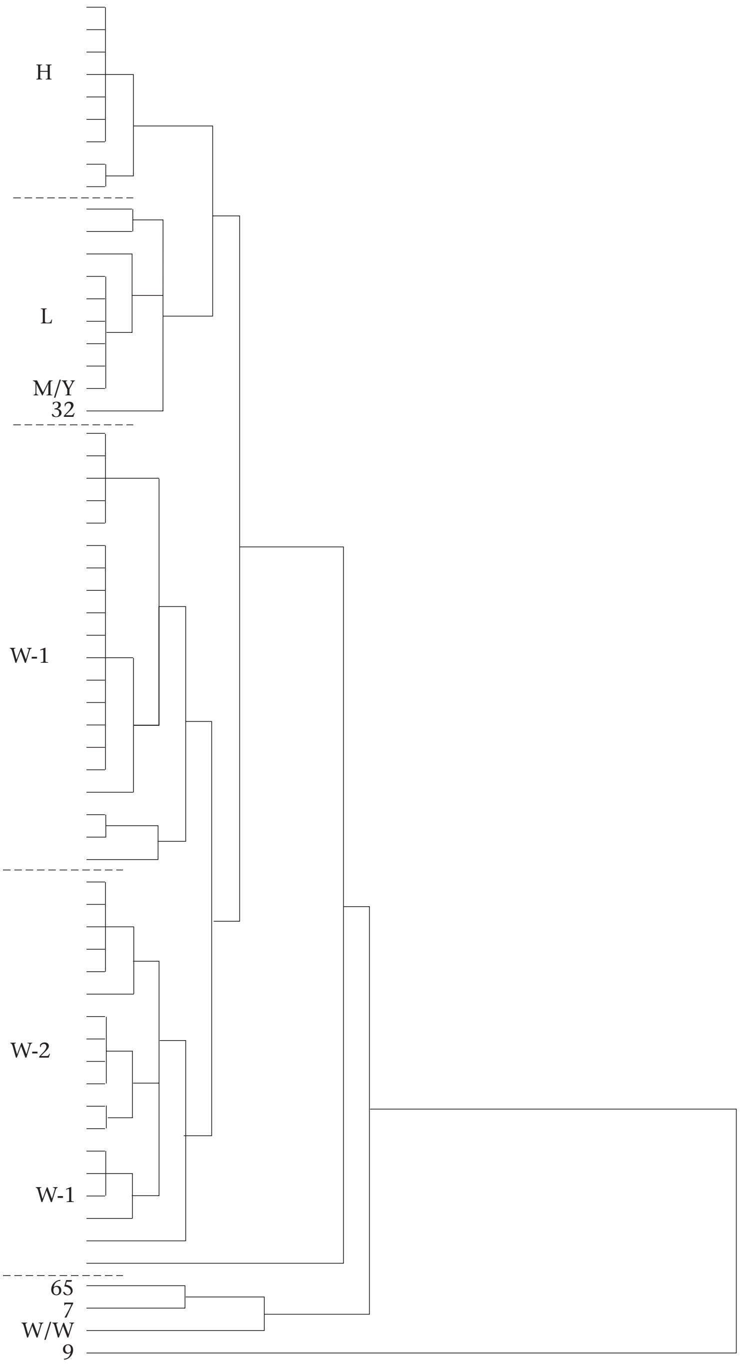

**Figure 4.** Dendrogram of songs recorded at Churchill in 1996 based on acoustic structure. Acoustic measurements (see text) were clustered using a hierarchical, unweighted, between-groups average, procedure based on squared Euclidean distances. Song types corresponding to groups are shown in Figs 3 and 5 (males M/Y and W/W).

### *Song overproduction*

No male overproduced in either 1995 or 1996. Of the 106 males sampled, all but two sang a single song type when I first encountered them. One male, R/W, sang two song types on the same territory from 1995 to 1997. Another male sang two song types throughout 1996. He was not banded, but a bird sang identical songs on the same territory in 1997.

The majority of males were recorded on the day they arrived (and sang). Six males were recorded and banded within a week of arrival in 1996. Two of them were replaced by unbanded birds singing different song types, while the remaining four sang the same song when recorded later in the season (Fig. 5). Eight other males were recorded on the day of their arrival, but were not banded until 2–3 weeks later. All eight retained the same

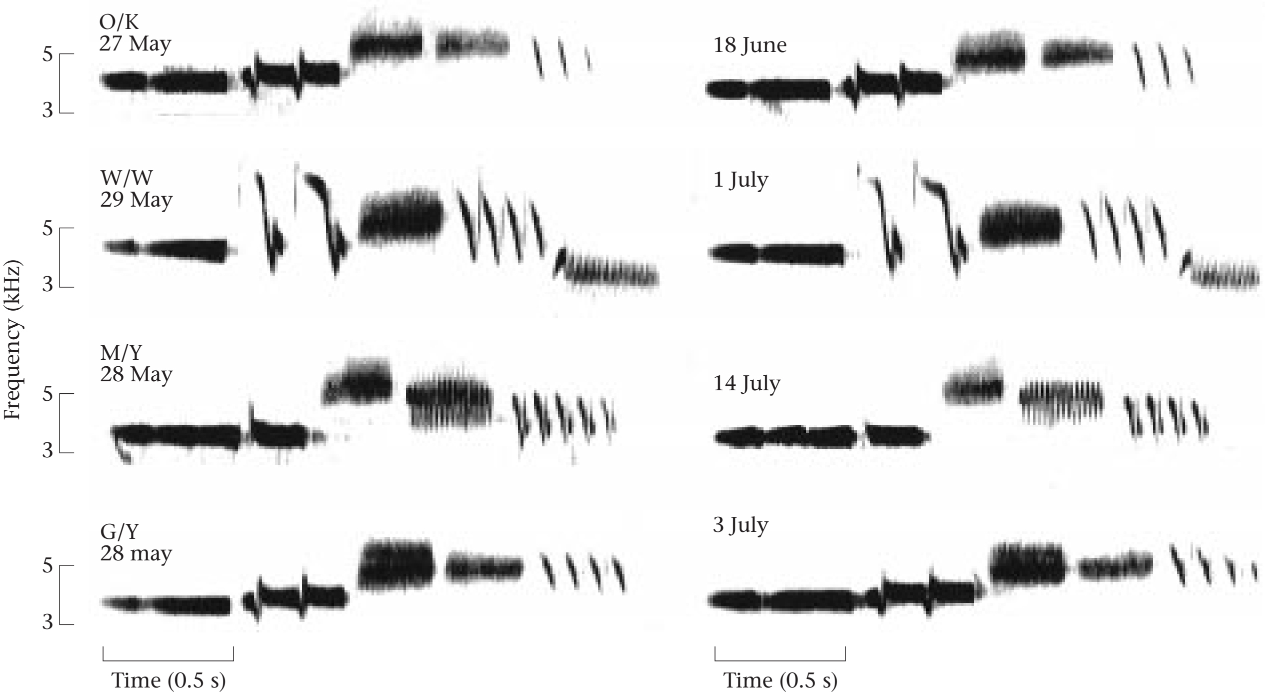

**Figure 5.** Songs of four males recorded on the day of arrival and again later on the same territories in the 1996 breeding season demonstrating stability of song. W/W was a '*leucophrys*' whose song resembled those of spring migrant *leucophrys* in Ohio (unpublished data). The paired notes after the whistle are atypical in *gambelii* song (DeWolfe et al. 1974).

song when recorded later. Four banded males were recorded in 2 consecutive years, and one (R/W) in 3 years. All five retained the same song types from year to year. I conclude that male *gambelii* arrive on the breeding grounds singing their adult repertoire, typically one song, which they do not alter within or between breeding seasons.

### Song sharing

In both 1995 and 1996, males on neighbouring breeding territories sang songs that were no more similar than were the songs of non-neighbours (Table 1). There was also no significant correlation between song dissimilarity and the reciprocal of the map distance between males' territories (Table 1). As recommended by Shackell et al. (1988), these analyses were performed using a continuous representation of song dissimilarity derived from 41 acoustic measurements (i.e. songs were not subjectively classified into 'types'). To illustrate the distribution of song variation over the study area, I used cluster analysis to classify the songs into three common types (warble, high and low) and a fourth category of rare songs. These four categories of song did not cluster within the study area (Fig. 6).

**Table 1.** Results of Mantel tests of three hypotheses concerning the spatial patterning of song variation in white-crowned sparrow song at Churchill, Manitoba

| | 1995 | | 1996 | |
|---|---|---|---|---|
| | *N* | *Z** | *N* | *Z** |
| Neighbour | 45 | −1.18 | 61 | 1.41 |
| Single neighbour† | 17 | −0.07 | 38 | −0.40 |
| 1/Map distance | 45 | −0.88 | 61 | 1.26 |

No *Z* statistics were significant (Bonferonni $P<0.013$) when compared to a $t_\infty$ distribution.
*A negative *Z* statistic indicates neighbours sing more similar songs than non-neighbours.
†Only birds singing 'warble' song types were analysed (see text).

The all-neighbour matrix compared the average song dissimilarity between all territory neighbours to the average dissimilarity between all other birds in the local population. If males learn their song from a single neighbour, the all-neighbour matrix would overestimate the dissimilarity to the tutor male, especially when a male's neighbours sing several different song types. To determine whether a male learned from a single neighbour that sang the same song type as his own, I restricted the analysis to the most common 'warble' song type in the population. I then searched the song dissimilarity matrix for the neighbour with the lowest dissimilarity and set the corresponding cell in the all-neighbour matrix to 1; all other neighbours and non-neighbours were set to 0. The single neighbour with the most similar song was no more similar than other males singing the same song type in the population (Table 1). I conclude that males do not learn their songs from breeding territory neighbours, nor do males preferentially settle on territories next to males singing similar songs. There is no evidence for local song dialects or neighbourhoods in this subspecies.

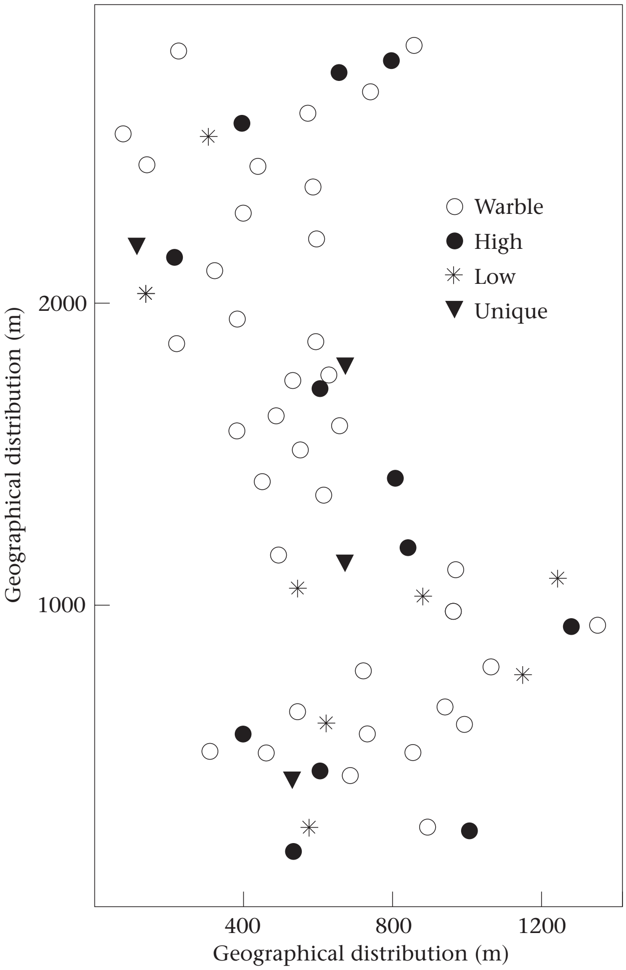

**Figure 6.** The distribution of the three song types (warble 1 and warble 2 are lumped) and a fourth category comprising all rare types on the Churchill study area in 1996. The song types are distributed at random (Table 1).

## Summary

My field observations on the breeding cycle agree with those of previous observers that have documented the rapidity with which *gambelii* initiate breeding upon reaching their sub-Arctic breeding grounds. Males arrived a few days before females and paired immediately on the females' arrival. Females started egg laying about 2 weeks after the first males had arrived. The song development process appeared to be complete by the time males arrived on the breeding grounds in late May. Males sang a single song type that they did not alter either within or between years. There was no correlation between song structure of males on neighbouring breeding territories, as would be expected, because males did not overproduce songs nor did they alter their songs after arrival.

# LABORATORY EXPERIMENT

## Methods

### *Subjects*

I collected 23 nestling white-crowned sparrows in seven broods between the ages of 4 and 6 days on 3 July 1996 and transported them to my laboratory in Columbus, Ohio. All seven females and six males attending the nests were *gambelii*. I hand-reared the young birds using animal husbandry techniques described elsewhere (Nelson et al. 1995, 1996a). I housed birds within 6 days of fledging at 9–10 days of age in pairs or trios in sound-isolation chambers. I sexed birds initially by listening for subsong, the first phase of vocal development in males. Fourteen birds produced subsong and were housed individually in sound chambers at the beginning of tutor block 2 (defined below). I moved the nine quiet birds, assumed to be females, into open cages in a neighbouring room. One of these birds began producing plastic song on 11 January 1997, and was immediately moved into a sound chamber. This bird, and 13 of the 14 assumed males, produced loud song in the next few months. I examined 12 males in 1997 when they were on long days and singing. All had cloacal protuberances measuring, 5–7 mm long a testosterone-dependent character used to sex songbirds. I maintained birds on the same photoperiod as in previous work: the ambient photoperiod for 38°N, advanced by 1 month (Nelson et al. 1996a). Gambel's white-crowned sparrows commonly winter at this latitude (Cortopassi & Mewaldt 1965).

### *Early tutoring*

I tutored males with the 'rich' tutoring regime used previously (Nelson et al. 1996a). I tutored males beginning at an average of 13.7 days of age (range 13–15) for 40 days with 16 different white-crowned sparrow song types (block 1), and then changed to 16 different song types for the subsequent 40 days (block 2). Block 1 contained eight *gambelii* song types (four recorded in Alaska, four in Churchill) and eight mountain white-crowned sparrow, *Z. l. oriantha*, song types. Block 2 contained eight *gambelii* song types (four Alaskan, four Churchill), four *oriantha*, and four Puget Sound white-crowned sparrow, *Z. l. pugetensis*, song types. Gambel's and mountain white-crowned sparrows are sympatric in Alberta (Lein & Corbin 1990), and *gambelii* migrate through *pugetensis* (Chilton and Lein 1996) and *oriantha* (Morton & Pereyra 1987) habitat, and so encounter these songs in nature. To facilitate identifying tutor imitations, I chose song types as acoustically distinct as possible (Nelson & Marler 1993).

I prepared seven different versions of the block 1 tape and 14 versions of block 2. The same 16 song types were presented in each of the versions but in different random orders. An individual bird heard one version every day during the 40 days. I played each tape twice daily in the morning and afternoon. On all tapes I repeated each song type 18 times, six times per min, before changing to the next type after a pause of 40 s. With the exception of using multiple versions of each tutor block, these procedures followed closely the procedures used in Nelson et al. (1996a), to which my results are compared. The only obvious difference is that the *pugetensis* males in Nelson et al. (1996a) did not begin tutor block 1 until 20 days of age, while all other subspecies began tutoring at 5–15 days.

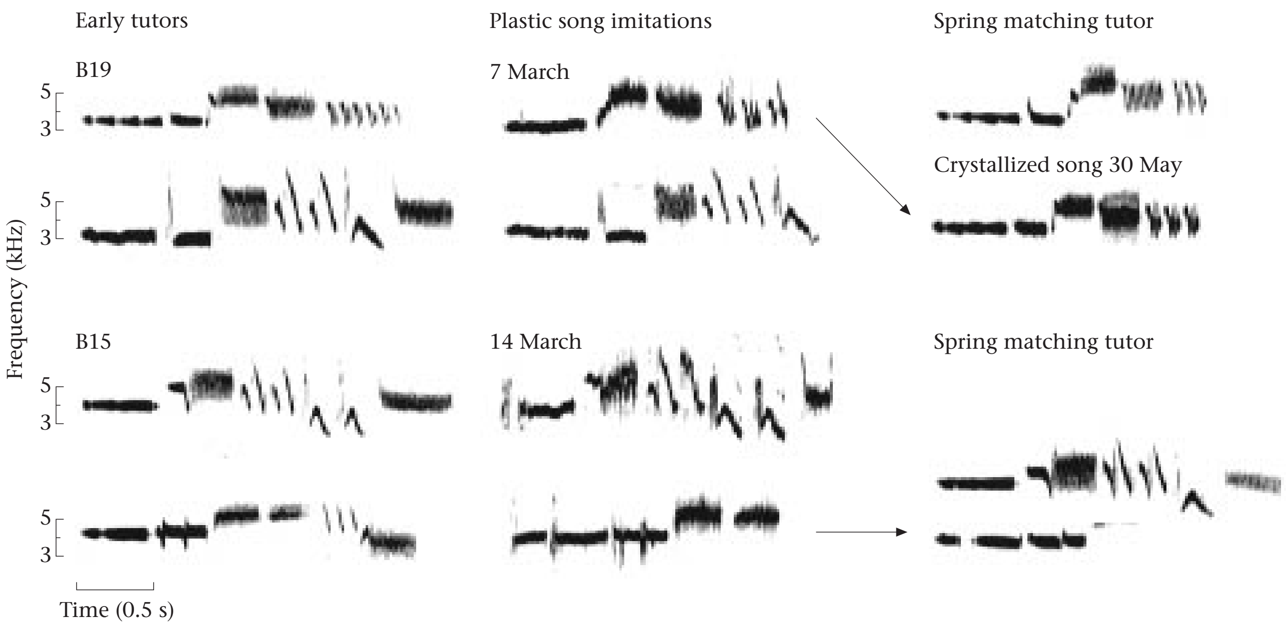

**Figure 7.** Results of the matched countersinging experiment for two hand-reared males. The middle column shows the imitations of two early tutors (left column) sung by each subject. For each male in the right column, the top song is the matching song presented during plastic song in the spring, and below it, the subject's final crystallized song. Arrows connect a bird's plastic and crystallized renditions of the same song type. Both males had spring matching tutors that were slightly different variants of one of the early tutors. B19 was one of two *gambelii* males in the experiment to crystallize the matching song; all other birds deleted the matching song from their repertoire.

### *Late tutoring (spring)*

The goal of the spring tutoring, beginning at approximately 210 days of age, was to test whether *gambelii* would selectively crystallize the song in their overproduced repertoire that matched the song type broadcast to them through a loudspeaker (Nelson & Marler 1994). As in previous work, to stimulate singing, I resumed tutoring the 14 males on 5 February 1997 with tapes that contained two novel song types. I repeated each song on these tapes 72 times before changing to the second type after a pause of 40 s. After imitations became recognizable in the birds' plastic song, I switched to playback of a single song type that either was the same tutor song that the bird imitated in block 1 (seven males), or a slightly different variant (4 males) of the imitated tutor (Fig. 7). The three remaining males did not participate in this phase of the experiment because they did not overproduce (one bird), they were played a novel song by mistake (one bird), or they were played an experimentally altered song (one bird). Before switching to a single matching song type, I waited until each male was singing imitations of two different tutor types with approximately equal frequencies. Most of the males were infrequently singing one to five other types. The matching type was chosen by flipping a coin. Matching playback began on 9 March for the earliest bird and 10 April for the latest. I played tapes twice daily in the morning and afternoon.

### *Song recording and analysis*

I recorded birds weekly beginning 3 January 1997 using techniques described elsewhere (Nelson et al. 1995). Three students and I analysed the recordings for evidence of imitations of tutor songs. We matched spectrograms of vocal material by eye to a catalog of spectrograms of the tutor songs, and we made identifications by consensus. On each recording date, I counted the number of tutor songs represented, in whole or in part, in each bird's singing. For most birds, the number of tutor imitations produced peaked early in plastic song (see below). White-crowned sparrows sing with near-immediate variety in plastic song, that is, they do not repeat a song type, or only repeat it two or three times before switching to a different one (Nelson et al. 1996b). We generally examined 25–50 songs on each day's recording.

I defined a song 'type' as a stable, repeated pattern, that was sung over at least 2 weeks. Song types usually became apparent in the first month of plastic song. Song types could be complete or partial imitations derived from one tutor song type, or 'hybrids', formed by combining phrases from two or more tutor song types. A song was considered crystallized when a male sang only one type that was repeated with little variation in note structure, especially the introductory whistle, which had to be produced with little random frequency modulation. Three birds did not reach this criterion when I terminated the experiment. Two of these males (the third died) were kept on short days until 28 November 1997, when I transferred them to long days (16:8 h light:dark cycle). I then tape-recorded them weekly until each sang a single song type in January 1998. They were tutored again with the same matching song types they heard the previous spring.

## Results

### *Timing of song production*

Male *gambelii* began plastic song, production of imitations of tutor songs, at a median of 228 days of age ($N=14$, first quartile=215, third quartile=229). Because the birds were kept on a photoperiod advanced by 1 month, they would probably begin plastic song at 260 days (8.6 months) on a natural photoperiod in the laboratory.

I compared the acquisition and production of songs by *gambelii* in the present experiment to previous results for *nuttalli, pugetensis* and *oriantha* obtained under comparable conditions (Nelson et al. 1996a). The date on which birds crystallized their single song type varied significantly among the four subspecies (Kruskal–Wallis test: $\chi^2_3=30.5$, $P<0.01$). Sedentary *nuttalli* males crystallized their song significantly earlier (10 March) than the other three subspecies (Bonferonni $P<0.05$ for multiple comparisons). The two subspecies breeding at high elevation, *oriantha*, or high latitude, *gambelii*, crystallized the latest, both on about 28 May (360 days of age; Nelson et al. 1996a). Male *pugetensis* crystallized significantly earlier (17 April) than the latter two subspecies, and significantly later than *nuttalli*. To estimate crystallization dates on a natural photoperiod, 1 month should be added to these dates. The timing of song production varies with photoperiod in this species (Whaling et al. 1998).

### *Sensitive phase for song acquisition*

Male *gambelii* acquired the vast majority of their imitations from block 1 when they were less than 55 days old (Fig. 8). Of 237 total phrases learned by the 14 *gambelii* males, 234 were learned in block 1, and only two males learned in block 2. No bird learned either novel type presented in February 1997. The proportion of the plastic song repertoire learned in block 1 was significantly higher than in any of the other three subspecies (Mann–Whitney $U$ tests: Bonferroni $P<0.05$).

On this tutoring regime, the acquisition age of all tutor songs reproduced in plastic song was the same in male *nuttalli, oriantha* and *pugetensis* (Nelson et al. 1996a). In another study using 10-day-long tutor blocks, male *oriantha*, which have a very short breeding season, memorized their single crystallized song at a significantly younger age than did male *nuttalli* (Nelson et al. 1995). A similar result held across all four subspecies using 40-day-long blocks. The rank order of breeding season duration (shortest to longest: *gambelii, oriantha, pugetensis* and *nuttalli*; Oakeson 1954; Morton 1976) was significantly correlated with the proportion of subjects learning their crystallized song in block 2 (Spearman's $\rho=0.48$, $N=43$, $P<0.002$). That is, *nuttalli* (44%) and *pugetensis* (63%) males were more likely to select their crystallized song from tutor block 2 (age 55–95 days) than were either *oriantha* (17%) or *gambelii* (0%). I conclude that male *gambelii* have the earliest sensitive phase for song acquisition of the four subspecies of white-crowned sparrow studied to date. Across four subspecies, duration of the breeding (and singing) season is positively correlated with duration of the sensitive phase.

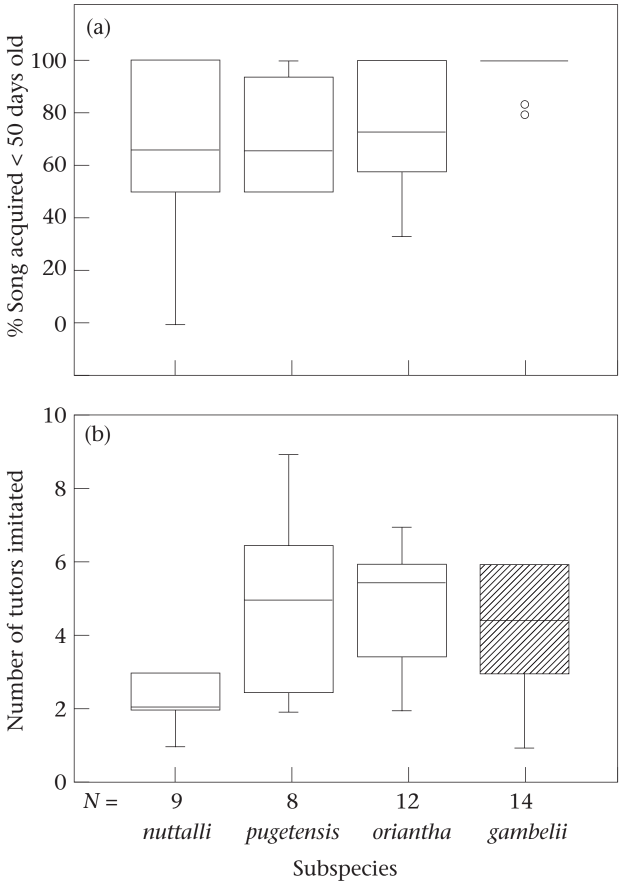

**Figure 8.** Results of the laboratory experiment using hand-reared *gambelii* males (▨). Data are compared to three other subspecies as reported in Nelson et al. (1996a). Male *gambelii* differed significantly from the other three subspecies by learning almost all their songs prior to 50 days of age (a). Male *gambelii* resembled *pugetensis* and *oriantha*, but differed from *nuttalli*, in the number of tutors imitated (b). The lower and upper edges of the boxes represent the first and third quartiles, the median is the horizontal line within each box. The vertical lines ('whiskers') include the range of values within 1.5 times the interquartile range. Individual outliers are small open circles. *N* is shown below each bar.

### *Overproduction*

Male *gambelii* learned as much vocal material as did the two other migratory subspecies (*oriantha* and *pugetensis*). There were no significant differences in the number of different tutors imitated (Kruskal–Wallis test: $\chi^2_2=1.19$, NS), the number of tutor phrases imitated ($\chi^2_2=3.74$, NS), or the number of song types produced among these three subspecies ($\chi^2_2=1.46$, NS; Fig. 8). Nelson et al. (1996a) documented that all three of these variables were significantly lower in sedentary *nuttalli* than in either *oriantha* or *pugetensis*. Thus, male *gambelli* resemble other migratory subspecies of white-crowned sparrow in their capacity to memorize songs from a standardized tutor regime.

### *Accuracy of imitations*

Figures 7 and 9 show the crystallized song and putative tutors for 12 of 14 *gambelii* males observed in the present experiment. Although some males truncated part of the

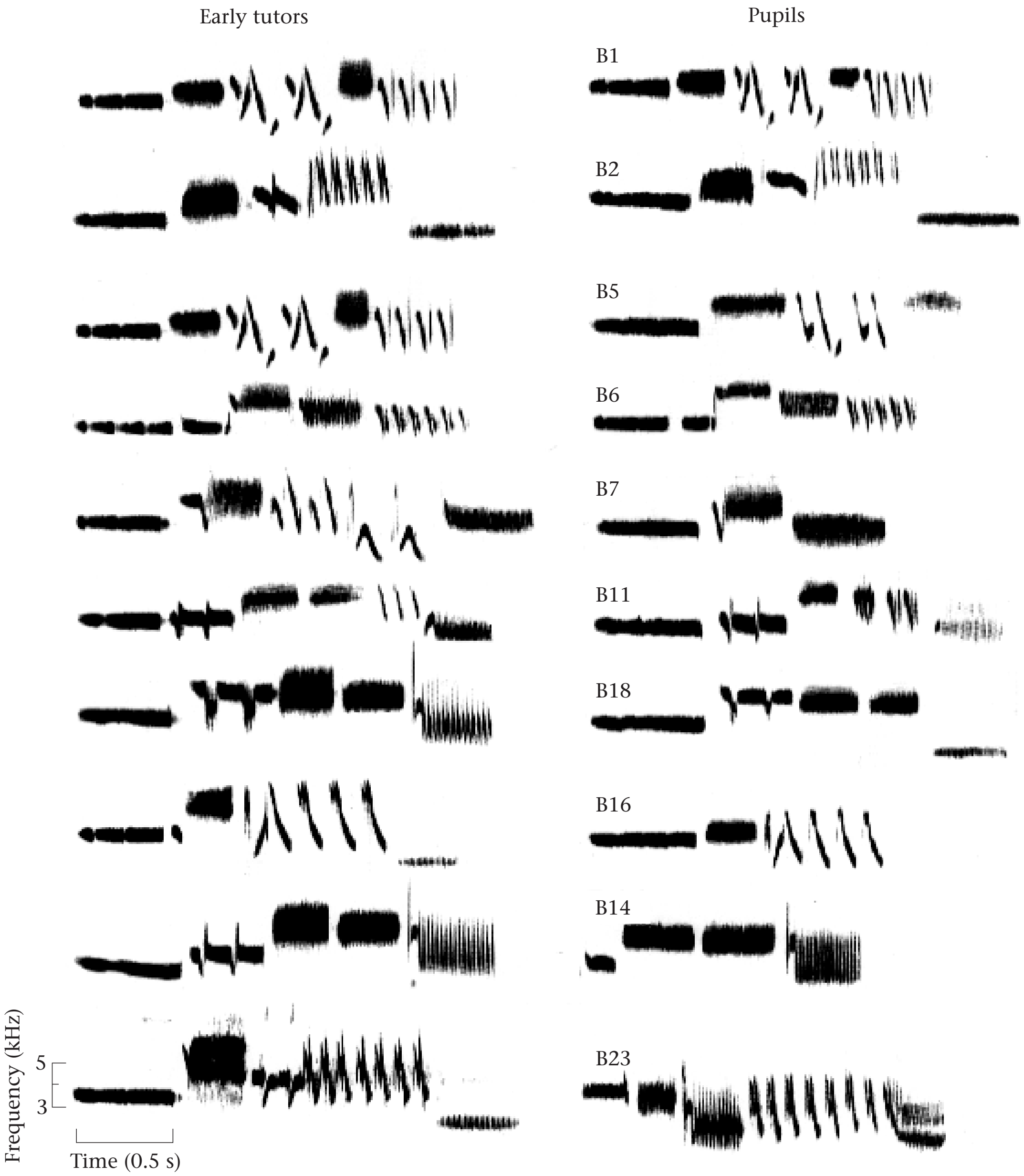

**Figure 9.** Songs of the presumptive tutors and their crystallized imitations by 10 *gambelii* subjects (two other males are in Fig. 7). In general, the imitations are accurate, although some birds dropped notes from their songs (B5, B7, B16, B14). B23's song is a 'hybrid' formed from his and B14's tutor.

tutor song in their imitations (B7, B14), this tendency exists in the other subspecies also. The number of imitated phrases in the final crystallized song did not differ significantly among the four subspecies (Kruskal–Wallis test: $\chi^2_3=6.42$, $N=42$, NS). Improvisation was not common in the hand-reared *gambelii*. The songs of three males (B7, B18 and B23) were 'hybrids', or combinatorial improvisations (Marler & Peters 1982b), derived from two different tutors. The proportion of male *gambelii* that crystallized hybrid songs (3/14=21%) did not differ significantly from the proportion in *pugetensis* or *oriantha* ($G_2=0.70$, $N=45$, NS). Nelson et al. (1996a) reported that *nuttalli* males were significantly more prone to produce hybrid songs than were males of the latter two subspecies.

### *Matched countersinging*

Late in song development, other white-crowned sparrow subspecies have a strong tendency to match songs heard with the best match available from their overproduced repertoire. When presented with playback of a song type in the spring that resembled one type currently being sung in their plastic song repertoire, only two of 11 male *gambelii* subsequently crystallized the matching type (Fig. 7). The two males that crystallized the matching song type were each tutored with variants of the tutor song they had initially memorized. All but two males (B5 and B16) crystallized one of the two most common song types they were practising when matching playback began. However, differences in the relative frequency of song performance in the week prior to when matching playback began did not influence which song was eventually crystallized (Wilcoxon signed-ranks test: $Z=-0.711$, $N=11$, $P=0.48$). The tendency to mismatch the playback type was almost significant (binomial test: $P=0.07$).

## GENERAL DISCUSSION

Gambel's white-crowned sparrow is a long-distance migrant that breeds across sub-Arctic Alaska and Canada near the tree line. The pattern of geographical variation in song appears quite different from any other white-crowned sparrow subspecies known to date. (The singing behaviour of the nominate form, *Z. l. leucophrys*, on the breeding grounds east of Hudson's Bay is still undescribed. Based on its far northern breeding distribution, I expect it resembles *gambelii*, as did the 20 *leucophrys* encountered at Churchill in this study.) Unlike other subspecies, the songs of neighbouring male *gambelii* are no more similar than are the songs of non-neighbours (DeWolfe et al. 1974; Austen & Handford 1991; Table 1). A small number (four to seven) of discrete song types exist in a random spatial distribution within local populations in Alaska and Canada. The goal of the present research was to determine how the process of vocal development in male *gambelii* differs from that of males of other subspecies of white-crowned sparrow in which vocal dialects are prominent (Marler & Tamura 1962; Baptista 1975, 1977; Orejuela & Morton 1975; Baptista & King 1980).

### Temporal Aspects of the Learning Process

My field observations on the progress of the breeding cycle agree with those of previous workers that have documented the extremely short period of time available for breeding at high latitudes in *gambelii* (Blanchard & Erickson 1949; Oakeson 1954; Irving 1960; Morton 1976; Wingfield & Farner 1978). The compression of the early phases of the breeding cycle in *gambelii* at Churchill, located on the shore of Hudson's Bay, appears to be even more pronounced than that of lowland populations breeding at higher latitudes in Alaska. Males in Alaskan populations may arrive in early to mid-May (Chilton et al. 1995), while my observations and those of Taverner & Sutton (1934) and Rees (1973) indicate that conditions at Churchill do not allow return until the last week of May and first week of June. The delayed and extremely short breeding season may have influenced at least two aspects of the learning process: (1) the lack of dialects in the wild and (2) the short sensitive phase for song acquisition (Fig. 8).

### Vocal Dialects

Three hypotheses were outlined earlier to explain the random distribution of song types in *gambelii*: (1) males might overproduce song learned in an early sensitive phase, but then, in contrast to other subspecies, select a song at random for retention as the crystallized song; (2) males might not overproduce; or (3) males might improvise their songs, rather than imitate tutors. A fourth possibility, that males would imitate neighbours upon arrival on the breeding grounds, was considered unlikely a priori as this would tend to produce vocal convergence among neighbours. I used a combination of field and laboratory evidence to evaluate these possibilities.

My field observations indicate that male *gambelii* arrive on their breeding grounds in late May and early June singing but a single song type. Therefore, they do not have the option of choosing one song type from an overproduced repertoire in order to match or mismatch countersinging with their territory neighbours. For wild males, therefore, hypothesis 1 is rejected, and hypothesis 2, that *gambelii* do not overproduce, is supported.

Observations of wild and hand-reared males reject the hypothesis 3 that male *gambelii* improvise, rather than imitate their songs. In the wild, songs fell into three or four common song types (Figs 3, 4). About 5% of males both years sang unique song types, but most of these were clearly incomplete versions of common types. Other unique types resembled songs recorded from other parts of the subspecies' range and were therefore probably learned elsewhere by immigrants to the local population. In the laboratory, with a few exceptions, all males developed good imitations of the tutor songs (Figs 7, 9). Some crystallized songs were incomplete imitations of tutors, but examination of plastic song indicated that all of these males had sung complete imitations of the tutor earlier in development.

As expected, there was little evidence from either the field or laboratory to suggest the sensitive phase for song acquisition was open in yearlings (hypothesis 4). My small sample suggests that males do not alter their single song after arrival. Four males banded within 1 week of arrival, and three other males that sang unique songs, kept the same song until late June of 1996. If males do alter their song within the first week after arrival, they do not appear to imitate their neighbours' songs (Fig. 6, Table 1). If imitation by males settling on territories occurred, then we would expect the spatial distribution of song types to be clumped and the relative proportions of song types in the local population to be stable from year to year. As in Alaskan populations (DeWolfe et al. 1974), neither prediction was met in this study. In contrast, in *oriantha* (Harbison et al. 1999) and *nuttalli* (Trainer 1983; Chilton & Lein 1996; unpublished data) the same song type may persist for decades at one locality. The very short period, 1–3 days (Fig. 2), that most male *gambelii* spent singing immediately after arrival could also render imitating neighbours difficult. Little data exist on how long the period of sensorimotor learning of song lasts in wild birds.

### Short Sensitive Phase

A second feature of the song learning process that appears to have been influenced by the extremely short breeding season at high latitudes is the duration of the sensitive phase. Even when measured by the relatively imprecise technique of presenting tutor songs for blocks of 40 consecutive days, hand-reared male *gambelii* display the shortest sensitive phase of any of the four subspecies of white-crowned sparrow studied to date (Fig. 8). This does not mean that *gambelii* are incapable of acquiring song beyond the age of 50–60 days in the wild. The results do suggest that *gambelii* are predisposed to be most sensitive to song stimulation at a significantly younger age than the other subspecies that experience longer breeding, and presumably, longer singing seasons. The truncation of the sensitive phase is even more dramatic than in *oriantha*, which also has a short breeding season at high elevations relative to *nuttalli/pugetensis* (Nelson et al. 1995). The relative brevity of the sensitive phase was not accompanied by a decrement in the capacity to learn: male *gambelii* learned just as much tutor material as did the other migratory sparrows. Therefore, the failure to overproduce on the breeding grounds at Churchill does not appear to be the result of a memory constraint (Stoddard et al. 1992).

## Matched Countersinging

Matched countersinging is a widespread behaviour among songbird species in which territory neighbours exchange similar songs (Marler 1960; Falls et al. 1982). Matched countersinging is a key component in the selective attrition model of song dialect formation (Marler 1960; Marler & Peters 1982a). Field studies have shown that males can achieve song matching via the selective attrition process (Baptista & Morton 1988; DeWolfe et al. 1989; Nelson 1992). Even though wild male *gambelii* on the breeding grounds did not overproduce song types and countersing matching songs, it was of interest to see how males in the laboratory would behave.

In contrast to two other subspecies that do form vocal dialects (*nuttalli* and *oriantha*, Nelson & Marler 1994), only two of 11 *gambelii* chose a song for crystallization from their overproduced repertoire that matched the song type played back to them. The other two subspecies always chose the matching song type. The song-matching playback experiment conducted in the laboratory gave male *gambelii* the opportunity to match song types during countersinging that they may not commonly experience on the breeding grounds at Churchill. In other parts of their extensive breeding range male *gambelii* return to lowland breeding sites in Alaska in early to mid-May (Blanchard & Erickson 1949; Wingfield & Farner 1978). It would be of interest to determine whether males in Alaskan populations are still in the overproduction phase in early May, but then discard, rather than retain matching song types, as did males in the laboratory. Yearling male *gambelii* overproduced song types on the wintering grounds in late March (Fig. 1).

## Why Mismatch Songs?

A tendency to discard the matching song type from the overproduced repertoire was expected as one possible mechanism that would produce a random assortment of song types within local populations. This result, obtained in hand-reared birds, indicates that the difference in the response to matching song stimulation between a subspecies that does not form vocal dialects (*gambelii*), and those that do (*oriantha* or *nuttalli*), has a genetic basis. Marler & Peters (1982a) originally suggested that some species might match, and others mismatch during countersinging, but they did not speculate on what circumstances might favour these different responses. One functional explanation for mismatching, and the consequent random distribution of song types, might be that mismatching increases the acoustic differences among neighbours' songs. Individual recognition of neighbours' songs is widespread among songbirds, but it is not known how long it takes for males to memorize their neighbours' songs at the beginning of the breeding season (Lambrechts & Dhondt 1995). Given the very short premating song period (Fig. 2), having a distinct song might speed learning neighbours' songs and thereby facilitate setting territory boundaries. Females that arrive a few days after males might prefer to mate with males on well-established territories. Another possibility is that if female choice is more important than male–male competition during the short *gambelii* breeding season, females might prefer males with distinctive songs. Song matching might be more prominent in subspecies where prolonged male–male competition is possible.

## 'Meme' Flow

The behaviour described in this paper can account for the maintenance of a pattern of random distribution of song types within local populations of *gambelii*. Other factor(s) must be responsible for the genesis of the diversity of song types. Possibly the different song types originally arose by cultural 'drift' (accumulation of copying errors) in isolated populations (Lemon 1975; Lynch & Baker 1994; Mundinger 1980). Dispersal could then spread song types widely. A 'meme' is the unit of cultural transmission (Dawkins 1976). The common occurrence of several song components in southeastern Alaska, Alberta and Churchill populations (Nelson 1998) indicates that 'meme flow' (Lynch & Baker 1994), mediated by large natal and/or breeding dispersal distances, is substantial in this subspecies. The few data available are consistent with this. I found breeding return rates of males of 33% ($N$=6) and 21% ($N$=14) in 2 years. Hahn et al. (1995) did not recover any *gambelii* of either sex the next year ($N$=12) in Alaska. Adult banding returns were variable and averaged 33% ($N$=32) over 3 years in a Northwest Territories population (Norment 1992). No banded nestlings were recaptured as adults in the latter population. While based on small samples, these estimates are all smaller than the approximate 50% return rates typical of other subspecies of the white-crowned sparrow (Chilton et al. 1995). The low breeding return rates in *gambelii* probably indicate some breeding dispersal, rather than low adult survival, because return of banded adult *gambelii* to wintering sites averages 50–60% (Blanchard & Erickson 1949; Mewaldt 1964, 1976). It is not clear whether large dispersal distances are sufficient to produce the random distribution of song types observed at the level of local populations. An inability to modify song on the breeding grounds may also be necessary to prevent the formation of local dialects. If yearlings, roughly half the population, could modify their songs to match their neighbours', then some degree of vocal convergence might be expected. Computer modelling (Williams & Slater 1990, 1991) incorporating varying degrees of dispersal and learning by yearlings might profitably reveal the interaction between these two factors.

Thus the general picture that emerges from these studies is that male *gambelii* learn from tutors exceptionally early in a very short sensitive phase, necessitated by the short breeding season. The failure to develop 'dialects' seems to be due to their high natal and breeding dispersal tendencies, and to their failure to match song types with their countersinging rivals.

## Song Learning and Perception

This study has focused on local, microgeographical, variation in song and the developmental processes that give rise to it. Bird songs also vary over larger distances as the result of populations being separated by time and space (macrogeographic variation). *Gambelii* songs do display significant differences between Alaska and Churchill (Nelson 1998), but in a playback experiment to territorial males at Churchill, local and Alaska songs elicited equivalent strong responses. This result is in striking contrast to the common pattern found in dialect-forming subspecies of white-crowned sparrow and other species in which males give different responses to local and distant dialects (Nelson 1998). The broader acceptability of song in adult *gambelii* may reflect the different range of song types the males experience during tutoring. Males of subspecies such as *nuttalli, oriantha* and *pugetensis* that learn the relatively invariant songs within a local dialect may acquire a highly focused representation of song. If this representation serves as a perceptual standard to which song stimuli are compared, then an alien dialect might be easily discriminated from the local dialect. In male *gambelii* in contrast, song production is not guided by tutoring and interaction with territory neighbours, either by direct imitation or by selective attrition from an overproduced repertoire. Their different developmental pathway, guided by innate differences in sensitive period duration and responsiveness to matching song playback, appears to have resulted in a more permissive tolerance of song variation in adults. It appears then, that variation in the timing of reproduction among different populations of the white-crowned sparrow has had far-reaching effects on the song learning process, the spatial distribution of song types, and the perception of song variation.

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