

Song repertoires of Harris' sparrows (*Zonotrichia querula*)

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The songs of 34 male Harris' sparrows were recorded at Churchill, Manitoba. The songs are composed of one to three whistled notes, all at the same frequency. Individuals sing from one to three song types, each at a discrete frequency. Males are very accurate at returning to the same frequency, both within a bout and between days. Individuals seem to structure their repertoire on the basis of the frequency ratio between types, rather than on the absolute frequency of each type. Males responded to playback of a 3-kHz song with the song in their repertoire that was closest to it in frequency. We suggest that the frequency ratio between song types may be species specific, whereas the absolute frequency of song types may facilitate individual recognition. This species has been previously described as having only a single song type. Our study and other recent work suggest that there is no sharp distinction in the wild between bird species with single and multisong repertoires.

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Les chants de 34 Bruants à face noire mâles ont été enregistrés à Churchill, Manitoba. Les chants de ce bruant se composent de une à trois notes sifflées, toutes de même fréquence. Chaque individu possède de un à trois types de chant de fréquences différentes et discrètes. Les mâles sont très fidèles à retourner exactement à la même fréquence au cours d'une phrase et d'un jour à l'autre. Les individus semblent structurer leur répertoire en fonction du rapport des fréquences entre les types plutôt qu'en fonction de la fréquence absolue de chaque type. Les mâles ont réagi à l'écoute d'un enregistrement d'un chant de 3 kHz en exécutant le chant de leur répertoire à la fréquence la plus proche de celle du stimulus. Nous croyons que le rapport des fréquences des divers types de chant est peut-être spécifique à l'espèce, alors que la fréquence absolue des types de chant peut contribuer à la reconnaissance entre individus. L'espèce a déjà été décrite comme n'ayant qu'un type de chant. Notre étude et d'autres travaux récents indiquent qu'il n'y a pas de distinction très nette en nature entre des espèces d'oiseaux à répertoire constitué d'un seul chant et des espèces à répertoire constitué de plusieurs chants.

[Traduit par la rédaction]

Introduction

Semple and Sutton (1932) described the song of the Harris' sparrow (*Zonotrichia querula*) as a "single, whistled note . . . repeated once, twice, even four or five times, the notes trailing into each other uncertainly." Harris (1920) stated that "this song is repeated . . . with variations in the number and the pitch of the notes." Based on this sketchy information, Harris' sparrows have been typically characterized as having only one song type (Bondesen 1977). This assumption has been used in developing hypotheses concerning the phylogeny of bird song (Irwin 1988) and the evolutionary significance of geographic variation and dialects in this genus (Baker 1982).

On the basis of limited recordings of seven male Harris' sparrows made at Churchill, Manitoba, in 1986, it appeared to us that individuals sang from one to three songs, at distinct frequencies (itches) (A. G. Horn, unpublished data). Interestingly, Nice (1929) also observed that individual Harris' sparrows shifted between pitches during premigratory singing, but her observations have not been widely cited. These observations suggested that Harris' sparrows have multiple song types.

The purpose of this study was to determine whether Harris' sparrows do have song repertoires, that is, whether they possess multiple song types. Following the terminology proposed by Shiovitz (1975), we define a song type as a specific version of a discontinuous song. Song types must be consistently reproduced between renditions, and there must be no continuous variation among types. Similar definitions have been used for great tits, *Parus major* (McGregor and Krebs 1982), and western meadowlarks, *Sturnella neglecta* (Horn and Falls 1988). The alternative hypothesis is that this species does not possess song types, that is, that the songs at different frequencies are not consistently discontinuous.

If Harris' sparrows do have repertoires (i.e., multiple song types), we also wanted to determine how the songs in an individual's repertoire were related to each other. We term the relationships among songs within an individual's repertoire the repertoire structure. Work by Whitney (1981) has shown that varied thrush (*Ixoreus naevius*) repertoires are structured to decrease the similarity among song types.

A phenomenon common to many repertoire species is song matching (Falls et al. 1982; Falls 1985). A third purpose of this study was to test whether Harris' sparrows also match songs, that is, whether individuals would respond to a stimulus song with a song type that was close in frequency to the stimulus song. Our intent was to assess whether the birds categorize songs sung at different frequencies as different. Matching is one way in which individuals may respond differentially to songs they perceive as being of different types. We also measured response strength and switching rate in response to playback, to determine whether the similarity of a song would affect the response.

Methods

Study species

Harris' sparrows winter in flocks in the south-central United States and breed along the northern tree line from the MacKenzie Delta southeast through the District of MacKenzie, N.W.T., to Hudson Bay and northern Manitoba (Rees 1973; Godfrey 1979). Nesting occurs in areas of scrub, where there is a heterogeneous environment of open tundra, stunted spruce, and willow (Semple and Sutton 1932; Rees 1973). The species is reported to be monogamous, and males defend territories against conspecific males (Semple and Sutton 1932). Interspecific territorial aggression has been observed between Harris' sparrows and white-throated sparrows (*Z. albicollis*) and white-crowned sparrows (*Z. leucophrys*) in the Churchill region (Rees 1973; C.T. Naugler, unpublished data).

Study area

The study was conducted from 3 to 20 June, 1986, 1 to 30 June, 1989, and 4 to 30 June, 1990, in the region between the town of Churchill, Farnsworth (Landing) Lake, and Twin Lakes. In the Churchill region, nest initiation usually begins by 31 May, incubation by 12 June, and fledging by 30 June (Rees 1973). In 1989 and 1990, territorial male Harris' sparrows were first sighted on the 7 and 6 of June, respectively. Fieldwork was performed during peak singing hours near dawn and dusk, usually from 04:00 to 11:00 and 19:00 to 23:00.

Subjects

The location of males was determined as soon as possible after their arrival at the breeding grounds. Individuals were not banded, but because of their strong site fidelity within a breeding season, identification was possible by flagging territories (Rees 1973). Individuals sang consistently from certain perches. All repeated recordings, observations, and playback experiments during a particular breeding season (1989, 1990) were carried out only at these known perches. Within each year, individuals could also be reliably identified by analyzing sonograms (unpublished data).

In 1986, individual males were recorded on a single occasion only, whereas in 1989 and 1990 we tried to record each male at least twice. It is possible that some individuals were recorded in both 1989 and 1990. This is unlikely because recordings were not made from exactly the same locations and no two sets of sonograms were identical. However, if male shift territories and (or) change their songs between years, resampling could have occurred.

Song recording

In 1986 recordings were made with a Uher 4000 tape recorder and a Beyer 26-C microphone mounted in a Sony PBR 330 parabola. In 1989 and 1990, recordings were made with either an Audiotechnica AT815a Line Cardioid/Electret microphone, or a Sennheiser ME 88 'shotgun' microphone and a Sony Walkman Professional WM-D6C cassette recorder. The recording system was calibrated before each session using a 660-Hz tone from a pitch pipe. The fourth harmonic (2.64 kHz) of this tone was measured during analysis.

Song-matching experiments

The majority of playback experiments reported here were performed during the 1989 field season. A small number of trials (five, with two birds) were performed in 1990, using identical procedures.

Playback stimulus tapes were prepared from recordings made in 1986 to reduce the possible effects of song familiarity on subjects' responses (Falls et al. 1982). Stimulus songs were filtered before preparation of the tapes (<0.5 and >5 kHz; -20 dB). Each stimulus tape was of 2 min duration, containing 20 repetitions of a two-syllable song from one male. This singing rate (10 songs/min) was the estimated average from the 1986 recordings. Two-note songs were used as they were the most common during the 1986 recordings. Three stimulus tapes were made for each of two frequencies: 4.1 ± 0.06 and 3.0 ± 0.07 (SE) kHz. These frequencies were at the high and low ends of the species frequency range, respectively. Each of the three songs at a given frequency was from a different male. Amplitudes of the playback stimuli were standardized prior to the study at 93.7 dB; SE = 0.81 dB; $n = 6$; re 0.0002 dynes/cm² at 1 m ('slow' reading, Realistic sound-level meter). Volume settings were then held constant during all experiments. All manipulations during the preparation of stimuli were performed digitally on a Macintosh IIx computer, using MacSpeechLab 2.0, SoundEdit, and Soundwave software. Stimulus songs were then recorded onto a Panasonic RQ-330 cassette recorder.

Playbacks with each of the two song frequencies were attempted with each known male. Stimulus songs were played from the same Panasonic RQ-330 cassette recorder described above, through an Aiwa SC-A8 speaker-amplifier. The playback speaker was placed approximately 2 m above the ground. The order of stimulus presentation was counter-balanced (i.e., half of the subjects heard the low stimulus first and half heard the high stimulus first). The presentation order alternated between high and low stimuli, though the actual tape presented (one of three) was randomly chosen. To reduce any effects of previous countersinging

by a subject, a trial began by observation of the subject's territory for 8 min. In order to proceed with the trial, the subject could not be observed in an activity involving singing, calling, or other territorial or sexual behaviour during this period. Males were then played one of the stimulus tapes. The subject's response songs were recorded simultaneously with observations of its distance from the speaker and the number and direction of flights. A trial was ended if a bird did not respond by flying towards the speaker or singing within 2 min of the end of the stimulus song. If a male did respond, the trial was ended when it stopped singing for at least 2 min, or if it started singing in response to, and flying towards a neighbouring male.

An experiment was considered successful if males responded to the stimulus song by approaching the speaker and (or) singing. Experiments in which there was an approach but no song were used for analysis of response strength only, and were repeated later. If there was neither song nor approach to the speaker, the experiment was scored as 'no response' and repeated at a later date. Subsequent playback trials with each subject were performed at least 2 days apart to prevent habituation to the stimulus tapes.

A match was scored when the first response song following the onset of playback was the closest one (in frequency) in the bird's repertoire to the stimulus song. The expected frequency of matching was calculated as the sum of the proportional frequencies of use during spontaneous singing of the closest song type.

Analyses

Songs were digitized and analyzed using MacSpeech Lab 2.0 on a Macintosh IIx computer, or analyzed on a Kay Elemetrics DSP sonograph model 5500, with a resolution of 29 Hz. For each male, at least three songs of each frequency at which it sang were measured during each recording session. For the 1989 recordings, at least three renditions of one-, two-, and three-note songs were measured for each frequency level at which a subject sang during a recording session. The frequency of each song was measured as the peak frequency of a spectral slice at the midpoint of the first syllable.

Results

In 1986, 7 males were recorded. In 1989, 17 males were recorded more than once and 3 males were recorded once only. In 1990, 11 males were recorded, 4 of them once only. For the bulk of the analyses, only those males that were reliably recorded on more than 1 day were included.

Recording sessions lasted from 3 to 25 min, and ranged from about 25 to 300 songs per session (mean 68 ± 6 (SE) songs).

Singing behaviour

Males were singing upon arrival at the study area. Males usually sang for extended periods of time (up to 50 min) from the same perch at a rate of approximately 10 songs/min. Males were never observed to sing in flight. Most singing occurred during the morning and evening, but song was occasionally heard at other times during daylight hours. No song was heard between 23:30 and 04:00.

Song was usually directed at other, countersinging males. Only rarely were males heard singing alone. Singing decreased rapidly during incubation and was rare after hatching (S. A. Shackleton, personal observation). Males were never seen to direct their song at females (S. A. Shackleton and C. T. Naugler, personal observation).

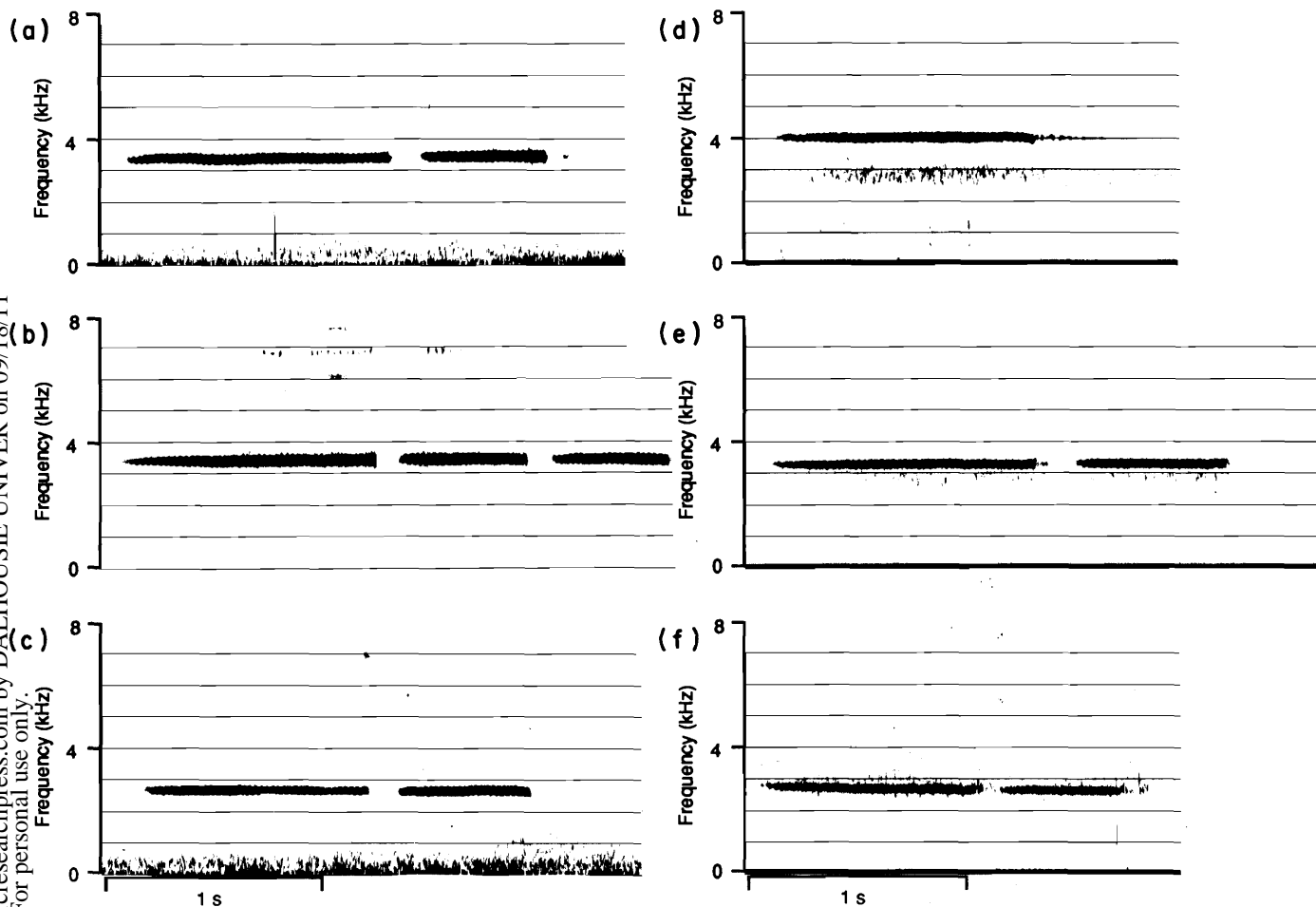
All the recordings in the following analyses were of spontaneous song (i.e., sung by males perched within their territory, and not involved in a territorial skirmish).

Song variation

A typical Harris' sparrow song is composed of one to three notes, all at the same frequency (Fig. 1). One four-note song was recorded during the study period. The first note is always the

Bird 89-02

Bird 90-04



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FIG. 1. Example sonograms of songs of two male Harris' sparrows recorded at Churchill in 1989 and 1990. (a–c) Bird 89-02 has a repertoire of two song types: *a* and *b* are a two-note and a three-note rendition of the high song type, respectively, and *c* is a two-note rendition of the low song type. (d–f) Bird 90-04 has a repertoire of three song types: *d* is a one-note high song type, *e* is a two-note medium song type, and *f* is a two-note low song type.

longest, and the second and third notes are approximately half as long as the first (Table 1). The pause between notes within a song was never greater than 150 ms.

The peak frequency was measured every 250 ms in a subsample of songs recorded in 1989 (65 songs, 5 birds). The mean of these measures was strongly correlated with the frequency at the midpoint of the first note ($r = 0.998$, $n = 65$ songs, 5 birds). The average coefficient of variation (CV) of these measurements was 1.4 ($n = 65$ songs, 5 birds). This represents fluctuations of frequency of approximately 40 Hz (SD) within a song sung at 3 kHz.

Figure 2 illustrates a typical bout of Harris' sparrow song (a bout was defined as a period of singing uninterrupted by pauses >120 s). Within a bout, songs were sung at highly stereotyped, exclusive frequencies, with a mean CV of only 0.5 (Table 2). Harris' sparrows were also extremely accurate at returning to these same frequencies on later days, with a mean CV of 1.3 between bouts (Table 2, Fig. 3a). CVs between bouts ranged from 0.23 to 4.25 (Table 2). In 31 of the 34 males there was no significant variation in the accuracy with which they returned to the same frequency on later days ($F_{\max} = 3.0$, $p > 0.1$, $df = 18$). Even the 'sloppiest' of the four outlier males, however, had a CV

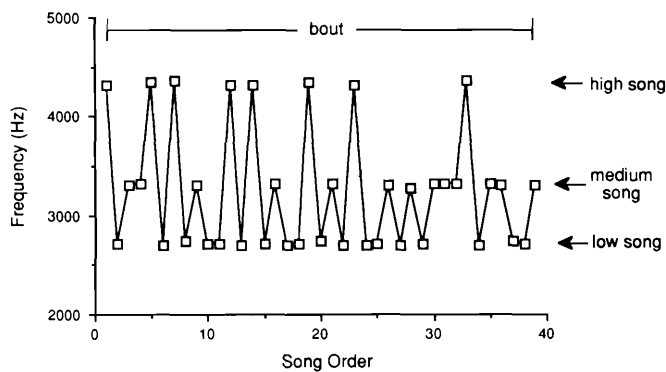


FIG. 2. Example bout of Harris' sparrow song; a bout is defined as a period of singing uninterrupted by pauses >120 s. Note that there is immediate variety among song types (high, medium, and low), and that song order is apparently random.

of only 4.25 (Table 2). This represents a fluctuation (SD) of about 130 Hz for a 3-kHz song type among five bouts recorded over a period of 18 days.

Although the frequency of song types was highly stereotyped

TABLE 1. Temporal measurements of songs of 15 male Harris' sparrows recorded at Churchill in 1986 and 1989

No. of notes	Duration (ms)					N
	First note	Interval one	Second note	Interval two	Third note	
One	1229±26	—	—	—	—	51
Two	1148±13	100±3	543±7	—	—	122
Three	1044±23	95±3	528±13	92±3	459±10	29

NOTE: Values are given as the mean ± SE. N is the number of songs.

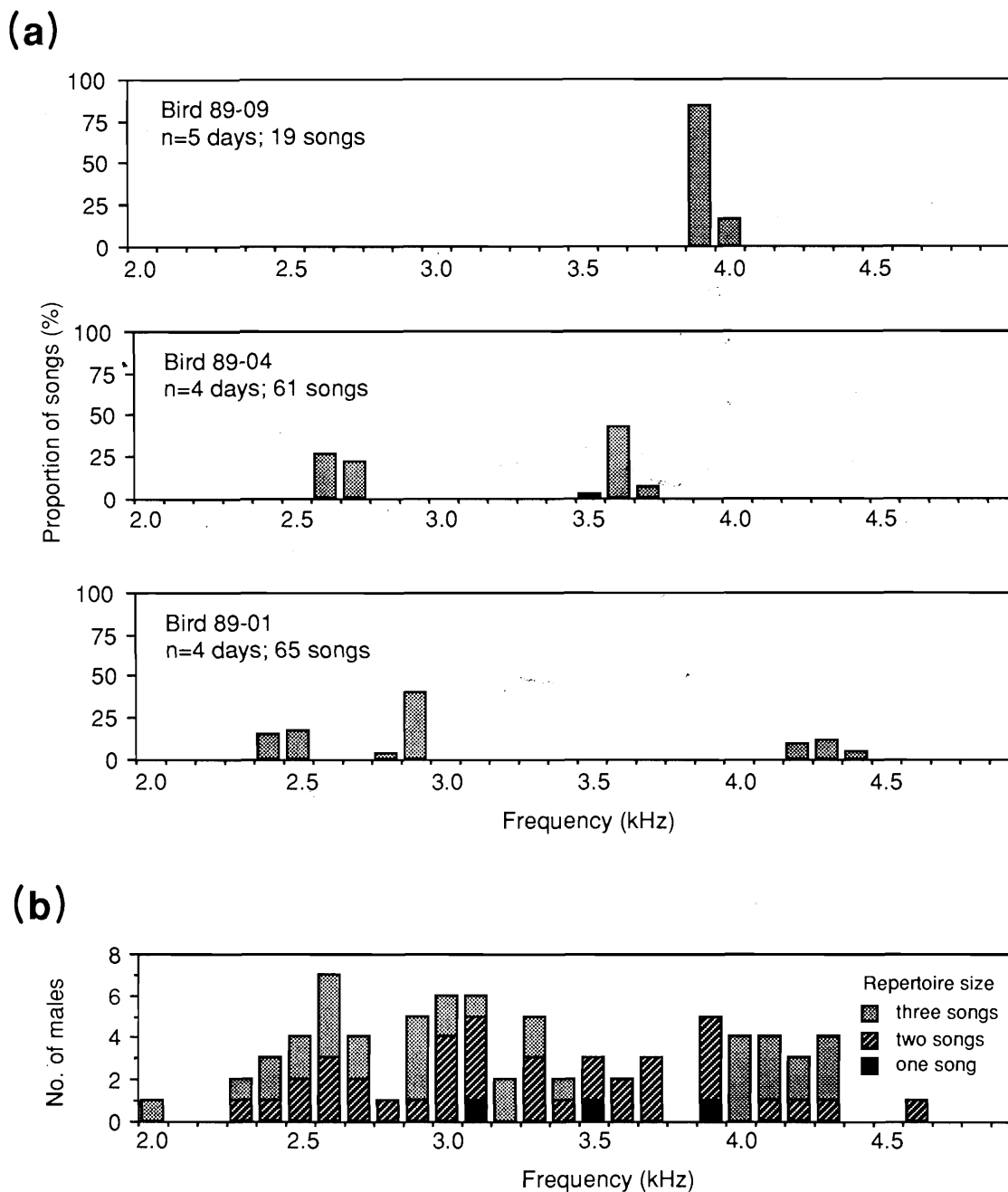


FIG. 3. Histograms of frequency use by Harris' sparrows. (a) Singing patterns of exemplary one-, two-, and three-repertoire males recorded in 1989. The accuracies with which these males returned to the same frequency on later days were near the mean (within 1 SD) for the population recorded. Columns indicate the percentage of songs that the individual sang at the frequency indicated. (b) Histogram of frequency use by all males recorded during the 3-year study period. Stacked columns indicate the repertoire size of the male that sang within the frequency range indicated. Each song type represents one unit, e.g., a male with three song types is indicated at three points on this histogram.

TABLE 2. Variation in frequency between repetitions of song types of Harris' sparrows recorded in 1989

	CV				
	Mean	SE	Eange	N_1	N_2
Within bouts ^a	0.504	0.026	0.0–1.70	17	120
Between days ^b	1.257	0.197	0.23–4.25	17	27

NOTE: CV = SD × 100/mean.

^aVariation in the frequency of each song type within a bout. (N_1 is the number of birds; N_2 is the number of song types × the number of bouts recorded).

^bVariation between the mean frequency of each song type between bouts, i.e., days (N_1 is the number of birds; N_2 is the number of song types).

within a bout, the number of notes in a song type often varied within a bout. There was no correlation between the number of notes and the frequency of the song ($r = 0.08$, $n = 452$ songs, 17 birds). There was also no significant variation in the frequencies of one-, two- and three-note songs across the population (Kruskal–Wallis, $H = 0.093$, $p = 0.95$, $df = 2$). Song types were consistently different in frequency, but were not consistently different in note number.

Repertoire structure

Individuals sang one to three song types, two being most common (3 males sang one song, 19 males sang two, and 12 sang three). The high switching rate (Fig. 2) enabled us to record the entire repertoire of each individual with a sample of only 15 songs (unpublished data). No new song types were ever recorded for any male after a sample of 15 songs.

We examined the distribution of song frequencies used by the population in order to determine whether it reflected the discrete nature of individuals' repertoires. The frequency of songs ranged from 2.0 to 4.7 kHz (Fig. 3b). Across all males, this distribution was almost continuous. In other words, different males do not 'agree' on the frequency of their song types.

Using the distribution shown in Fig. 3b, we divided the species range into low, medium, and high categories (<2.9, 2.9–3.8, and >3.8 kHz, respectively). These breakpoints were chosen as frequencies at which one or no males sang (Fig. 3b). We then classified the repertoires of all males with more than two song types (31) according to these categories. Of these males, only one possessed two song types within a single category. Moreover, of all males with only two song types (19), none lacked a song in the medium category, regardless of whether its other song was high or low, that is, multiple song types were always in adjacent categories. Of the three males with one song type, two sang in the medium and one sang in the high category (Fig. 3b). This suggests that individual repertoires are not composed of songs chosen at random from the species' frequency range.

Further analyses were conducted to determine the nature of the relationship between songs within a repertoire (repertoire structure). This could be either a ratio function or a difference function of frequency. To determine which was the case in Harris' sparrows, we compared the frequency ratio (FR) to the frequency difference (FD) between adjacent song types. (Adjacent song types are those types next to each other in rank order by frequency). The FR between two songs was calculated as the frequency of one song type divided by the frequency of the next lower type, and FD was calculated as their arithmetic difference. We used the mean FR (1.34 ± 0.012 (SE)) and mean FD (927 ± 37 Hz (SE)) between the songs of only those birds with a repertoire of two to create expected values of lower song

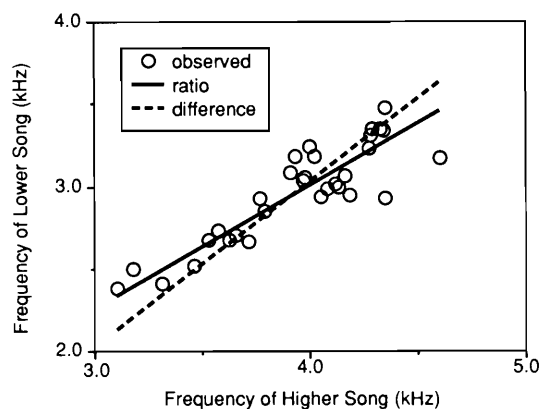


FIG. 4. Comparison of the frequency ratio with the frequency difference between the songs of Harris' sparrows with a repertoire of two. The hypothetical ratio line gives a better fit to the observed data ($\chi^2 = 82$) than does the hypothetical difference line ($\chi^2 = 183$).

frequencies from the observed higher song frequencies. The ratio values were more similar to the observed data than the difference values (goodness of fit; $\chi^2 = 82$ for ratio, $\chi^2 = 183$ for difference; Fig. 4). Therefore, a ratio function is a better predictor of the relationship between adjacent songs than is a difference function.

Males with three song types have two FRs, one between the high and medium songs (FR_{3H}) and between the medium and low songs (FR_{3L}). FR_{3L} is significantly smaller than FR_{3H} (repeated measures ANOVA, $F_{[1,12]} = 8.82$, $p = 0.02$; Table 3); thus, there is not a single relationship between adjacent types. Using the categories outlined above, two-song males could be divided into two classes; those with a high and a medium song (10) and those with a medium and a low song (9). There was no significant difference between the FRs of these two classes, so they were pooled as FR_2 (one-factor ANOVA, $F_{[1,17]} = 1.20$, $p = 0.29$; Table 3). FR_{3H} was not significantly different from FR_2 (one-factor ANOVA, $F_{[1,29]} = 0.32$, $p = 0.58$) but FR_{3L} was significantly smaller than both FR_2 and FR_{3H} (one-factor ANOVA, $F_{[1,29]} = 14.23$, $p = 0.001$; Table 3).

Song matching

Fifty-six playback trials were attempted in 1989. In 27 of these the subject responded with song, and in 6 it responded without song. Six of the 27 responses with song were by males with only one song in their repertoire and were used only in the analysis of response strength.

Males varied in the proportional use of each song type. In 17 of the 18 responding multisong males, the proportional use of each song did not vary significantly between recording sessions (χ^2 contingency table; all $p > 0.05$). The remaining male did not alter the results, so was included in these analyses, using mean values for proportional use. The proportional use values were used to determine the number of matches expected by chance.

Individuals responded with the song from their repertoire that was closest to the stimulus song significantly more often than expected for the 3-kHz stimulus ($N = 11$ birds; Table 4). Individuals did not match significantly the 4.1-kHz stimulus, however ($N = 9$ birds; Table 4). It is clear that individuals matched the 3-kHz stimulus, because more non-matches than matches were expected by chance. For the 4.1-kHz stimulus, however, more matches were expected by chance. In this case, a much larger sample may be necessary to demonstrate a significant difference, even though matching may be occurring. Matches outnumbered non-matches for five of the six stimulus

TABLE 3. Comparison of frequency ratios between song types of Harris' sparrows

Ratio	Mean \pm SE
FR _{3H}	1.339 \pm 0.021a
FR _{3L}	1.236 \pm 0.023b
FR ₂	1.326 \pm 0.012a

NOTE: FR_{3H}, ratio between the high and medium songs of three-song males; FR_{3L}, ratio between the medium and low songs of three-song males; FR₂, ratio between the songs of two-song males. Values followed by the same letter are not significantly different from each other ($P < 0.05$) (see text for test statistics).

TABLE 4. Results of matching experiments

Playback	Observed	Expected	χ^2	
4100 Hz				
Matches	6	5.18		
Nonmatches	3	3.82	0.08	$p > 0.50$, $df = 1$
3000 Hz				
Matches	8	3.9		
Nonmatches	3	7.8	7.07	$p < 0.01$, $df = 1$

NOTE: Harris' sparrows matched the 3000-Hz stimulus more often than expected by chance, but did not match the 4100-Hz stimulus. χ^2 values are corrected for discontinuity.

tapes. Individuals did not match the note number (two notes) of the stimulus song ($\chi^2 = 1.42$, $p > 0.05$, $df = 1$); however, there were significantly more one-note songs in response to playback than in spontaneous song ($\chi^2 = 6.38$, $p < 0.05$, $df = 1$).

The number of responses (an approach to the speaker and (or) a song) to each of the six playback tapes did not differ significantly from that expected by chance ($\chi^2 = 7.47$, $p > 0.1$, $df = 5$). There was also no significant variation in the latency of response among the six tapes (one-factor ANOVA, $F_{[5,27]} = 1.21$, $p = 0.34$). There was also no difference in the number of song matches to each tape, given the number of responses ($\chi^2 = 1.92$, $p = 0.9$, $df = 5$). In other words, we detect no differential effect of tape version on these results.

There was no correlation between the similarity of the stimulus song (to the subject's own song) and the number of songs in the response ($r = 0.3$, $N = 37$), the latency to response ($r = 0.06$, $N = 37$), the number of flights in response ($r = 0.33$, $N = 37$), or the minimum distance to the speaker ($r = 0.01$, $N = 37$). Also there was no significant difference between the matched responses and the non-matched responses in the number of songs (Mann-Whitney $U = 38.5$, $p = 0.61$, $N = 15,6$), the latency ($U = 39$, $p = 64$, $N = 15,6$), the number of flights ($U = 34.5$, $p = 0.41$, $N = 15,6$), or the minimum distance ($U = 27$, $p = 0.16$, $N = 15,6$). Thus, it appears that the matching response is qualitatively different from the strength of a response.

There was also no significant difference in the switching rate (measured as the mean number of repetitions of a type before switching) between spontaneous singing and response to playback in a subsample of six subjects who responded to playback with more than 10 songs (repeated-measures ANOVA, $F_{[1,6]} = 0.4878$, $p = 0.516$). Since switching rates are high during spontaneous singing (Fig. 2), differences in this rate would be difficult to detect.

Owing to time limitations, only five playback trials were performed in 1990 ($N = 2$ birds). The procedures were identical

with those used in 1989, but new stimulus tapes of songs at 2.4, 2.8, 3.8, and 4.3 kHz were used. Three of the five responses were matches (using the same criterion as in the 1989 experiments). This proportion was not significantly different from that expected by chance ($\chi^2 = 3.21$, $p = .05$, $df = 1$).

Discussion

Song types

Over 75% of songbird species have song repertoires, that is, males sing more than one variant of the species-characteristic song (Hartshorne 1973). Although the functional significance of repertoires has been the subject of much research (Krebs and Kroodsma 1980; Slater 1981; Kroodsma 1982), a major problem has been defining what constitutes a song type. In some species whose song types have been extensively studied (e.g., great tits), an individual's song types can be easily distinguished from each other on the basis of several frequency and temporal parameters (McGregor and Krebs 1982). Types are discrete, that is, there is no continuous variation between types. Although there may be variation between two birds' renditions of the same type, they are usually more similar to each other than they are to other types.

The main finding of this study is that Harris' sparrows do not have a single stereotyped song. In terms of song production, the songs sung at different frequencies can be considered discrete types. As with other repertoire species (e.g., McGregor and Krebs 1982; Horn and Falls 1988), there is no continuous variation in structure between an individual's different song types, and the variation between types is much greater than the variation within types.

Harris' sparrows appear to be unique in producing distinct song types differing only in one obvious parameter: frequency. Although the note number may encode some information, such as aggressive motivation (playback elicited more one-note songs), we do not believe it to be a parameter of song types. Song types must be consistently reproduced between renditions. The same note number, however, was not consistently repeated by a given male. Whitney (1981) found that the song types of the varied thrush could be distinguished by means of only two parameters: frequency and amplitude modulation. Although some song types are differentiated by researchers on the basis of a single parameter, the birds use multiple parameters to discern different types (Weary et al. 1990a).

One way in which birds demonstrate that they categorize different songs as different is by song matching. There is good evidence that Harris' sparrows did match the 3-kHz stimulus, but no evidence that they did not match the 4.1-kHz stimulus. Males matched both stimuli more often than they did not. The lack of a significant difference for the higher playback is because a high level of matching was expected by chance, not because matching was not occurring. The results from playbacks performed in 1990 similarly support the conclusion that Harris' sparrows match songs. The way in which Harris' sparrows perceive different frequencies and note numbers is a topic for further research.

Unlike other repertoire species, the discrete nature of individuals' song types is not reflected in the distribution of song types across the population. In other repertoire species there is usually less variation within a song type among individuals than there is among the types. Harris' sparrows do not all 'agree' on what constitutes a 'type' and seem to structure their repertoire on the basis of differences within the repertoire rather than on external standards. Harris' sparrows are dissimilar to other

repertoire species in that individuals do not share song types. They do, however, possess consistently produced, discrete song types. There is continuous variation in the frequency of songs among males, but we define song types on the basis of differences within the repertoire of an individual male.

Repertoire structure and possible functions

Although the absolute frequencies of different males' song types are not the same, there is consistency among individuals in the way repertoires are structured. There is a constant interval between the two highest song types an individual has ($FR_2 = FR_{3H}$), and if there is a third song, it is added by a constant interval (FR_{3L}) at a lower frequency. In this way, individuals may have one-, two-, or three-song types within the species' range that are not necessarily at the same frequencies as any other male's songs. These intervals are better predicted by a ratio than by a difference. The way in which Harris' sparrows structure their repertoires is similar to the way other species' structure notes within songs (Hurly et al. 1990; Weisman et al. 1990). To determine whether Harris' sparrows actually use a ratio rule to perceive the differences among song types requires further experiments.

Becker (1982) suggested that species-specific information should be encoded in characters of bird song that are relatively invariable among males, and that characters which are relatively variable among males may encode information about the individual. The ratio between song types, then, may be a species-specific cue while the absolute frequency of a male's song types may encode information about the individual. It has also been suggested that the relative and absolute frequencies provide information for species and individual recognition, respectively, in black-capped chickadees (*Parus atricapillus*) (Weisman et al. 1990).

Having multiple song types could facilitate neighbour recognition in Harris' sparrows, as has been suggested for great tits (Weary et al. 1990b). We found it possible to identify males reliably through the absolute frequency of their songs (unpublished data). The combination of song-type frequencies was unique to each individual. Neighbour recognition by song would require that an individual remember the absolute frequencies of his neighbour's song types, since the relationship between an individual's songs is relatively constant.

The way in which Harris' sparrows structure their repertoires suggests that switches between song type could encode information, such as agonistic intensity (as has been found in song sparrows, *Melospiza melodia*; Kramer et al. 1985). We found no difference in switching rate between spontaneous singing and response to playback. More detailed examination of switching rates by males in different behavioural contexts might yield different results. However, since males with more than one song type always sing with a high degree of immediate variety, changes in switching rate would be difficult to detect, both statistically and by other birds.

Another possible function of repertoires in Harris' sparrows is that individuals are trying to avoid masking by conspecifics. Each male could be utilizing a set of clear 'frequency channels.' However, if there was strong selection to avoid masking, more complex songs would be expected to develop. Also, our finding that Harris' sparrows match playback songs with the closest song in their repertoire contradicts this hypothesis.

Conclusions

Our study, along with other recent work, suggests that there are several levels of 'song types.' Traditionally, songbirds have

been divided into two groups: repertoire species, and those with a single song type (e.g., Krebs and Kroodsma 1980). Perhaps, however, there is a continuous spectrum ranging from birds that sing a single stereotyped song to those with large repertoires of discrete 'types' which are shared among individuals. Only recently have any studies focused on the area between these two end points. Our results indicate that Harris' sparrows have discrete types which are not shared among individuals. Morton and Young (1986) found that Kentucky warblers (*Oporornis formosus*), which have only a single song type, can match stimulus songs that have been artificially raised or lowered in pitch, by shifting the emphasized frequency within their song. The phenomenon of song matching was previously known to occur only in repertoire species such as great tits (Falls et al. 1982). Shifting between song types has also only been extensively studied in repertoire species (e.g., western meadowlarks, *Sturnella neglecta*; Horn and Falls 1988). Black-capped chickadees do not have discrete song types (contrary to Hill and Lein 1987), but they do repeat songs at a given frequency many times before shifting to a new frequency (A. G. Horn, M. Leonard, L. Ratcliffe, S. A. Shackleton, and R. G. Weisman, submitted for publication). Japanese bush warblers (*Cettia diphone*) also shift the frequency of song types (C. L. Whitney, personal communication). In these species, shifting could perhaps have similar functions to the shifting between song types in repertoire species. Observations of these species call attention to the need for clear definitions of terms such as 'song types,' which may have multiple levels of meaning, and further demonstrate that many of the phenomena which have been studied in typical repertoire species may occur in those species commonly thought to have a single song type.

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