

FREQUENCY SHIFT IN THE FEE BEE SONG OF THE BLACK-CAPPED CHICKADEE

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The two-note, whistled *fee bee* of the Black-capped Chickadee (*Parus atricapillus*) is considered one of the most simple and stereotyped of parid songs (Dixon and Stefanski 1970, Latimer 1977, Ficken et al. 1978). Individual males may add a third note (*fee bee bee* or *fee bee yee*; e.g., Saunders 1935; Odum 1941, 1942, Brewer 1961), but within-individual variation in note frequency (pitch) has seldom been reported. Saunders (1935) and Odum (1942) mentioned hearing single males occasionally singing *fee bee* at different pitches. Ficken et al. (1978), however, reported virtually no individual variation in the frequency characteristics of *fee* and *bee* notes in a sonographic analysis of five males that were singing alone, although pitch changes were heard during countersinging (M. Ficken, pers. comm.). Hence, during recent work on *fee bee* song recognition, we were surprised to record extensive frequency shifts in the *fee bees* of captive male chickadees. Here, we describe the pattern of frequency variation and its context, and examine Saunders' (1935) suggestion that males will shift frequency in response to hearing conspecifics.

We mist-netted a flock of seven chickadees near Kingston, Ontario, on 31 January 1984, and kept them indoors in adjacent individual cages. Four males were identified by singing behavior (loud *fee bees*, Ficken et al. 1978). From March to August, 1984, we recorded males in two contexts: either alone (solo context), or within earshot of *fee bee* song playback (playback context). In the playback experiments, males were presented with eight bouts of *fee bee* song; bouts consisted of two consecutive, unshifted *fee bees* and were separated by 3-min silent intervals. Solo songs were obtained from males who had not been exposed to any playback during the previous 48 h. Songs were recorded on either a BASF cassette recorder with a Realistic 200 Dynamic microphone, or a SONY VU-matic audio/video cassette recorder with a SONY cardioid microphone. In every case, we isolated males from their flockmates overnight and then recorded their songs the following morning. We analyzed all songs that produced clear traces on a Kay Elemetrics Digital Sonagraph (using the 45 Hz band setting), following the methods of Ficken et al. (1978).

All four males sang two kinds of loud *fee bee* songs, which we classified as either "normal" (the most common song form in each male's overall repertoire) or "shifted." The proportion of shifted songs that were given within any one recording session varied from 4-73%. Males tended to intersperse single, shifted songs between bouts of normal song. Table 1 gives the frequency characteristics of normal and shifted songs for each male. Frequency varied but little within individuals in either type of song, as shown by the SE values which ranged from 0.01 to 0.08. Shifted songs were always lower in frequency than were normal range songs, which contrasts with Saunders' (1935) observation that individuals shifted pitch both upwards and downwards from the normal song. In all cases, the mean frequency of both *fee* and *bee* notes was significantly lower in the shifted songs than in the normal songs: Male

TABLE 1. Frequency characteristics (kHz) of normal and shifted *fee bees*.

Male		Normal		Shifted	
		<i>Fee</i>	<i>Bee</i>	<i>Fee</i>	<i>Bee</i>
1	\bar{x}	3.96	3.39	3.57	3.09
	SE	0.01	0.04	0.08	0.06
	n^*	(25, 122, 59)		(21, 38, 12)	
2	\bar{x}	3.97	3.43	3.71	3.22
	SE	0.04	0.02	0.03	0.06
	n	(10, 47, 0)		(9, 9, 0)	
3	\bar{x}	3.83	3.19	3.54	3.15
	SE	0.01	0.01	0.03	0.01
	n	(15, 47, 38)		(12, 16, 12)	
4	\bar{x}	4.08	3.53	3.94	3.20
	SE	0.04	0.02	0.02	0.01
	n	(6, 24, 24)		(6, 12, 12)	

* n = sonagrams measured, total songs recorded, songs recorded in solo context.

1: $t > 18.70$, $df = 44$, $P < 0.01$; Male 2: $t > 3.28$, $df = 17$, $P < 0.01$; Male 3: $t > 2.08$, $df = 25$, $P < 0.05$; Male 4: $t > 3.51$, $df = 10$, $P < 0.01$. Also, the mean difference between the *fee* and *bee* notes (the frequency span) was less in shifted than it was in normal songs of all males, significantly so for Males 1 ($t = 5.27$, $df = 44$, $P < 0.01$), 3 ($t = 9.13$, $df = 25$, $P < 0.01$), and 4 ($t = 4.97$, $df = 6$, $P < 0.01$).

The mean frequency span of normal and shifted songs changed little as a function of either recording context or repeated observations. Two males, 1 and 3, were recorded in both solo and playback contexts. We noted no significant differences in mean frequency span between contexts for either normal or shifted songs (t -tests, $P > 0.05$). Similarly, of the three males recorded on more than one occasion (Males 1, 2, and 3), none differed significantly in mean frequency span among occasions for shifted songs (Male 1: $F = 0.55$, $df = 2, 6$, $P = 0.61$; Male 2: $F = 1.48$, $df = 2, 18$, $P = 0.25$; Male 3: $F = 0.01$, $df = 1, 10$, $P = 0.91$). Only one male (No. 2) showed significant heterogeneity in mean frequency span among occasions for normal song ($F = 6.10$, $df = 2, 7$, $P < 0.05$). This result was due to a slightly higher mean frequency of *fee* on the first of three recording occasions.

We found no evidence that Males 1 and 3 (for which there were sufficient data) sang significantly more shifted songs when they could hear conspecifics (i.e., during playback context) than when they could not. The overall percentage of shifted songs was: Male 1: 17% in solo context, 29% in playback context, $\chi^2 = 3.31$, $P > 0.05$; Male 3: 24% in solo context, 45% in playback context, $\chi^2 = 0.25$, $P > 0.50$). Although we found no significant effect of context on the production of shifted songs, the fact that both males sang more shifted songs during playback suggests that more extensive experiments are needed to answer this question.

Our analyses support earlier field observations (Saunders 1935, Odum 1942) of frequency shift in Black-capped Chickadees, with two differences: each male had a single version of shifted song (lowered in frequency), and shifted songs were sung quite regularly. This behavior seems to be widespread at the local level, since we have both heard wild chickadees singing shifted songs (of lower frequency) up to 90 km from Kingston. The functional significance of shifted song remains unclear and will require intensive recording of marked individuals in the field. We conclude that variation within individuals in the frequency characteristics of *fee bee* songs is greater than recent sonographic work on lone males (Ficken et al. 1978) has implied.

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SEASONAL CHANGES IN DETECTABILITY OF SAGE AND BREWER'S SPARROWS

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Seasonal changes in the detectability of individual bird species may confound efforts to estimate population densities. This is particularly true during the breeding season, when such changes may be pronounced (e.g., Best 1981). The time and duration of the period within the breeding season when detectability is greatest for one species may differ substantially from those for another, necessitating adjustments in scheduling and interpreting census counts. Also, seasonal fluctuations in detectability may change from one year to the next. At present, little information is available on seasonal patterns of detection (or song) of North American birds during counts; the best documentation comes from European studies (see references in Best 1981:260). Best (1981) presented seasonal profiles of detection for selected bird species breeding in woodland and forest habitats of Iowa, and Emlen (1984) reported seasonal trends in song frequency of birds breeding in an arboretum in Wisconsin. Seasonal patterns of detection have not been reported for bird species occupying the vast areas of shrubsteppe in the western United States, although many studies conducted in that region have depended upon bird census results for their conclusions (e.g., Walcheck 1970, Best 1972, McGee 1976, Rotenberry et al. 1979, Wiens and Rotenberry 1981).

The Sage Sparrow (*Amphispiza belli*) and Brewer's Sparrow (*Spizella breweri*) are two of the dominant bird species breeding in the sagebrush-grasslands of Idaho, Oregon, and Washington (Wiens and Dyer 1975, Wiens and Rotenberry 1981, Reynolds and Trost 1981). Best and Petersen (1982) documented the effects of stage of the breeding cycle on Sage Sparrow detectability, but seasonal changes in detectability could not be derived directly from the breeding cycle data because the birds nested asynchronously. Seasonal changes in detectability of this species and the Brewer's Sparrow have yet to be reported. In this study, our objective was to document changes in the detectability of these two species during the breeding season.

Because most birds were marked and all territories were mapped (see below), we could derive seasonal profiles of detectability, adjusted for seasonal changes in bird densities. Such profiles may be used when planning bird-count schedules and when interpreting census results for sagebrush-grassland bird communities.

The study was conducted in 1981 and 1982 on the Idaho National Engineering Laboratory (INEL), approximately 11 km south of Howe, Butte County, Idaho. The topography is flat to gently rolling. Dominant plant species included big sagebrush (*Artemisia tridentata*), green rabbitbrush (*Chrysothamnus viscidiflorus*), bluebunch wheatgrass (*Elytrigia spicata*), Indian rice grass (*Oryzopsis hymenoides*), and bottlebrush squirreltail (*Elymus elymoides*). Substantial portions of the ground were bare. Four 6.25-ha study plots, gridded throughout at 25-m intervals, were established. Most birds were mist-netted soon after their arrival on the study area and were marked with colored leg bands. In May and June, we mapped territories of all males by using the "flush" technique (Wiens 1969). Forty-three Sage Sparrow and 27 Brewer's Sparrow territories were delimited in 1981; 41 and 25 territories of the respective species were mapped in 1982. Each plot was visited at least twice weekly, thus enabling us to closely track seasonal fluctuations in population densities and pairing status of all territorial males.

Birds on each plot were counted weekly during the breeding season (5 May-2 July 1981 and 22 May-8 July 1982), by using field procedures similar to those for the spot-map method (Robbins 1970). Counts were started later in 1982 because the breeding phenology was delayed that year (see below). Counts began 15 min before sunrise and ended 2.5 h after sunrise. On a given day, birds on two plots were counted, and we alternated from week to week the plot that we visited first. Counts were not made on days with rain or strong wind (>15 kph). Every other grid line was followed during a count until the plot had been completely traversed; the location and behavior of birds that we observed were recorded on grid maps of the plot. When we saw individual birds moving from one location to another during a count, only the initial sighting was included. We assumed that the circumstances under which birds are first observed are influenced less by the observer's presence, thus providing the best indication of seasonal changes in detectability. Multiple sightings of individual birds were regarded as separate observations only if the observer lost visual and/or auditory contact with the bird between observations. Daily weather information, measured at Howe, was obtained from the National Climatic Center, Asheville, North Carolina.

Seasonal changes in detectability of the two sparrow species were expressed in two ways: Total Observations and Singing Observations. All bird observations on each