

ABSOLUTE AND RELATIVE PITCH PRODUCTION IN THE SONG OF THE BLACK-CAPPED CHICKADEE¹

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Abstract. Black-capped Chickadee (*Parus atricapillus*) song consists of two notes, termed *fee* and *bee*. Frequency measures at three key points (at the start and end of *fee*, and at the start of *bee*) were obtained from the songs of a large sample of chickadees ($n = 151$) in the wild. In this sample, 19 birds produced songs shifted downward in frequency as well as their normal songs. Analysis of normal song revealed that *fee* declines in frequency in a glissando of nearly pure tone, then continues at greatly reduced amplitude at the start of *bee*; whereas *bee*, also a nearly pure tone, is always lower in frequency than either the start or end of *fee*. The absolute pitches (frequencies) of these measures vary substantially among birds, but much less within individuals. In contrast, pitch intervals (ratios of higher to lower frequencies) for frequency changes among the three measures are highly invariant among birds. Moreover, chickadees with normal and frequency-shifted songs maintain virtually the same pitch intervals in both. This analysis suggests that the absolute and relative pitch constancies in chickadee song production may provide information for individual and species recognition, respectively.

Key words: Song production; pitch change; species recognition; Black-capped Chickadee; *Parus atricapillus*.

INTRODUCTION

The normal *fee-bee* song of the Black-capped Chickadee (*Parus atricapillus*) consists of two clearly whistled notes, the second slightly lower in pitch than the first (Dixon and Stefanski 1970). Males sing loud *fee-bees*, usually in the context of long distance territorial advertisement (Ficken et al. 1978). Saunders (1935) and Odum (1942) observed that individual chickadees sometimes sing two versions of the *fee-bee* song; one version is shifted downward from the frequency of the normal, more commonly sung version. Recently, we (Ratcliffe and Weisman 1985) presented frequency measurements of normal and shifted songs for a small sample ($n = 4$) of chickadees. Subsequently, Hulse and Cynx (1986) analyzed these songs in terms of absolute and relative pitch.

Here we report further on absolute and relative pitch production in chickadees.

Absolute and relative pitch are studied in human music perception, but they may be important in passerine song production and recognition as well. Absolute pitch production refers to the ability to produce notes with little variation in frequency between renditions (Ward and Burns 1982). Relative pitch production refers to the ability to produce notes that bear constant ordinal or ratio relationships to temporally adjacent notes in repetitions of a song (Sundberg 1982). Melodious song in accomplished human singers is characterized by constancy in pitch contour and most often by constancy in pitch interval as well. Specifically, maintaining the pitch contour of a song means to maintain the ordinal, directional changes between adjacent notes in all renditions of the song. Maintaining the pitch intervals in the production of a song means to preserve the same frequency ratios between adjacent notes in all renditions of the song. For example,

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the interval of chickadee song is the ratio of the frequency of *fee* to *bee*. Hulse and Cynx (1986) suggested that the pitch interval was constant in the normal and frequency-shifted songs in our small sample of chickadee songs (Ratcliffe and Weisman 1985). In other words, it appears that chickadees may transpose their song downwards in frequency, showing pitch interval constancy, much as human singers produce the same melody in a lower key.

This report analyzes the frequency information from a large sample of chickadee songs recorded from a population in eastern Ontario. The purpose is to assess both absolute and relative pitch constancy and their implications for individual and species recognition in chickadees. Our assessment was guided by suggestions that relatively invariant song features tend to be important (Marler 1960, Becker 1982), or at least that oscines tend to weight such features more (Nelson 1988), in species song recognition. Conversely, features used to recognize individuals tend to vary greatly among birds, but tend to be much less variant within individuals.

METHODS

This study was conducted on a 50-ha study site at the Queen's University Biological Station at Lake Opinicon, Ontario, about 50 km north of Kingston, during April and May of 1987 and 1988. Most recorded songs were spontaneous, but some were elicited by playback or whistled human imitation of the *fee-bee* song. A Sony Walkman Professional WM-D6C cassette recorder and a Sennheiser M-816 "shotgun" microphone, or occasionally, a Dan Gibson P200 parabolic microphone, were used to record song. We recorded on BASF or TDK 90-min "Normal" cassette tapes, without Dolby noise reduction.

We recorded songs from 156 chickadees, identified by color bands or territory location. Our main sample consisted of three songs in a single bout from each of 132 birds ($n = 396$ songs). A second bout of three songs was recorded 8–16 days later from 11 birds in the main sample. A second sample, which yielded only one or two songs from an additional 19 birds, was included with the main sample in comparisons requiring only averages for individual birds ($n = 32$ songs).

In the main sample, 19 birds produced both normal and shifted songs. Shifted songs were lower in pitch by at least 200 Hz, as measured

at the end of the *fee* note. We included only the normal songs in analyses of the main sample. Finally, an additional five birds sang abnormal songs (*fee-fee*, only *fees*, etc.) and were excluded from these analyses.

Songs were digitized at a sampling rate of 22-k points/sec using a work station comprising a Macintosh SE computer, 8-bit Impulse digitizer, SoundCap, SoundWave, and SoundEdit software (Gibson 1988), and a Bessel filter, which yielded a useable frequency range from 0.2 kHz to 10.5 kHz. Graphic measurement of peak frequency from 1-k point spectrograms produced on the work station using SoundWave software had a resolution of about 20 Hz and a remeasurement error of about 10 Hz. Occasionally, frequency measurements from the work station were verified visually on a Kay Elemetrics Digital SonaGraph Model 7800, at the narrow band (45 Hz) setting.

We measured and averaged the peak frequency (absolute pitch) of two 1-k point (46-msec) samples taken at the start (FEE_{Start}) and end (FEE_{End}) of high energy (≥ 25 dB) production of *fee* and at the start of high energy production of *bee* (BEE). Also, using the onset of *bee* as the zero point, we measured the number of 46-msec segments in which energy at FEE_{End} and BEE peak frequencies was present simultaneously (3 dB above adjacent frequencies).

RESULTS

SPECTRAL ANALYSIS

In Figure 1, we show a temporal series of acoustic frequency spectrograms in 1-k point (46 msec) samples for a typical chickadee song, from the start of *fee* to the end of *bee*. This series discloses several facts about chickadee song. First, *fee* and *bee* approximate pure tones (i.e., most of the energy is at or near their peak frequencies). Second, the peak frequency of *fee* shifts downward (to the left in Fig. 1) for 184 msec after the start of *fee*. Third, the peak frequency of *bee* is constant, several hundred hertz lower than *fee*. Fourth, *fee* and *bee* are present simultaneously for a time. Energy at the peak *fee* frequency is markedly reduced during this period of overlap, but continues at a low level for several samples (duration ≥ 138 msec) after *bee* has started. It is clear from Figure 1 that only a few key measurements are needed to represent frequency and frequency change during song.

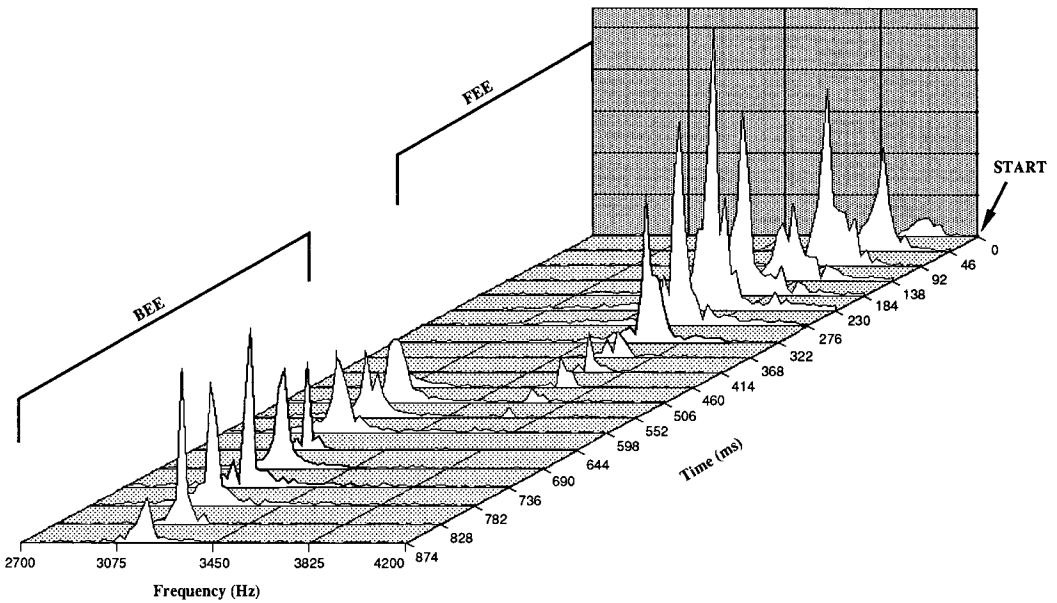


FIGURE 1. Successive spectral slices (at a sampling rate of 22-k points/sec) of a typical Black-capped Chickadee song from the start of *fee* to the end of *bee* (at the top and bottom of Fig. 1, respectively). Each slice is 1-k points or about 46 msec in duration. The vertical axis is amplitude, reduced by 40% to accommodate the peak frequency of all the slices within the plots drawn by the SoundWave frequency spectrum software.

ABSOLUTE PITCH

As a necessary precondition, if chickadees use absolute pitch in song recognition, then the frequencies of *fee* and *bee* notes must be easily distinguishable. This means that distinctive frequency information in FEE_{Start} , FEE_{End} , and BEE must be produced with little variability either within or among birds. Table 1 shows that variability about mean frequency at FEE_{Start} , FEE_{End} , and BEE in normal songs was considerable among birds, but smaller within birds. For example (c in Table 1), the SD for the frequency of BEE is ± 184 Hz among individuals, whereas within birds the SD is ± 49 Hz between days, and only ± 36 Hz within song bouts on the same day. Measuring variability among birds another way, the overlap of the distribution of peak FEE_{End} frequencies (in 100-Hz frequency bins) with the distribution of peak FEE_{Start} frequencies is 84%, and overlap of the distribution FEE_{End} with BEE is 58%.

RELATIVE PITCH

Chickadees could use either pitch contour or pitch interval to recognize conspecific song. If chickadees use contour in recognition, then they must produce songs in which the frequencies of

FEE_{Start} , FEE_{End} , and BEE maintain the same ordinal relationship among and within birds. In fact, the ordinal relationship was $FEE_{Start} > FEE_{End} > BEE$ in the songs of 151 of 156 birds studied; recall that five birds sang abnormal songs. If chickadees use pitch interval in song recognition, then they must produce songs in which both the ordinal and ratio information in song has little variability either among or within birds. That is, the notes must be easily distinguishable among birds on the basis of pitch interval. There are two pitch changes of interest in the *fee-bee* song; one for the change during *fee*, FEE_{Start}/FEE_{End} (f in Table 1), and a second for the change from the end of *fee* to the beginning of *bee*, FEE_{End}/BEE (g in Table 1). In expressing a pitch interval as a decimal number, the higher frequency is divided by the lower frequency, regardless of the temporal order of the two (Hall 1980). For comparison, we provide statistics for two absolute pitch differences, $FEE_{Start} - FEE_{End}$ (d in Table 1) and $FEE_{End} - BEE$ (e in Table 1). The coefficients of variation for pitch interval (f and g in Table 1) are much smaller than those for absolute pitch differences (d and e in Table 1). In contrast with other song pitch measures, these intervals are remarkably constant among birds.

Figure 2 shows obtained average values of

TABLE 1. Frequency and frequency change among Black-capped Chickadees ($n = 132$ birds), between days and within bouts ($n = 11$ birds, 2 days, three songs each). Measurements were taken at the start (FEE_{Start}) and end (FEE_{End}) of high energy production of *fee* and at the start (BEE) of high energy production of *bee*.

	Among birds			Within birds			
	\bar{x}	SD	CV	Between days		Within bouts	
				SD	CV	SD	CV
(a) FEE_{Start}	3,814 Hz	251 Hz	6.6	79 Hz	2.1	47 Hz	1.3
(b) FEE_{End}	3,609 Hz	215 Hz	6.0	57 Hz	1.6	41 Hz	1.2
(c) BEE	3,183 Hz	184 Hz	5.8	49 Hz	1.6	36 Hz	1.1
(d) $FEE_{Start} - FEE_{End}$	204 Hz	72 Hz	35.2	29 Hz	13.4	27 Hz	12.6
(e) $FEE_{End} - BEE$	426 Hz	68 Hz	15.9	24 Hz	5.9	20 Hz	5.0
(f) FEE_{Start}/FEE_{End}	1.056	0.018	1.7	0.008	0.7	0.008	0.7
(g) FEE_{End}/BEE	1.134	0.018	1.6	0.007	0.7	0.007	0.4

¹ Coefficient of variation = $(SD \times 100)/\bar{x}$.

FEE_{Start} and of FEE_{End} (the higher frequencies) as a function of FEE_{End} and BEE (the lower frequencies), respectively, in 151 birds ($n = 428$ songs). The regression lines shown in Figure 2 are linear equations based on the theoretically derived pitch intervals shown in Table 1; i.e., $FEE_{Start} = 1.056 FEE_{End}$ and $FEE_{End} = 1.134BEE$. In equations fitted from both intervals, agreement between obtained and predicted frequencies is high ($R^2s > 0.90$), and no empirically derived polynomial regression equation accounts for even 0.5% more variance than these theoretically based linear equations. It is clear from Figure 2 that, although the distributions of FEE_{Start} and FEE_{End} overlap considerably, the frequencies of these measures are easily distinguished when viewed as pitch interval functions of FEE_{End} and BEE, respectively.

To assess further whether chickadees use an absolute or a relative pitch rule in song production, we performed Model II empirically derived regressions (Sokal and Rohlf 1981) of FEE_{Start} on FEE_{End} and BEE on FEE_{End} . If chickadees use absolute pitch, in effect, subtracting a constant (d in Table 1) from FEE_{Start} to find FEE_{End} and subtracting another constant (e in Table 1) from FEE_{End} to find BEE, then the slopes of the empirically derived regression lines should be 1. If, on the other hand, chickadees use pitch interval, then the regression lines should have slopes equal to the intervals (f and g in Table 1). The empirical equations were $FEE_{Start} = 1.057FEE_{End} - 1.560$ and $FEE_{End} = 1.134BEE - 0.449$. Notice that these are virtually identical to the equations derived from the interval model. In the empirical equations, the slopes are significantly greater than 1, $t_{s150} \geq 8.758$, $Ps < 0.001$, but not different from the theoretically derived pitch intervals, $t_{s150} < 1$. These analyses support the interval

model against a model based on absolute differences.

SHIFTED SONGS

If chickadees simply transpose their normal song downward in pitch during shifted song, then the same intervals and equations that describe normal song should describe frequency-shifted song. We used pitch intervals derived from the main sample (f and g in Table 1) to predict FEE_{Start} and FEE_{End} (the higher frequencies) from FEE_{End} and BEE (the lower frequencies), respectively, in the shifted and normal songs of a sample of birds that sang both. These intervals, shown as regression lines in Figure 3, accurately predict FEE_{Start}

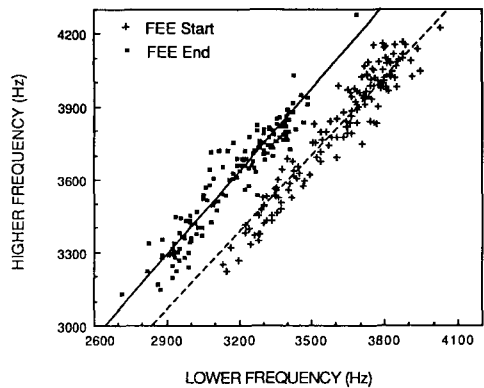


FIGURE 2. Average values of FEE_{Start} and of FEE_{End} (the higher frequencies) as a function of FEE_{End} and BEE (the lower frequencies), respectively, for 151 Black-capped Chickadees ($n = 428$ songs). The regression lines shown in Figure 2 are based on the theoretically derived pitch intervals: $FEE_{Start} = 1.056FEE_{End}$ (the dashed line) and $FEE_{End} = 1.134BEE$ (the solid line). Note that in calculating pitch interval as a decimal number, the higher frequency is expressed as a function of the lower frequency, regardless of the temporal order of the two.

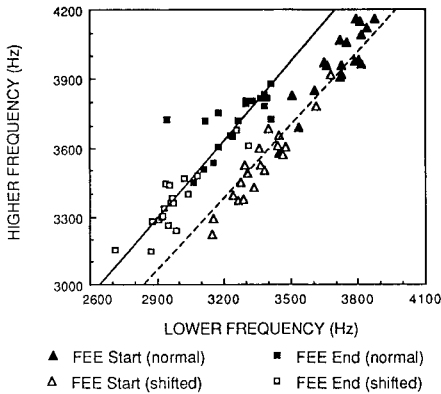


FIGURE 3. Average values of FEE_{Start} and of FEE_{End} (the higher frequencies) as a function of FEE_{End} and BEE (the lower frequencies), respectively, in the normal and frequency shifted songs of 19 Black-capped Chickadees ($n = 114$ songs). The regression lines shown in Figure 3 are based on theoretically derived equations: $FEE_{Start} = 1.056FEE_{End}$ (the dashed line) and $FEE_{End} = 1.134BEE$ (the solid line).

and FEE_{End} frequencies obtained in the shifted and normal songs in this sample ($R^2s > 0.85$). In addition, the intervals derived from frequency-shifted songs in this sample and those derived from normal songs in the main sample did not differ significantly, $t_{17} < 1$. Nonetheless, the normal songs of birds that did not sing shifted songs differed somewhat from the normal songs of birds that did. Birds with normal and shifted songs start their normal songs approximately 150 Hz above the mean for birds with only normal songs, $t_{17} = 3.01$, $P < 0.01$. Also, birds with both songs have a slightly larger interval during *fee* (about 0.01) than birds with only normal songs, $t_{17} = 2.73$, $P < 0.05$. In other respects, the normal songs in this sample were not significantly different from those of other birds, $t_{17} < 1$. In summary, it appears that chickadees transpose their songs downward to sing frequency-shifted songs.

COMPARISONS BETWEEN MODELS

We conducted comparisons between the interval and additive models in their goodness of fit to observed pitch change in the main sample (Fig. 2) and in our sample of birds with normal and frequency-shifted songs (Fig. 3). Pitch interval constancy requires the higher frequency in the ratio to increase proportionally with the value of the lower frequency, whereas absolute pitch change constancy requires the higher frequency to increase a fixed amount independent of the

value of the lower frequency. If the interval model provides the better fit, then in comparisons of deviations from the values predicted by the two, the additive model should overestimate observed pitch change at lower frequencies (below the mean) and underestimate it at higher frequencies (above the mean); similarly, the additive model should overestimate the pitch change in shifted songs, which tend to be below average in frequency. In tests comparing deviations between the two, in predicting FEE_{Start} and FEE_{End} from FEE_{End} and BEE , respectively, the additive model performed precisely as stated above, both for the normal songs shown in Figure 2 ($t_{S_{149}} \geq 8.49$, $P < 0.001$), and for the shifted songs shown in Figure 3 ($t_{S_{18}} \geq 2.65$, $P < 0.03$). Once again, the analysis supports the interval model against an absolute pitch model.

COMPARISONS WITH OTHER POPULATIONS

If the interval derived from our main sample describes a general characteristic of song, then it should predict change in the normal and frequency-shifted songs of chickadees from other populations (e.g., Ficken et al. 1978, Ratcliffe and Weisman 1985, Hill and Lein 1987). Published frequency measures are from eight birds with both normal and frequency-shifted songs and five birds with normal songs only. These investigators measured the frequency of *fee* at mid-note, not at the start and end of *fee*. We estimated end of *fee* from mid-note frequencies using a Model II regression equation computed from our main sample: $FEE_{End} = 0.991FEE_{Mid-note} + 0.531$, $R^2 = 0.97$. Figure 4 shows good agreement between these FEE_{End} frequencies and those predicted by the model ($R^2 = 0.87$), indicating that the interval was maintained in both shifted and normal published songs. In addition, there was no significant difference between the intervals of shifted and normal songs available in the published data ($t_7 = 1.16$, $P > 0.20$ in a paired test), again suggesting that chickadees maintain the interval in normal song when they sing shifted song.

THE PERIOD OF OVERLAP

Although the human ear recognizes two distinct notes in the chickadee *fee-bee* song, the *fee* note overlaps with the *bee* note at very low energy (approximately -25 dB). The mean overlap was 0.772 segments (36 msec), which is reliably greater than zero overlap ($t_{150} = 6.05$, $P < 0.0001$). Furthermore, birds maintain approximately the

same period of overlap from song to song; only about 28% of the variance in song overlap is due to differences within birds. This latter finding makes it unlikely that overlap is the result of echo in the environment, as the overlap in notes would not then be so consistent among birds recorded in so many different locations. Also, song notes whistled in the field by humans ($n = 6$), although similar in absolute and relative pitch, never overlapped in time.

DISCUSSION

We found that the absolute pitch information produced at three key points in chickadee song was considerably less variable within than among birds. Thus, birds might be identified individually, at least in part, by the absolute pitch of their songs. Recent playback experiments show that territorial male chickadees respond more aggressively to the *fee-bee* songs of strangers than neighbors, and suggest that the recognition of a neighbor's song is influenced by the absolute pitch of *fee* (Ratcliffe, unpubl.). By contrast, absolute pitch difference information is probably too variable among birds to be useful in species recognition.

If the absolute pitch changes in chickadee song are not useful species markers, then, perhaps, the range of frequencies used in song production provides more reliable species information. In support of that idea, we (Weisman and Ratcliffe 1989) found that songs played within the normal frequency range elicited more response than songs which started or ended outside that range. However, chickadees share both song frequencies and geographical range with several species. For example, White-throated Sparrows (*Zonotrichia albicollis*) sing clearly whistled notes over a frequency range which subsumes that of chickadees (Borror and Gunn 1965). Plainly, the frequency range of song can provide only an approximate marker to either species.

Chickadees produce pitch changes during the *fee* note and from *fee* to *bee* with remarkable constancy among birds in both contour and interval. Constancy in the direction of frequency change in song makes it impossible to deny contour perception a role in song perception in chickadees. However, there is now extensive evidence favoring interval over contour perception. The most convincing single piece of evidence is that chickadees transpose not only the contour but also the interval of *fee-bee* song. As first suggested by Hulse and Cynx (1986) from our small

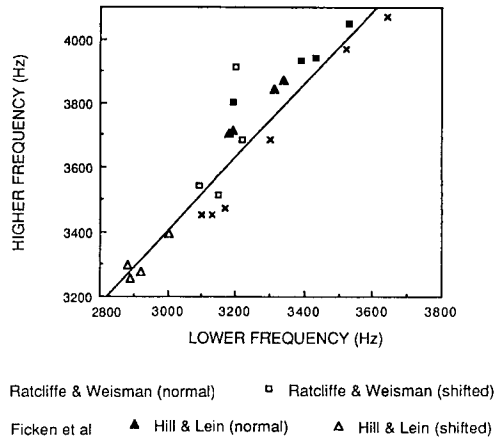


FIGURE 4. Average values of FEE_{End} (the higher frequency) as a function of BEE (the lower frequency), in the normal and frequency-shifted songs of 14 Black-capped Chickadees ($n = 172$ songs) in three published studies: Ficken et al. 1978, Hill and Lein 1987, Ratcliffe and Weisman 1985. The regression line shown in Figure 4 is based on a theoretically derived equation: $FEE_{End} = 1.134BEE$. The published studies measured frequency at the midpoint of *fee*. FEE_{End} was estimated with high accuracy ($R^2 = 0.97$) to maintain consistency with the other analyses.

sample of laboratory recordings, and confirmed in the wild by us and by Hill and Lein (1987), chickadees maintain the same interval in normal and frequency-shifted songs. Also, important evidence comes from our finding (Weisman and Ratcliffe 1989) that chickadees respond less to songs with increased intervals during playback experiments. Contour perception judges only direction, whereas interval perception judges both direction and amount of pitch change. In summary, the evidence leaves little doubt that interval perception plays an active role in chickadee song production and recognition.

In addition to this analysis of absolute and relative pitch, two additional observations are worth noting. First, although others (e.g., Ficken 1981) have published sonograms showing frequency change during *fee*, we have identified and analyzed this glissando. Second, we have observed that the *fee* note continues at greatly reduced amplitude during *bee*. According to the Nowicki and Marler (1988) explanation of how oscines produce song, the simultaneous voicing of two nearly pure tones in chickadee song most likely originates in productive activity by both medial tympaniform membranes, coupled with active suppression of harmonics in the vocal cavity.

Ficken (1981) described *fee-bee* as a simple two-note vocalization lacking in the complexities often associated with song in oscines. Clearly, the present results require reexamination of that evaluation. The *fee-bee* song encodes both absolute and relative pitch information in the glissando during the *fee* note and a discrete pitch change between the *fee* and *bee* notes. Absolute pitch is probably important in individual recognition while relative pitch likely functions as a species marker. Finally, the evidence suggests that chickadees use their vocal tracts in a manner similar to other oscines during song production.

It is tempting to speculate about the general importance of absolute and relative pitch in song recognition. White-throated Sparrows use absolute pitch in individual recognition (Brooks and Falls 1975), and the pitch interval in their most common song appears to vary geographically (Borrer and Gunn 1965). These results are similar but not identical to those for chickadees, which show no evidence of geographical differences in pitch intervals. Even so, both species produce and recognize nearly pure tones at fixed pitch intervals. We plan to extend our study of pitch interval to species which produce more complex frequency information in their songs.

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