

RELATIVE FREQUENCY PARAMETERS AND SONG RECOGNITION IN
BLACK-CAPPED CHICKADEES¹

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Marler (1960) proposed that those features of bird song which are the least variable should be the most important for species recognition (termed "the invariant features hypothesis"). This hypothesis has been tested on several species of song birds, with mixed results. For example, Field Sparrows (*Spizella pusilla*) and Chipping Sparrows (*S. passerina*) do not use the least variable features to classify conspecific song (Nelson 1989). On the other hand, Veeries (*Catharus fuscescens*) and White-throated Sparrows (*Zonotrichia albicollis*) do use features with very little variation to recognize conspecific song. Altering the normally stereotypic between-note frequency ratios in these species' songs reduces the amount of aggressive response to playback (Weary et al. 1991, Hurly et al. 1990). Similarly, Chiffchaffs (*Phylloscopus collybita*) and Firecrests (*Regulus ignicapillus*) respond less strongly to playback of songs where the within-note frequency sweeps have been altered (Becker 1982).

Black-capped Chickadee (*Parus atricapillus*) song consists of two pure tonal notes: "fee bee" (see NORM in Fig. 1). Frequency descends during the fee note (termed glissando), and there is a drop in frequency between the fee and the bee (termed pitch interval; Weisman et al. 1990). The frequency ratio of the glissando (fee-start/fee-end), and the ratio of the pitch interval (fee-end/bee) are highly stereotypic, varying by less than two percent among and within birds in populations from Alberta, Wisconsin and Ontario (Weisman et al. 1990). The frequency at any given point within a song is highly predictable from any other point, that is, highly correlated to all other points. Although chickadees shift their songs over a wide range of absolute frequencies (Shackleton 1991), the glissando and pitch interval remain constant. Playback studies conducted in the laboratory showed that adult male Black-capped Chickadees respond less aggressively to songs where the pitch interval (fee-end/bee) had been altered, compared to normal songs (Weisman and Ratcliffe 1989). Therefore, to examine the importance of the glissando (fee-start/fee-end) to song recognition in this species, we played back songs to wild males in which we altered both of these relative frequency parameters.

METHODS

We synthesized three playback songs using the Mitsyn sound synthesis package (Bregman 1982). The amplitude envelopes of the three songs were identical and the volume settings were held constant during playback sessions. All three songs had identical bee notes. The only difference between the normal (NORM) and altered songs (ALT1 and ALT2) was the presence or absence of a glissando within the fee note. All frequency ratios in NORM were set at the species' mean (fee-start/fee-end = 1.06, fee-end/bee = 1.13; Weisman et al. 1990) and the absolute frequency of NORM was set at the mean frequency of songs recorded during the year previous to this study (fee-start = 3.8 kHz). Both ALT1 and ALT2 had no frequency sweep within fee (i.e., fee-start/fee-end = 1.0). The frequency of fee in ALT1 was equal to the frequency at fee-start in NORM and the frequency of fee in ALT2 equalled the frequency at fee-end in NORM. Thus in ALT1, the pitch interval was larger than normal, while in ALT2 the pitch interval was normal (Fig. 1). Since all other features of these songs were identical (amplitude, bee note and frequency), any difference in response between the normal and the altered songs must therefore be due to the presence or absence of the glissando in fee.

A repeated measures experimental design was used to account for inter-subject variation. All three stimulus songs were presented to each subject in a single session consisting of a priming phase followed immediately by three playback trials. Sessions were always performed near the center of the subject's territory. During the priming phase we played a tape consisting of 30 sec of chickadee calls, which simulated an intruding male and served to attract the subject to the vicinity (<40 m) of the playback speaker. The effect of these calls on subsequent response was controlled by presenting the same tape to all birds. The calls on the priming tape were from another population, and were unfamiliar to any of the subject birds. During each trial, we played the test song at a rate of 10 songs/min for 90 sec followed by 120 sec of silence. This playback rate simulates natural counter-singing. We fully counterbalanced the assignment of songs to trials in a block randomized list prepared prior to the experiment. One observer (SAS) recorded the subjects' movements (number of flights and distances from the speaker) and vocalizations (fee bees, "chickadees" and "gargles"; Ficken et al. 1978) at a distance of 10 m from the speaker. As an aid to distance estimation, a 20 m measuring tape was laid on the ground with the

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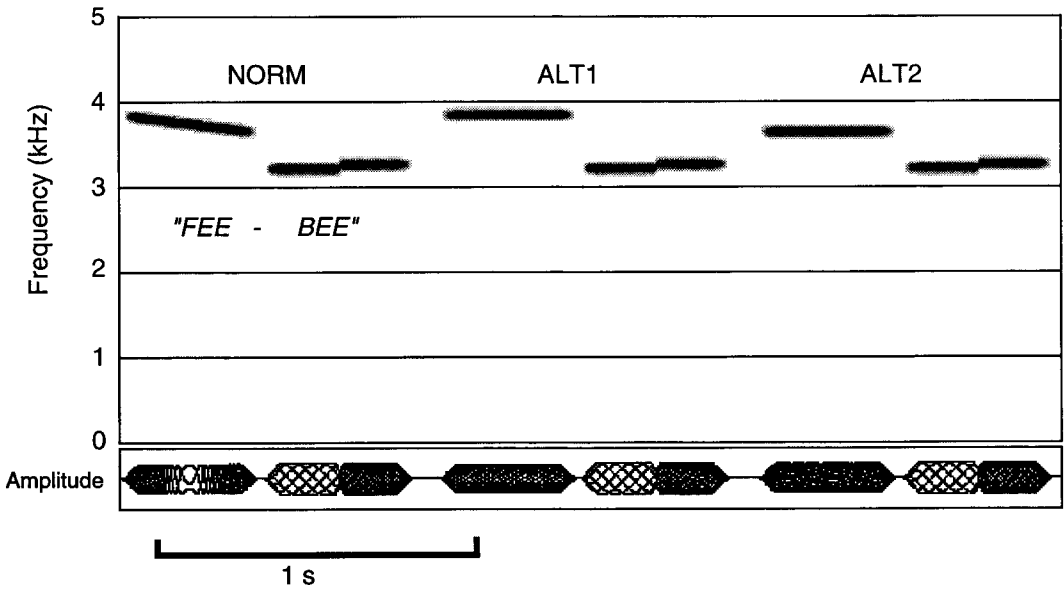


FIGURE 1. Sonograms of three synthetic stimulus songs, above, with corresponding amplitude oscillograms below. NORM is a normal song, and ALT1 and ALT2 are altered songs. The two notes of the normal song are termed *FEE* and *BEE*.

speaker at the center. Distances were estimated to the nearest meter. In equivocal cases, perch locations were noted during the trial, and distances measured directly thereafter. Playback songs and calls were played on a Sony Professional WM D6C cassette recorder and broadcast through an Aiwa SC-A8 speaker/amplifier.

Playbacks were performed between 26 April–20 May 1991 to territorial males in two populations: at the Queen's University Biology Station (QUBS), Chaffey's Locks, Ontario ($n = 18$ birds) and near Chelsea, Quebec ($n = 6$ birds). These two sites are separated by approximately 200 km. These populations were part of a larger study of the singing behavior of this species

(Shackleton 1991). Each male was tested only once. Males at QUBS were color-banded. Males at Chelsea were identified by territory location alone and none of the males used as subjects had adjacent territories. Birds never approached playback outside their territory at QUBS, so we are confident that birds were not resampled at Chelsea. No differences in general singing behavior were observed between the two sites (Shackleton 1991). A two-way ANOVA revealed no significant interactions between playback songs and location (F -tests, all $P > 0.05$). Moreover, the results were not qualitatively altered when we conducted separate ANOVAs for each population. All differences re-

TABLE 1. Results of a repeated measures analysis of variance (ANOVA) on response measures to playback by 24 adult male Black-capped Chickadees. Playback songs which share the same letter elicited responses that were not significantly different from each other (Fisher's post hoc comparison; $P > 0.05$). Response values are given as mean (\pm SE). Songs labelled "A" elicited significantly stronger responses than those labelled "B" ($P \leq 0.05$). $df = 2, 23$ for all tests. All P -values have been corrected using the sequential Bonferroni technique (Rice 1989).

Response	Repeated measures ANOVA		Playback songs		
	F	P	NORM	ALT1	ALT2
Min. distance (m)	5.29	0.025	5.9 (\pm 1.0) A	8.6 (\pm 1.2) B	9.6 (\pm 1.1) B
Mean distance (m)	5.78	0.023	9.1 (\pm 1.1) A	11.4 (\pm 1.0) B	12.0 (\pm 1.0) B
Number of flights	11.81	0.0005	4.3 (\pm 0.7) A	2.2 (\pm 0.4) B	1.5 (\pm 0.3) B
Number of calls*	4.41	0.036	3.0 (\pm 0.9) A	1.8 (\pm 0.7) AB	0.7 (\pm 0.3) B
Number of songs*	0.57	0.56	19.3 (\pm 3.3) n/a	21.7 (\pm 3.0) n/a	24.0 (\pm 3.0) n/a

* Means and SEs are from untransformed data.

mained unchanged for the QUBS birds, and although there were fewer statistically significant differences (due to reduced sample size) for the Chelsea birds, all trends remained unchanged. All statistics reported below are from repeated measures ANOVAs and Fisher's post hoc comparisons on the pooled data ($n = 24$ birds). The number of calls and songs in response to playback were square-root transformed to normalize the data.

RESULTS

There was significant variation among the playback songs in the minimum distance (m) to which birds approached the speaker (Table 1). Pairwise comparison revealed that birds approached significantly more closely to NORM than to either of the altered songs, but there was no significant difference in response to ALT1 and ALT2. Moreover, the same results were found for the mean distance (m) from the speaker (calculated as the distance from the speaker multiplied by the time at that distance summed and divided by total time). Subjects made significantly more flights in response to NORM than to either of the altered songs, and again there was no difference between ALT1 and ALT2 (Table 1). There was significant variation in the number of "chickadee" and "gargle" calls (as defined by Ficken et al. 1978) uttered in response to the three stimuli. Post hoc comparison revealed that birds called more to NORM than to ALT2, with no other significant differences. There was no significant difference in the number of songs given in response to the three stimulus songs (Table 1).

DISCUSSION

These results indicate that the presence of a glissando in the first note, *fee*, is important to song recognition in Black-capped Chickadees. Territorial males make more flights, approach more closely, and utter more calls to songs containing a glissando than to those that do not. These results also suggest that the glissando may affect responsiveness as much as, or more than, the drop in frequency in the pitch interval. If the pitch interval was more important, we might expect a stronger response to ALT2 than to ALT1. This was not observed. However, we altered the glissando to a much greater extent than the pitch interval. In contrast, Weisman and Ratcliffe (1989) altered the pitch interval much more than we did here. Determining how both of these relative frequency parameters interact in song recognition clearly requires further experimentation.

Our manipulation of the glissando had a greater effect on approach to the speaker and calls than on song. Like several other parids, territorial male Black-capped Chickadees sing to neighbors at long distances (> 50 m), but approach, call and physically displace intruders at shorter distances. A possible explanation for our results is that subjects responded to the altered songs as they would to males singing further away, and to the normal song as they would to a nearby intruder. The drop in frequency within the first note, then, may be important for distance estimation. That is, frequencies within this note may be differentially attenuated by the environment and provide distance estimation cues, as in Carolina Wrens (*Thryothorus ludovicianus*; Richards 1981). In natural songs, amplitude is lower

at the start of the *fee* note, where the frequency is highest (Weisman et al. 1990), which may enhance this differential attenuation effect. To determine whether the altered songs are perceived as a more distant signal, or are merely less effective at eliciting a territorial response also requires further experimentation.

Our results, together with those of Weisman and Ratcliffe (1989), demonstrate that relative frequency parameters are important in eliciting territorial behavior in male black-capped chickadees. We altered the glissando in an all-or-none manner, however, so exactly what aspects of the glissando the birds are attending to remains to be determined. More experiments need to be performed to determine whether frequency ratios, frequency differences or merely ordinal changes in frequency are important for song recognition. Hurly et al. (in press) have shown that White-throated Sparrows respond less aggressively to songs with alterations in frequency ratio, but do not respond differently to songs where the arithmetic difference in frequency has been altered while preserving the normal ratio. In this species, then, the frequency ratio (a logarithmic function) is important for song recognition, rather than the frequency difference (a linear function). To test whether frequency ratios are more important than frequency differences in general requires similar experiments in a greater number of species. A growing number of studies (reviewed above) show that relative frequency features, especially frequency ratios, can be classified as "invariant features" important for song recognition. A larger survey of the variation in relative frequency parameters and their importance in recognition may help us understand how birds decode and process the information contained in songs.

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SONGS OF TWO MEXICAN POPULATIONS OF THE WESTERN FLYCATCHER *EMPIDONAX DIFFICILIS* COMPLEX¹

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Johnson (1980) provided a detailed treatment of the Western Flycatcher (*Empidonax difficilis*) complex, and more recently Johnson and Marten (1988) recommended that coastal and interior populations of *E. difficilis* be considered specifically distinct. This course was followed by the American Ornithologists' Union (1989), naming coastal birds the Pacific-slope Flycatcher (*E. difficilis*) and interior birds the Cordilleran Flycatcher (*E. occidentalis*). Johnson's (1980) analysis of vocalizations lacked the advertising songs from several key areas, and included none from Mexico. Recordings from two areas would be of particular interest: (1) interior-breeding birds in Mexico, which Johnson (1980) suggested might not have a complete advertising song; and (2) the distinct population (*E. d. cineritius*) in the Cape District mountains of southern Baja California which was given "megasubspecies" status by Johnson (1980).

During recent field work, one of us (Howell) recorded the advertising songs of birds from both these areas;

they are described here to contribute to our understanding of this interesting complex. Vocalizations were recorded on a Sony TCS 430/450 cassette-recorder using a Radio Shack Electret tie-pin microphone mounted in a plastic funnel, and analyzed on a Kay 7029A sound spectrum analyzer. As in Johnson (1980), measurements were made from the single clearest recording from each bird. Although our sample sizes are very low, advertising songs in the *E. difficilis* complex tend to be similar over broad geographic areas (Johnson 1980), so recordings of single birds can be quite meaningful in a study of geographic variation.

E. d. cineritius: this bird is common in the fairly arid pine-oak forests of the Sierra Laguna (= Sierra Victoria), southern Baja California. Two singing individuals were tape-recorded at the northern end of La Laguna meadow on 9 and 10 June 1991; representative songs from each individual are shown in Figure 1 (A and B). In the field, the songs clearly recalled those of birds in coastal California, but they are lower pitched (cf. Johnson 1980:fig. 28, Santa Barbara sample), particularly syllable 1 (Table 1). Also, the peak of syllable 2 is not as acute as in typical coastal songs, being similar in this respect to songs from the California Channel Islands population. Channel Islands birds also tend to have low pitched songs, although not as low as the Sierra Laguna birds (Table 1). Syllable 3 is clearly typical of coastal populations (Johnson 1980:fig. 26).

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