lationships within a raptor guild in the central Canadian Arctic. Can. J. Zool. 66:2275–2282.

- RADCLIFFE, D. A. 1980. The peregrine falcon. T. and A. D. Povser, Calton.
- RICKLEFS, R. E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115: 177-201.
- SCHMUTZ, S. M., AND L. W. OLIPHANT. 1987. Chromosome study of peregrine, prairie and gyrfalcons with implications for hybrids. J. Heredity 78:388– 390.
- STEENHOF, K., AND M. N. KOCHERT. 1988. Dietary responses of three raptor species to changing prey densities in a natural environment. J. Anim. Ecol. 57:37-48.
- TARBOTAN, W. 1984. Behavior of the African Peregrine during incubation. Raptor Res. 18:131-140.

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- THIOLLAY, J. 1988. Prey availability limiting an island population of peregrine falcons in Tunisia, p. 701–710. In T. J. Cade, J. H. Enderson, C. G. Thelander and C. M. White [eds.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Inc.
- VASINA, W. G., AND R. J. STRANECK. 1984. Biological and ethological notes on *Falco peregrinus cassini* in central Argentina. Raptor Res. 18(4):123–130.
- WHITE, C. M., AND T. J. CADE. 1971. Cliff-nesting raptors and ravens along the Colville River in arctic Alaska. Living Bird 10:107–150.
- YALDEN, D. W., AND P. E. YALDEN. 1985. An experimental investigation of examining Kestrel diet by pellet analysis. Bird Study 32:50-55.

PITCH PRODUCTION IN CAROLINA CHICKADEE SONGS¹

Bernard Lohr and Stephen Nowicki Department of Zoology, Duke University, Durham, NC 27706

Ron Weisman

Department of Psychology, Queen's University, Kingston K7L 3N6, Canada

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The fee-bee song of the Black-capped Chickadee (*Parus atricapillus*) consists of two clearly whistled notes, the first *fee* slightly higher in pitch than the second *bee* (Dixon and Stefanski 1970, Ficken et al. 1978). Weisman et al. (1990) reported that frequency relationships in Black-capped Chickadee songs represent simple transformations of constant ratios between adjacent notes across the frequency range of the species. That is, both the frequency sweep (glissando) during the *fee* note and the change in frequency from *fee* to *bee* have constant frequency ratios among and within individuals.

Whereas the perception of absolute pitch is related to the frequency of a sound, the perception of relative pitch by pitch interval is related to the frequency ratio between adjacent sounds (Hall 1980). Weisman et al. (1990) presented four kinds of evidence in favor of relative pitch production in Black-capped Chickadees: (i) distributions of the absolute pitches of *fee* and *bee* overlap extensively; (ii) the absolute pitches of the notes are highly predictable from one another, i.e., highly correlated with each other and with values predicted from one another; (iii) the pitch interval ratios between the start and end of *fee* and between *fee* and *bee* are much less variable than the absolute pitches of the notes; and (iv) when individual birds shift the absolute pitches of their song notes, they maintain constant species-typical pitch intervals.

Carolina Chickadees (*P. carolinensis*) are closely-related congeners (Braun and Robbins 1986, Gill et al. 1989), who also sing clearly whistled notes in their territorial songs. Ward (1966) and Smith (1972) described the song of the Carolina Chickadee as a series of alternating high and low pitched notes. A variety of song types are observed, which appear to vary across geographical regions (Ward 1966). We here examine relationships among the absolute pitches in two song types of Carolina Chickadees to determine whether they show relative pitch constancies similar to those observed in the songs of Black-capped Chickadees.

METHODS

We recorded the songs of 23 Carolina Chickadees within a 10-km radius of Duke University, Durham, North Carolina in May 1990. Most birds sang more than one song type; we recorded six song types of which two were by far the most frequent in our area (see A and B in Fig. 1). We obtained at least five exemplars of song A from 19 birds, and five exemplars of song B from 11 of these same birds. We obtained five exemplars of song B from four additional birds, who did not sing song A in our recordings, raising our sample of song B to 15 birds. Individuals were identified by territory location and recorded in a single session, with all territories separated by at least ½ km, to insure that all recorded birds were different individuals.

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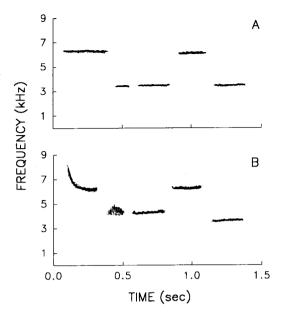


FIGURE 1. Sonagrams of the two Carolina Chickadee song types analyzed in this study; song type A above, song type B below. Sonagrams were generated digitally using "SIGNAL" software (512 pt FFT, frequency resolution = 44 Hz, temporal resolution = 23 ms).

A Sony TC-D5M cassette recorder and either a Sennheiser ME88 shotgun microphone or an Audiotechnica 2AX Pro omidirectional microphone mounted in a Sony PBR330 parabola were used to record birds. Songs were digitized at a rate of 22.6 kHz (Compaq 386/25 computer, DT2821 A/D board) using "SIGNAL" sound analysis software (Beeman 1989). Peak frequency measures were made from 1024 point FFTs (resolution 22 Hz) calculated at the start, midpoint, and end of each note. Additional frequency measures during rapid FM sweeps were made from 256 point FFTs (resolution 88 Hz).

RESULTS AND DISCUSSION

Song types A and B (Fig. 1) both consist of alternating high and low notes. Except for the buzzy second note in song B, these sonagrams resemble two typical song types described by Ward (1966). In song type A (Fig. 1A), two low notes, Note 2 shorter in duration than Note 3, intercede before the second high note (Note 4). Statistical analyses are based on note frequencies averaged over the middle and end points of each note as these two estimates did not differ significantly (Ps > 0.20). We found significant frequency differences among the notes of song A ($F_{4,72} = 3,209.37, P <$ 0.0001). Pairwise post hoc comparisons (Scheffe's test, P < 0.05) found Notes 1 and 4 significantly higher in frequency than Notes 2, 3, and 5. The frequencies of these low notes did not differ significantly, but Note 1 was significantly higher than Note 4.

In song type B (Fig. 1B), Note 1 begins in a glissando, then a short buzzy note (Note 2) and low frequency pure tonal note (Note 3) intercede before the second high note (Note 4). We found significant frequency differences among the notes of song B ($F_{4,56} = 575.66$, P < 0.0001). Pairwise comparisons (P < 0.05) revealed an only slightly different pattern of frequencies than observed in song A: Notes 1 and 4 were significantly higher than Notes 2 and 3, which were in turn significantly higher than Note 5. Neither the higher notes (1 & 4) nor the middle lower notes (2 & 3) differed within pairs. To summarize, both song types present alternating patterns of high and low pitched notes, with much smaller differences either among the high (song A) or low (song B) notes.

We examined the distributions of high and low pitched notes in both song types and found no instances of overlap. The probability of overlap between a randomly sampled low note with the range of the most similar high note (i.e., Notes 1 and 2 of song B) is less than 0.0001. These results are in good agreement with those of Ward (1966) for song types from other geographical regions.

Correlations among the notes in songs A and B are shown in Tables 1a and 1b. Song A includes more notes that are significantly correlated than does song B (P < 0.05), suggesting a greater overall relationship among pitches in song A. However, only Notes 2, 3, and 5 in song A, and Notes 1 and 4, and Notes 2 and 3 in song B are highly correlated (rs > 0.80). Notice that these high correlations are all between notes at very similar frequencies (Table 2). The absence of high correlations between high and low notes in these songs suggests that frequency ratios are not highly predictive of pitch changes in Carolina Chickadee songs.

Constancy in absolute and relative pitches among adjacent notes was evaluated by comparing the coef-

TABLE 1a. Correlations among the notes in song A (19 birds, 5 songs each).

	Note 1	Note 2	Note 3	Note 4	Note 5
Note 1	1.00				
Note 2	0.60 ²	1.00			
Note 3	0.64 ²	0.96 ³	1.00		
Note 4	0.57 ¹	0.49 ¹	0.59 ²	1.00	
Note 5	0.61 ²	0.90 ³	0.95 ³	0.66 ²	1.00

TABLE 1b. Correlations among the notes in song B (15 birds, 5 songs each).

	Note 1	Note 2	Note 3	Note 4	Note 5
Note 1	1.00				
Note 2	-0.39	1.00			
Note 3	-0.02	0.84 ³	1.00		
Note 4	0.80 ³	0.11	0.34	1.00	
Note 5	0.27	0.22	0.32	0.55 ¹	1.00

 $^{1}P < 0.05.$

 ${}^{2}P < 0.01.$ ${}^{3}P < 0.001.$

TABLE 2. Means and coefficients of variation (CVs) for the pitches (Hz) and intervals in song A (19 birds, 5 songs each) and in song B (15 birds, 5 songs each).

	Song A		Song B		
	Mean	CV ¹	Mean	CV ¹	
Pitches:			-		
Note 1 (N1)	6,498	3.2	6,385	3.8	
Note 2 (N2)	3,602	4.0	4,503	6.6	
Note $3(N3)$	3,607	3.9	4,298	5.7	
Note 4 (N4)	6,125	4.1	6,388	3.5	
Note 5 (N5)	3,585	3.8	3,683	4.1	
Intervals:					
N1/N2	1.81	3.2	1.43	10.1	
N2/N3	1.00	1.1	1.05	3.7	
N4/N3	1.70	3.7	1.49	6.0	
N4/N5	1.71	3.8	1.74	3.8	

 1 CV = SD × 100/mean.

ficients of variation (CV = SD × 100/mean, Sokal and Rohlf 1981, p. 59) for frequencies and frequency ratios (Table 2). Except for Notes 2 and 3 in song A, which are virtually identical in frequency, the CV for the ratio of any two adjacent notes is not significantly smaller than the CVs for the individual frequencies (P > 0.05, Sokal and Rohlf 1981 p. 150). Indeed, in song B, the frequencies of two notes (1 and 4) are significantly less variable than the ratios between their frequencies and those of adjacent notes (2 and 3, respectively, P < 0.05). Thus, unlike Black-capped Chickadees, the pitch intervals in Carolina Chickadee songs are not less variable than the absolute pitches of the notes.

Similar analyses were conducted on the glissando within Note 1 of song B. The probability of overlap between randomly sampled note start and end frequencies is less than 0.045. The correlation between start and end was r = 0.74 (P < 0.05), which predicts only slightly more than 50% of the variance among these frequencies. The CVs for the frequencies and frequency ratios within this note are not significantly different (*P*s > 0.05). In short, the glissando provides results similar to those obtained between notes in both song types.

We did not observe Carolina Chickadees shifting note frequencies in songs of the same type, as Blackcapped Chickadees do in fee-bee songs (Ratcliffe and Weisman 1985), but more extensive recordings are needed to examine this possibility. When Carolina Chickadees sing two alternating-pitch song types such as songs A and B, however, they do not necessarily maintain the same pitch intervals in both types (compare "Intervals" for songs A and B, Table 2).

Our analysis suggests an important difference between mechanisms underlying song production in Carolina and Black-capped Chickadees. In contrast to the fee-bee notes of Black-capped Chickadees, the alternating-pitch notes of Carolina Chickadees do not overlap in frequency, are no more variable than the intervals between them, and are not highly predictable from the pitches of adjacent notes. These differences suggest that, unlike their congeners, Carolina Chickadees may not rely on relative pitch relationships in song production and perception. The possibility that Carolina Chickadees emphasize absolute pitch while Blackcapped Chickadees utilize relative pitch is especially interesting given the overall similarity in the structure of the songs of these two species and their propensity to interbreed.

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LITERATURE CITED

- BEEMAN, K. 1989. "SIGNAL" user's guide. Engineering design, Belmont, MA.
- BRAUN, M. J., AND M. B. ROBBINS. 1986. Extensive protein similarity of the hybridizing chickadees *Parus atricapillus* and *P. carolinensis*. Auk 103: 667-675.
- DIXON, K. L., AND R. A. STEFANSKI. 1970. An appraisal of the song of the Black-capped Chickadee. Wilson Bull. 82:53-61.
- FICKEN, M. S., R. W. FICKEN, AND S. R. WITKIN. 1978. Vocal repertoire of the Black-capped Chickadee. Auk 95:34-48.
- GILL, F. B., D. H. FUNK, AND B. SILVERIN. 1989. Protein relationships among titmice (*Parus*). Wilson Bull. 101:182–197.
- HALL, D. E. 1980. Musical acoustics. Wadsworth, Belmont, California.
- RATCLIFFE, L., AND R. G. WEISMAN. 1985. Frequency shift in the fee bee song of the Black-capped Chickadee. Condor 87:555–556.
- SMITH, S. T. 1972. Communication and other social behavior in *Parus carolinensis*. Publ. Nuttall Ornithol. Club, Cambridge, MA.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. The principles and practice of statistics in biological research. Second edition. Freeman, New York.
- WARD, R. 1966. Regional variation in the song of the Carolina Chickadee. Living Bird 5:127-150.
- WEISMAN, R., L. RATCLIFFE, I. JOHNSRUDE, AND T. A. HURLY. 1990. Absolute and relative pitch production in the song of the Black-capped Chickadee. Condor 92:118–124.