FREQUENCY VARIATION IN SONGS OF BLACK-CAPPED CHICKADEES (*PARUS ATRICAPILLUS*)

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Abstract.—Recordings of dawn singing by male Black-capped Chickadees (*Parus atricapillus*) show that each individual sings its fee-bee song at a wide range of frequencies. Males tend to repeat songs at a given frequency but on average after every 41 ± SE of 8.8 songs a male shifts the frequency of its song by a statistically significant amount ($\geq$80 Hz). During any given morning, males may appear to shift among a limited set of discrete frequencies, but over longer time periods intermediate frequencies also are sung. These results suggest that chickadees can vary the frequency of their song more or less continuously over the species' frequency range. When songs of one of three widely spaced frequencies (recorded in previous years) were played back, males replied with songs that had approximately the same frequency as the playback song. Thus, frequency shifting appears, at least in part, to be a form of song matching. These results add to a growing body of evidence that some species with single-song repertoires have evolved effective matching strategies through manipulation of the frequency of their song. *Received 14 June 1991, accepted 20 January 1992.*

THE MAJORITY of songbirds possess multisong repertoires, in which song types can be easily distinguished from each other on the basis of several frequency and temporal features. There has been considerable effort to understand the inter- and intrasexual selective pressures favoring the evolution of multisong repertoires (e.g. Kroodsma and Miller 1982, Searcy and Andersson 1986). In contrast, the conditions that predispose species to maintain single-song repertoires have received comparatively little attention. By single-song repertoires, we mean those in which songs may vary in a graded fashion (e.g. longer or shorter), but cannot be divided into groups by discontinuities in any single parameter or combination of parameters.

Species with single-song repertoires may show little variation in song structure because of some advantage to stereotypy, for example, because low variation within and between males in a given area aids the recognition of dialects (e.g. Baker and Cunningham 1985). Alternatively, relatively subtle variations in song structure may serve functions that, in a repertoire species, would be served by abrupt changes in song type. For example, variation in the frequency of the songs of Kentucky Warblers (*Opornis formosus*; Morton and Young 1986) and Harris' Sparrows (*Zonotrichia querula*; Shackleton et al. 1991) allow males to match the frequency of each other's songs as a signal in territorial contests. In species with song types, this function is served by males matching each other's song types.

We examined the nature and significance of frequency variation in Black-capped Chickadees (*Parus atricapillus*), a species typically classified as having a single-song repertoire (Hailman 1989). The vocal repertoire of this species is one of the best known of any bird, especially its "chickadee" (Hailman and Ficken 1986, Nowicki 1989) and "gargle" (Ficken and Weise 1987) calls. In contrast to these complex calls, chickadee song is remarkably simple, consisting of a two-note whistle (fee bee). The form of this song is relatively invariant; the lengths of the component notes are relatively constant, and the frequency of the first note is higher than that of the second note by a constant ratio (Ficken et al. 1978, Weisman et al. 1990). Males repeat their song at a given frequency with a high degree of stereotypy. However, males sometimes lower or raise the frequency of their song by at least 100 Hz; these are described as "shifted" songs (Ratcliffe and Weisman 1985, Hill and Lein 1987).

Chickadees sing little during the day, so previous studies have sampled only one to three "normal" and "shifted" songs from each male. In work preliminary to our study, we observed chickadees singing the fee-bee song at more than two frequencies. We investigated whether

chickadee males sing: (a) just one song type, but potentially at any frequency within a given range (as in Kentucky Warblers; Morton and Young 1986); or (b) a fixed repertoire of song types, which in this case would be songs of essentially the same form at different frequencies. Chickadees, like many passerines, sing persistently at dawn, which enabled us to obtain a large number of songs from each male for analysis. We also conducted a song playback experiment to test whether the pattern of frequency variation we observed might be a consequence of song matching.

METHODS

Our study was conducted at the Queen's University Biological Station at Lake Opinicon, Ontario, about 50 km north of Kingston. Recordings were made from 1 April to 30 June 1989, and from 19 April to 8 June 1990. Subjects were color banded at winter feeding stations before the study began. Territories were mapped using song playbacks (Falls 1981) and/or observations of territorial interactions.

Recording and analysis of dawn singing.—Recordings of spontaneous song were made between 0415 and 0600 EST. The songs of one male were recorded on each morning. Selection of the male recorded on a particular morning was opportunistic, but we did not record males that had heard recorded playback songs within the last 24 h, and we avoided recording neighboring males on successive days if possible. We arrived on the target male's territory before he began singing and tried to record his entire dawn performance. Identification of males as soon as there was enough light always indicated that they were singing well within their own territories.

In 1989, we analyzed recordings of only one dawn performance from each of 15 males. Unfortunately, males changed perches, and it took us some time to relocate them, so we missed many songs. In 1990, with the help of a field assistant, we recorded complete performances on two different days from each of eight males. Sample sizes vary among analyses because recordings from 1989 were incomplete for some analyses. Most of the analyses presented below are based on the eight males recorded in 1990. We knew the breeding status of seven of these males; none was nesting or excavating nestholes on the first recording date, but by the second recording date four had mates laying eggs. Except where noted each datum represents one dawn performance by one male. Means and standard errors (SE) are reported.

Males were recorded using a Sony WM D6 cassette recorder and a Sennheiser MKH816 microphone, or a Panasonic RQ-330 cassette recorder and a Realistic microphone mounted in a Sony PBR330 parabola, at distances ranging from 3 to 50 m (median 10 m). A

standard tone from a pitch pipe was sounded during about 90% of recording sessions, and indicated no measurable variation in tape speed. The frequencies of the two notes in this species' song ("fee" and "bee") are highly correlated ($r = 0.95$, Weisman et al. 1990). The frequency of the first note, fee, changes by about 200 Hz from beginning to end, but the second note, bee, usually changes less than 20 Hz (Weisman et al. 1990). Therefore, we report measurements of bee. We used the "power spectrum between cursors" function on a Kay Elemetrics DSP Sonograph (Model 5500) to display the average spectrum of the entire note, and measured the frequency at its peak. This method provided nearly 100% repeatability, even in recordings with high background noise. We used a band width of 29 Hz, a transform size of 1,024 points and a Hamming window. The frequency cursor for this display provided frequency measurements at 20-Hz intervals, well above the resolution of the sonograph ($\pm 0.05\%$, or 1.7 Hz at 3,400 Hz).

Song playback experiment.—Playback songs were recorded on the study site in 1987 and 1988 using a Sony WM D6C cassette recorder and a Sennheiser MKH816 microphone. Three frequencies were selected for playback: the mode of "shifted" songs (3,133 Hz), the mode of all songs (3,381 Hz), and the mode of "normal" songs (3,628 Hz; Weisman et al. 1990). To ensure that song frequency effects would not be due to the peculiarities of particular tapes or individuals, two songs from different individuals were used to represent each song frequency. Also, each of these songs was made by joining the fee of one individual with the bee of another. Small sample sizes prohibited us from testing whether different tapes within a given treatment elicited different responses. We chose song notes that kept the frequency ratio of fee to bee constant, at approximately the species' mean (1.13), and the temporal separation of fee and bee constant at 110 ms. Playback songs were constructed at a work station consisting of a Macintosh SE computer and SoundCap, SoundWave, and MacSpeech Lab software, using 8-bit A/D and D/A conversion. We standardized the amplitudes of the playback tapes at 80 dB with an SPL meter (slow setting).

This experiment was performed between 1 and 30 April 1989, between 0700 and 1700 (usually between 1000 and 1200). Each male received one playback trial. Order of presentation of the playback songs was randomized in blocks of six birds. The male to be tested on a given day was selected randomly, and neighboring males were not tested on the same day. One trial consisted of a 1-min playback of one song that was repeated at a rate of 10 songs per min (the mean song rate in our dawn sample). Songs were broadcast from a Sony WM D6C cassette recorder and a Sony SRS-35 speaker. The speaker was placed 2 m above the ground roughly in the center of the subject's territory, and the observer was stationed about 10 to 15 m from the speaker. Responses were recorded with a

TABLE 1. Mean frequencies (±SE) of songs sung in response to playback of three different frequencies. Results of one-sample comparisons of playback with response frequencies also shown.

Frequency (Hz)			One-sample t-test	
Playback	Response	n	t	P
3,130	3,310 ± 64	7	2.80	0.03
3,380	3,410 ± 54	7	0.56	0.59
3,630	3,580 ± 35	10	−1.77	0.11

Sony ECM-155 microphone and WM D6C cassette recorder. Trials were excluded from analysis if the subject did not sing within 30 s of the end of playback, or if a male from a neighboring territory sang first. This yielded a total sample of 24 usable trials (Table 1).

We measured the bee of the first song elicited by playback, using the same methods as those described above for naturally occurring songs. Again, we measured the playback song immediately preceding the response song, and used its deviation from the original playback tape to correct the frequencies of response songs for variations in the tape speed in the playback or the recordings of responses.

RESULTS

Dawn singing.—Males spent approximately the first third of their dawn chorus near the center of their territory, and then sang at scattered perches throughout the territory. Because their neighbors were usually singing at the same time, the males we were recording rarely sang solo for more than 20 songs at the beginning or 50 songs at the end of their dawn performance.

Figure 1 shows the frequencies of songs sung by four males, comprising their entire dawn performances for a single morning in 1990. These four birds sang the longest dawn choruses of the eight males recorded in 1990. The average length of dawn chorus for all eight males was 284 ± 59 songs. Individuals usually repeated songs at close to the same frequency before switching to another frequency (Fig. 1). Occasionally, individuals shifted frequency a large amount in small successive steps (e.g. Fig. 1D), but this was uncommon.

To quantify the tendency to shift song frequency, we analyzed the distribution of all frequency shifts between successive songs on a particular morning. For each male recorded in 1989, the shift in frequency between successive
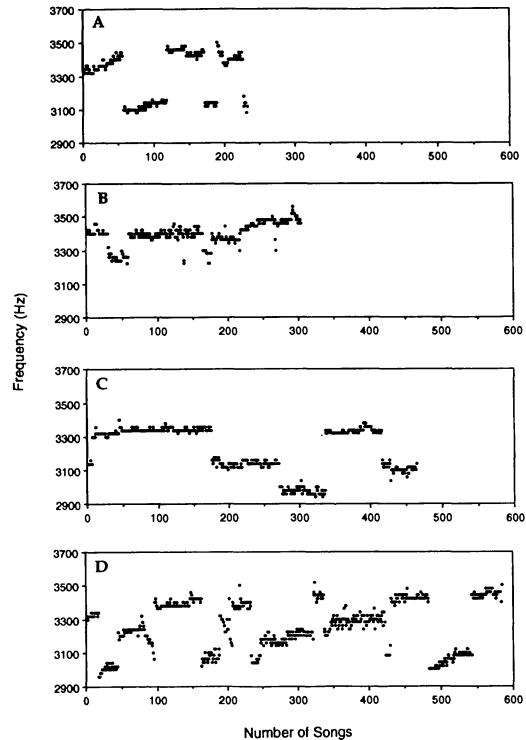

Fig. 1. Frequencies of all songs sung at dawn by four males. Males recorded on separate mornings, and each panel represents one male. Songs arranged along X-axis in order in which they were sung.

songs was less than 80 Hz in 95% of the instances. Figure 2 shows the results of a similar analysis performed on frequency shifts pooled across the eight males recorded in 1990; in this sample, 94.7% of shifts were less than 80 Hz. Using the common practice of regarding the 95% level as indicating a difference unlikely to have arisen by chance (i.e. statistically significant), we focused our analyses on shifts of 80 Hz or more. For the eight males recorded in 1990, the mean number of songs between shifts of 80 Hz or more was 41 ± 8.8.

It is important to ask whether, when males sing, they shift among a limited set of discrete frequencies (analogous to frequencies playable on a bugle), or among an unlimited set of frequencies (analogous to frequencies playable on a slide trombone). That is, can the mean frequencies of each series of repeated songs occurring after one shift and before the next (e.g. the first 50 songs in Fig. 1A) be sorted into a limited set of significantly different means? To evaluate this query, we treated the first five song
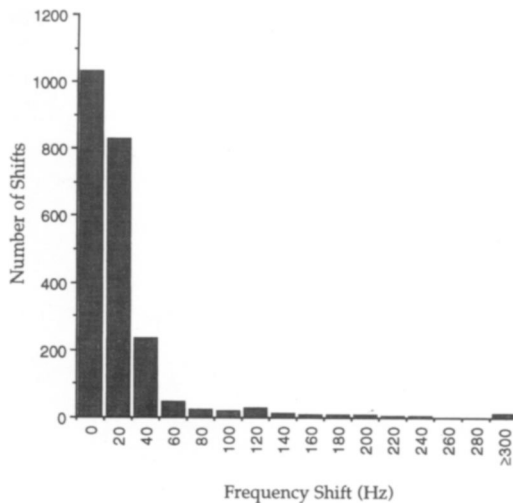
Fig. 2. Distribution of frequency shifts (Hz) in dawn choruses of eight males (n = 2,262 songs) recorded in 1990.

measurements after each shift of 80 Hz or more in an individual's morning performance as a separate sample in a Scheffe's multiple-comparisons test, which tests whether means can be sorted into significantly heterogeneous groups (Sokal and Rohlf 1981). Because males tended to repeat each frequency, successive songs are not statistically independent points. However, recall that every tenth song was measured (Methods), which would reduce the effects of such sequential dependence. Also, any effect of nonindependence would bias our results against grouping the means together (i.e. towards finding discrete frequencies).

Overall, the songs of a male on a given morning did not sort into a few discrete frequencies (i.e. song types). In 7 of 16 dawn choruses, Scheffe's tests revealed four or fewer discrete groups of means (P < 0.05). However, there were significantly fewer shifts of 80 Hz or more in those choruses than in the nine remaining choruses (Mann-Whitney U; day 1, U = 16, n = 8, P = 0.002; day 2, U = 14, n = 7, P = 0.05). That is, the gaps between frequencies fill in the more a bird shifts frequency. For example, recording 90 songs from the male depicted in Figure 1D would make one think he sang only three discrete frequencies, but after recording over 500 songs, one finds he sings most frequencies between 2,960 and 3,500 Hz.

Song playback experiment.—All males in the above analyses sang songs within 120 Hz of the

high, medium, and low playback frequencies, so we assume that males in the playback study could do likewise. A regression analysis showed that the frequency of songs sung by males in response to playback was significantly and positively related to the frequency of the stimulus song ($F_{1,22}$ = 19.68, P = 0.002), although responses to playback of the low stimulus were significantly higher in frequency than the playback frequency (Table 1).

DISCUSSION

Species are said to possess song types if discontinuous variation in frequency or temporal characters allows their songs to be divided into discrete types (e.g. McGregor and Krebs 1982, Horn and Falls 1988). In this limited sense, some Black-capped Chickadees, at least within the course of one morning, may be said to possess a repertoire of song types. However, Black-capped Chickadees differ from species with multisong repertoires in that, on different days and across the population, frequency variation appears to be continuous. Thus, we conclude that variation in Black-capped Chickadee song more nearly approximates that of species with a single fixed song type than a multisong repertoire.

Our results add to a growing number of studies (Morton and Young 1986, Shackleton et al. 1991) that suggest there is not a sharp distinction between species with a single song type and those with multisong repertoires. The case of Black-capped Chickadees is especially interesting, because this species displays at least two features once thought to be peculiar to species with song repertoires: (1) repetitive delivery of stereotyped songs punctuated by sudden shifts in song parameters; and (2) a form of song matching (discussed below).

The results of our playback experiment suggest that song matching plays an important role in determining what frequencies chickadees sing. In addition, field observations suggest that neighboring males match each other much of the time (Horn unpubl. data). This evidence suggests that the number of frequencies sung by each male could be determined by the number of neighbors he has and the frequency of interactions he has with each of them. Repetitions at a given frequency might reflect an ongoing vocal interaction with one neighbor, with shifts occurring when an interaction with an-

other neighbor is started. The quality of those interactions among males might also play a role. One way in which this might happen is suggested by the lower rate of matching to our lowest-frequency playback song. If songs at lower frequencies convey a stronger territorial message than songs at higher frequencies, as suggested by Hill and Lein (1987), then males might be more reluctant to match a lower song.

However, there may also be individual differences in singing behavior. Although the precise frequencies sung by each male may vary from one day to another, the total range of frequencies sung appears to be consistent within males (Spearman rank correlation of day 1 values with day 2 values by male: r_s [corrected for ties] $= 0.81$, $n = 8$, $P < 0.05$). Also, the number of significantly different subsets of frequencies, as identified by Scheffe's tests, is consistent within males ($r_s = 0.87$, $n = 8$, $P \leq 0.05$). If singing patterns among neighbors are relatively constant, then matching might account for this consistency. Individual differences in song structure other than repertoire size have received little attention, so this possibility deserves further study. Differences in song structure in the related Great Tit (*Parus major*) have been related to various measures of male quality (Lambrechts and Dhondt 1986).

Studies of the dawn chorus in other species suggest that dawn singing is at least partly directed to the singer's mate (Mace 1987, Cuthill and McDonald 1990). The different frequencies sung by Black-capped Chickadees, therefore, might be used in intersexual communication, even though the behaviors of song matching and of patrolling territory boundaries during the chorus in this species suggest an intrasexual function as well. Recordings of complete dawn performances from different nesting stages would be valuable; changes in the length of the dawn chorus in Great Tits in relation to laying date have been attributed to an increase in the risk of cuckoldry (Mace 1987). We found little difference in singing patterns between prelaying and laying stages, but our sample size was small.

The song of the Black-capped Chickadee was thought to be one of the simplest among songbirds (e.g. Ficken 1981, Hailman 1989). Although the structure of individual songs is simple, we have now shown that each male sings several frequencies and can match the frequencies of playback songs. To date there have been

relatively few examples of continuous variation in species with single-song repertoires (e.g. Morton and Young 1986, Shackleton et al. 1991). Our results confirm the common idea that chickadees have a single song type, and at the same time suggest frequency variation has an analogous function to multiple song types.

LITERATURE CITED

BAKER, M. C., AND M. A. CUNNINGHAM. 1985. The biology of bird-song dialects. Behav. Brain Sci. 8:85–100.

CUTHILL, I. C., AND W. A. McDONALD. 1990. Experimental manipulation of the dawn and dusk chorus in the Blackbird *Turdus merula*. Behav. Ecol. Sociobiol. 26:209–216.

FALLS, J. B. 1981. Mapping territories with playback: An accurate census method for songbirds. Stud. Avian Biol. 6:86–91.

FICKEN, M. S. 1981. What is the song of the Black-capped Chickadee? Condor 83:384–386.

FICKEN, M. S., FICKEN, R. W., AND S. R. WITKIN. 1978. Vocal repertoire of the Black-capped Chickadee. Auk 95:34–48.

FICKEN, M. S., AND C. M. WEISE. 1987. A complex vocalization of the Black-capped Chickadee. II. Repertoires, dominance and dialects. Condor 89: 500–509.

HAILMAN, J. P. 1989. The organization of major vocalizations in the Paridae: A study in the evolution of communication. Wilson Bull. 101:305–343.

HAILMAN, J. P., AND M. S. FICKEN. 1986. Combinatorial animal communication with computable syntax: Chick-a-dee calling qualifies as 'language' by structural linguistics. Anim. Behav. 34:1899–1901.

HILL, B. G., AND M. R. LEIN. 1987. Function of frequency-shifted songs of Black-capped Chickadees. Condor 89:914–915.

HORN, A., AND J. B. FALLS. 1988. Structure of Western Meadowlark song repertoires. Can. J. Zool. 66: 284–288.

KROODSMA, D. E., AND E. H. MILLER. 1982. Acoustic communication in birds, vols. I and II. Academic Press, New York.

LAMBRECHTS, M., AND A. A. DHONDT. 1986. Male quality, reproduction, and survival in the Great Tit (Parus major). Behav. Ecol. Sociobiol. 19:57–63.

MACE, R. 1987. The dawn chorus in the Great Tit Parus major is directly related to female fertility. Nature (Lond.) 330:745–746.

McGREGOR, P. K., AND J. R. KREBS. 1982. Song types in a population of Great Tits (Parus major): Their distribution, abundance and acquisition by individuals. Behaviour 79:126–152.

MORTON, E. S., AND K. YOUNG. 1986. A previously undescribed method of song matching in a species with a single song "type," the Kentucky Warbler (Oporornis formosus). Ethology 73:334–342.

NOWICKI, S. 1989. Vocal plasticity in captive Black-capped Chickadees: The acoustic basis and rate of call convergence. Anim. Behav. 37:64–73.

RATCLIFFE, L., AND R. G. WEISMAN. 1985. Frequency shift in the fee bee song of the Black-capped Chickadee. Condor 87:555–556.

SEARCY, W. A., AND M. ANDERSSON. 1986. Sexual selection and the evolution of song. Annu. Rev. Ecol. Syst. 17:507–533.

SHACKLETON, S. A., L. RATCLIFFE, A. G. HORN, AND C. T. NAUGLER. 1991. Song repertoires of Harris' Sparrows (Zonotrichia querula). Can. J. Zool. 69: 1867–1874.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. W. H. Freeman and Co., New York.

WEISMAN, R., L. RATCLIFFE, I. JOHNSRUDE, AND T. A. HURLEY. 1990. Absolute and relative pitch production in the song of the Black-capped Chickadee. Condor 92:118–124.