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Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees

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Abstract The *fee-bee* song of male black-capped chickadees (*Poecile atricapillus*) is considered a single-type song that singers transpose up and down a continuous frequency range. While the ability to shift song pitch in this species provides a mechanism for song matching as an aversive signal in male-male territorial song contests, the functional significance of this behaviour during the “solo” performances of males during the dawn chorus is unclear. We analysed the dawn chorus songs and singing behaviour of males whose winter-flock dominance status we determined. We used correlation analysis to show that pitch shifts were accompanied by changes to other fine structural characteristics in song, including temporal and relative amplitude parameters. We also found that songs of socially dominant males and songs of their most subordinate flockmates could be distinguished using these methods by the way they performed a between-note frequency measure accompanying pitch shifts. That is, a ratio measure of the internote frequency interval remained constant for songs of high-ranking birds despite changes in absolute pitch, while low-ranking males sang a smaller ratio as they shifted to higher absolute pitches. These findings identify previously unrecognised variation in the songs of black-capped chickadees. More importantly, they indicate a mechanism by which pitch shifting during the dawn chorus of black-capped chickadees could provide a reliable indicator of relative male quality.

Keywords Black-capped chickadees · Dawn chorus · Male quality · Pitch shifts · Song structure

Introduction

A number of songbirds demonstrate an ability to transpose songs (or song elements) up and down a species-shared frequency range (Shackleton and Ratcliffe 1994). This “shifting” of absolute frequency is used to match the frequency of rival songs during territorial disputes in several species of songbirds, including Kentucky warblers (*Oporornis formosus*; Morton and Young 1986), Harris’ sparrows (*Zonotrichia querula*; Shackleton et al. 1991), black-capped chickadees (*Poecile atricapillus*; Horn et al. 1992), stripe-breasted wrens (*Thryothorus thoracicus*; Mennill personal observation) and nightingales (*Luscinia megarhynchos*; Naguib et al. 2002). For species with single song types, matching a rival’s song pitch appears to function as an agonistic response similar to song-type matching in species with multiple song types (Horn et al. 1992). Frequency-matched counter-singing during territorial encounters has been well-documented in black-capped chickadees, a species with a single song type (Otter et al. 2002). In these territorial song duels, pitch matching is closely associated with conflict escalation (Shackleton and Ratcliffe 1994) and functions as a graded signal, significantly affecting male behaviour as more aversive than non-matching song (Otter et al. 2002; Mennill and Ratcliffe 2004). Moreover, females appear to evaluate frequency matching (in combination with song overlapping) as an indicator of relative male quality in overheard male-male song duels (Mennill et al. 2002).

Chickadees sing a tonal, two-note *fee-bee* that they can shift up or down a continuous frequency range of several hundred hertz (Hill and Lein 1987; Horn et al. 1992). Despite changes in absolute frequency, other elements of chickadee song structure show remarkable conformity across most of the species’ pan-North American range (Hailman 1989; Kroodsma et al. 1999). In particular, two within-song frequency relationships, the frequency ratios of fee_{start}/fee_{end} (the glissando ratio) and fee_{end}/bee_{start} (the interval ratio), have been found to vary by less than 2% across North America (Weisman et al. 1990; Kroodsma et al. 1999). These have been implicated as possible cues to

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species recognition for territorial males evaluating their aggressive response to playback songs of intruders (Shackleton et al. 1992) and females determining their sexual response to playback songs of potential mates (Ratcliffe and Otter 1996).

While chickadees shift absolute frequency to match rival songs during territorial encounters, they also regularly shift frequency during the breeding-season dawn chorus. Unlike the case of territorial song duels, pitch shifting during the dawn chorus does not appear to be a response to concurrent singing by neighbouring males (Shackleton and Ratcliffe 1994). While the possibility exists that shifts in frequency are in response to motor constraints such as exhaustion from repeating songs at the same frequency (Lambrechts 1996), the fact that birds do not sing lower frequency dawn chorus songs any more often than the putatively more physiologically demanding high frequency songs suggests this is not the case. Horn et al. (1992) found chorusing males typically sing 41 ± 8.8 (mean \pm SE) songs at a given frequency before switching to another. These frequency shifts are audibly distinctive (to humans) and statistically discernible. During a single performance on a given morning, these pitch shifts lend the appearance of falling into discrete frequency categories, but over a large number of shifts and across multiple dawn choruses, males demonstrate an ability to sing along a continuous frequency range of 465 ± 52.9 Hz (Horn et al. 1992). The role of this pitch shifting behaviour during "solo" dawn chorus song performances is, however, unclear.

The dawn chorus of many birds has been functionally implicated in mate attraction, mate stimulation and mate guarding, among other social functions such as territory defence and adjusting social dynamics (Staicer et al. 1996). Indeed, male chickadees who have lost their mates during the breeding season dramatically increase their dawn chorus song rate, suggesting the dawn chorus of chickadees is important to mate attraction (Otter and Ratcliffe 1993). Further, female chickadees appear to seek extra-pair copulations from neighbouring males during the period corresponding with the dawn chorus (Smith 1988; Mennill, unpublished data). Yet, how these choruses might encode useful information for females assessing mating opportunities is not well understood. Recent research provides some clues. For instance, Otter et al. (1997) found measures of dawn chorus song output, including song rate, chorus length and chorus start time, could distinguish males that rank high within the linear dominance hierarchies of winter flocks from males that rank low. Females evaluating the relative quality of males might rely on these acoustic cues since high-ranking males enjoy better access to food (Ficken et al. 1990), improved survival (Smith 1991), and better overall reproductive success (Otter and Ratcliffe 1996; Otter et al. 1998) than their low-ranking flockmates. The fine structure of dawn chorus song, on the other hand, provides no similar categorical cues to relative social rank (i.e. quality) per se (Christie et al. 2003). Instead, chickadee song fine structure is individually distinctive

and could indicate the identity of familiar males whose relative quality is known from previous experience, such as interactions within winter flocks.

Pitch shifting during the chickadee dawn chorus suggests this behaviour may be important for the intersexual communicative function of these performances (Horn et al. 1992). The aim of the present study is to explore this possibility and the likelihood that this behaviour is an indicator of relative male quality to females evaluating prospective mates. That is, we were interested in determining whether some aspect of pitch shifting behaviour or some feature of pitch shifted song correlated with relative social rank. We examined field recordings of dawn choruses by male chickadees whose winter flock dominance status we determined. We evaluated these recordings to test for differences in pitch shifting behaviour between high-ranking males and their low-ranking flockmates. Similarly, we examined five fine structural measures of dawn chorus songs to test for correlations between variation in song structure and different absolute frequencies and whether these relationships might provide cues to relative male rank.

Methods

We examined pitch shifting behaviour, song structure and male quality by analysing the dawn chorus singing behaviour and songs of male chickadees in a population of individually colour-banded birds at the Queen's University Biology Department's Biological Station near Kingston, Ontario. Twenty-five different distinguishable winter flocks (5 flocks from 1999 and 20 flocks from 2000) were caught before the breeding season at winter feeders and were sexed and aged using morphometric and plumage measures (Meigs et al. 1983; Desrochers 1990; Smith 1991). The relative social rank of subject males within their winter flocks was determined by monitoring interactions at feeders (using established methods; see Ficken et al. 1990; Otter et al. 1994). Social rank data used in this analysis were taken from the results of 5,700 interactions between about 170 birds in 35 flocks that were part of a separate study (Mennill et al. 2002). High-rank and low-rank males were selected for paired comparison when they represented a flock's dominant male and his most subordinate male flockmate. These represented the alpha male and the beta male in 10 of the 25 flocks in our sample (i.e. only two males in these flocks). In flocks used for the remaining paired comparisons, alpha males and their most subordinate male flockmates were separated by at least one other male (i.e. three-male flocks) and as many as three (i.e. five-male flocks).

We analysed nine songs randomly selected from a single dawn chorus performance from each of 46 males (a total of 414 songs; songs were not selected if they fell within 4 songs of a pitch shift). Recordings of entire or partial dawn choruses were made at between 0445 and 0630 hours during the pre-fertile and fertile period between 24 April and 10 May 1999 ($n=10$ males) and between 23 April and 16 May 2000 ($n=36$ males). Birds were recorded at distances of 4–8 m using SONY Walkman Professional Stereo Cassette Recorders (WM-D6C) or Marantz Portable Cassette Recorders (PMD222) and either a Sennheiser directional microphone (model BA3) or Audio-technica directional microphones (model AT815a) with Saul Mineroff pre-amplifiers (model BA3). Songs were digitised at a sampling rate of 22,050 Hz (16-bit format) using Syrinx-PC sound processing software (John Burt, Ithaca, N.Y.) and analysed using Avisoft SASLab Pro sound analysis software for Windows (Raimund Specht, Berlin, Germany).

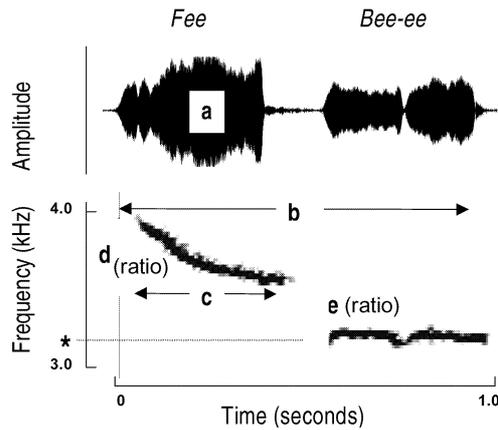


Fig. 1a–e An oscillogram and spectrogram representing a typical male black-capped chickadee (*Poecile atricapillus*) song from a dawn chorus recording. Song structural measures included in our analysis were **a** relative *fee* loudness (dB re maximum amplitude for the song), **b** song length (s), **c** *fee* length (% of song), **d** glissando ratio and **e** interval ratio. The absolute frequency of songs was calculated as the frequency of the start of the *bee* note (*)

We used five fine-structural song features in our analysis (Fig. 1). These were song length, the relative length of the *fee* note (*fee* length = percentage of song length), the relative loudness of the *fee* note (*fee* loudness = the logarithmic root mean squared measure (RMS) of the amplitude of the *fee* note (V_{Fee}) expressed in decibels relative to the RMS value for the song (V_{Song})) and the frequency ratios of the *fee* note (*glissando* ratio = frequency@*fee*_{start} / frequency@*fee*_{end}) and the internote interval (interval ratio = frequency@*fee*_{end} / frequency@*bee*_{start}) (see Weisman et al. 1990). The amplitude measure for the note and the song was determined using Avisoft software's "copy RMS of marked section" analysis tool and the ratio in dB was calculated as $20 \log V_{Fee}/V_{Song}$. We used a 2.5–5.0 kHz bandpass filter to reduce background noise outside the relevant frequency band to 0 dB SPL. Spectrograms were generated with an FFT length of 1,024 points and a spectral overlap of 87% (Hann window, 100% frame size). These parameters allowed a frequency resolution of 21 Hz and a temporal resolution of 5.8 ms. The start and end of signal elements were considered the points at which the amplitude of the sound within the envelope was less than 10% relative to the signal's maximum as determined using the Avisoft software's automatic parameter measurements (settings: –20 dB re max. amplitude, hold time 2 ms). The –20 dB threshold was chosen for its consistency for usefully delineating the signal while reducing the likelihood of interference from background noise. The absolute acoustic frequencies for the songs were determined by the frequency at the start of the second, more-constant *bee* note (Otter and Ratcliffe 1993).

We used only recordings from 2000 to analyse bout length, acoustic frequency range, and the pitch shifting behaviour of male chickadees during the dawn chorus, and we used recordings from both 1999 and 2000 to analyse song structure. The recordings of 45 males from 2000 included 36 high- and low-ranking males used in subsequent song analysis as well as 9 other males which occupied middle ranks in their flock hierarchies. All birds were from 18 winter flocks where flocks varied in size from two males per flock to five males per flock. Dawn chorus recordings were sometimes incomplete because we missed the beginning of the chorus while we located the bird, because continuous recording was disrupted by the bird's perch changes, or because the observer left off to record a second bird. The recordings were transcribed using a simple notation that tracked songs, discernible pitch shifts and interruptions in the recordings. We used the pitch shift criteria of Horn et al. (1992) for these transcriptions, considering males to have significantly altered their song pitch if they moved the absolute frequency of their songs up or down the frequency range by a

change ≥ 80 Hz. A smaller sample of complete chorus transcriptions were used to calculate chorus length ($n=17$) and a sample of chorus recordings that were uninterrupted for the first 300 continuous songs ($n=32$) were used to calculate the number of songs per shift and to compare these parameters between high-ranking ($n=16$) and low-ranking males ($n=16$). We also visually compared the song spectrograms and oscillograms to explore other obvious structural differences.

We used the randomization procedures available in Resampling Stats for Excel software (Resampling Stats, Arlington, Va.) to test for correlations between song features and absolute acoustic frequency using nine songs selected (as above) from a single dawn chorus from each of 10 males in 1999 and 36 males in 2000 (216 songs from 24 high-ranking males and 198 songs from 22 low-ranking males for a total of 414 songs). Randomisation procedures contrast a test statistic (in this case, the correlation coefficient r) against a null distribution empirically generated using a large number of random allocations of our observed data. The probability of the observed test statistic is determined as the proportion of values in the null distribution that are equal to or more extreme than the observed (Manly 1997). Since our sample included feature measures from nine songs from each of 46 birds, we used randomisation to generate our test statistic in a manner that would avoid pseudo replication effects: we repeatedly randomly selected one song from each bird to generate a number of correlation coefficients for song features and acoustic frequency based on the 46 birds. The mean of this population of results became our test statistic. In all cases, randomisation was performed using 5,000 replications to assure a stable probability value (Adams and Anthony 1996). We repeated these procedures on subsets of our sample to explore whether correlations between song features and the absolute acoustic frequency of the song existed for the categories of high-ranking or low-ranking males and the age categories of second year (SY: $n=108$ songs from 12 birds) or after second year males (ASY: $n=306$ songs from 34 birds). In our sample, nine SY birds (the youngest group) were also low-ranking males, while three from this group ranked high in flock dominance despite their young age. Among the ASY group (older birds), 21 were high-ranking males while 13 were low-ranking. We used statistical power analysis to explore whether any apparent consistency in song measures across the absolute frequency range of our population (no significant correlation, or $H_0: P=0$) might be the statistical consequence of a Type I error. We made no assumptions about possible correlations so all significance tests were two-tailed and $\alpha=0.05$. Unless otherwise indicated, all values are expressed as means \pm SE.

Results

We found male chickadees in our population sang dawn chorus songs within an 860 Hz absolute frequency range (between 2,770 and 3,630 Hz). The number of songs per individual chickadee's dawn chorus recording in 2000 ($n=32$) was 282 ± 36 (as compared to 284 ± 59 reported by Horn et al. 1992), and the maximum number of songs in a continuous chorus recording was 793. Meanwhile, the rate at which singers pitch shifted songs was highly variable between males. For instance, one bird did not shift at all during a recording of 443 songs, while another shifted 71 times during a recording of 464 songs. Overall, however, we found the rate of dawn chorus pitch shifting in our sample was 30.7 ± 3.7 songs between shifts (somewhat lower than the 41.0 ± 8.8 reported by Horn et al. 1992).

We found no difference in the rate at which males pitch shifted songs during the dawn chorus for high-

ranking males versus low-ranking males (high-ranking = 35.1 ± 5.2 songs between shifts, low-ranking = 26.2 ± 5.2 songs between shifts; two-tailed t -test, $df=30$, $t=1.21$, $P=0.24$). Similarly, we found no rank-categorical differences in the size of the dawn chorus pitch shifts (change in frequency) performed by high-ranking and low-ranking males in our recordings (high-ranking = 331.1 ± 17.6 Hz, low-ranking = 340.5 ± 18.2 Hz; two-tailed t -test, $df=23$, $t=-0.371$, $P=0.71$).

Correlation analyses examining dawn chorus songs from 46 male chickadees (nine songs from each male) suggested three of the five fine structural features became significantly smaller when songs were performed at higher absolute acoustic frequencies (song length: $r=-0.27$, $P<0.0001$; *fee* length: $r=-0.27$, $P<0.0001$; relative *fee* loudness: $r=-0.24$, $P<0.0001$). In particular, songs of high- and low-ranking birds that were performed at the lowest frequency (for this sample, 2,790 Hz) were on average 8% longer than those performed at the highest frequency (for this sample, 3,610 Hz), while the relative length of the *fee* note (expressed as a percent of song length) showed songs at the lowest frequency were 8% greater than those at the highest frequency. The *fee* loudness relative to the loudness of the song at the lowest frequency was almost 6% more intense than at the highest. Meanwhile, the correlation of these temporal and relative amplitude measures with absolute frequency was equally characteristic of songs performed by high-ranking ($n=24$ males; 216 songs) and low-ranking males ($n=22$ males; 198 songs) (song length: high-ranking $r=-0.32$, $P<0.0001$; low-ranking $r=-0.22$, $P<0.0001$; *fee* length: high-ranking $r=-0.27$, $P<0.0001$; low-ranking $r=-0.25$, $P<0.0001$; relative *fee* loudness: high-ranking $r=-0.32$, $P<0.0001$; low-ranking $r=-0.16$, $P<0.0001$) (Fig. 2).

The two relative frequency measures, however, showed a different pattern. Unlike other measures, the frequency ratio for the glissando did not change significantly across the range of absolute pitch for both high- and low-ranking males (Fig. 2d; high-ranking $r=-0.07$, $P=0.08$; low-ranking $r=0.06$, $P=0.12$). By contrast, low-ranking males significantly reduced the frequency ratio of their internote interval as they performed songs at higher pitches (Fig. 2e; low-ranking $r=-0.20$, $P<0.0001$) while high-ranking males performed this interval with a consistent ratio across all pitch shifts (Fig. 2e; high-ranking $r=0.02$, $P=0.32$). At the highest frequency in the performance range for our population, the interval ratio for low-ranking males was 1.7% smaller than at the lowest.

The pattern of correlations between song measures and acoustic frequency was similar when examined in the context of the singers' age (Table 1). Songs from both categories of young males (SY; $n=12$) and older males (ASY; $n=34$) showed significant negative correlations between temporal measures and acoustic frequency, while the frequency ratio of the *fee* note remained consistent. Also, in a manner corresponding to the difference between high-ranking and low-ranking males, the interval ratio of the songs of younger males showed a significant

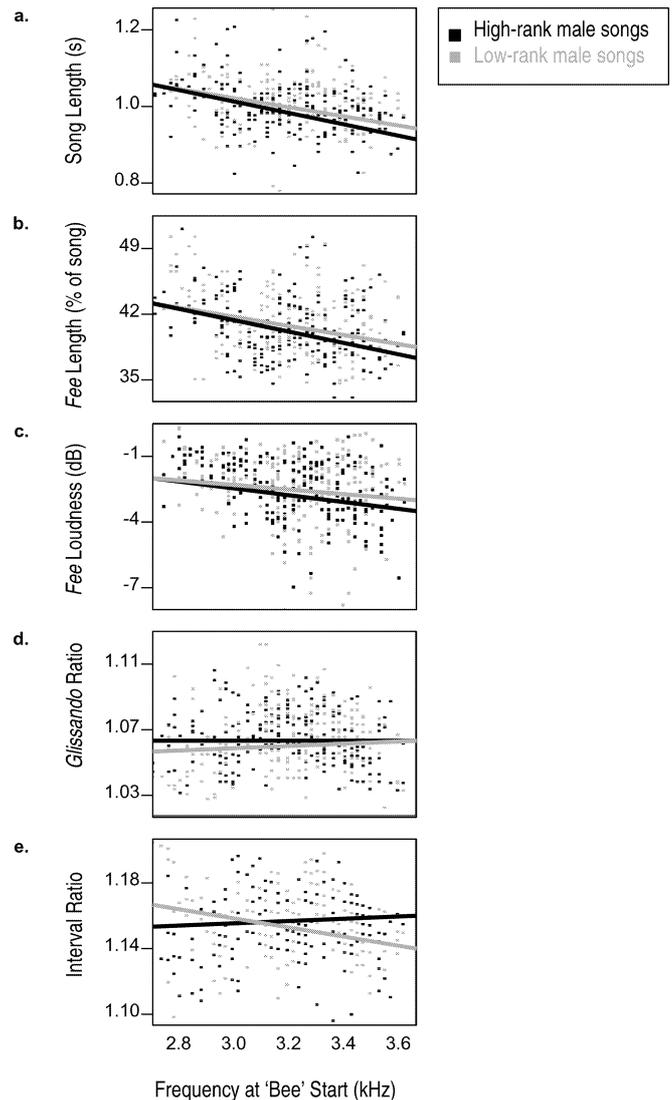
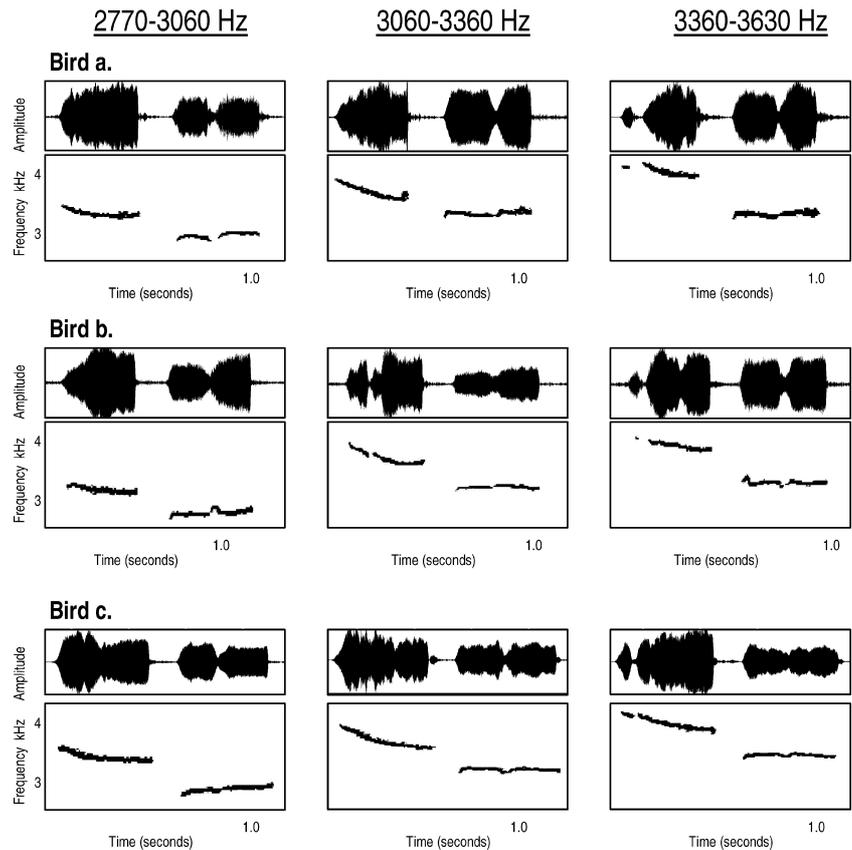


Fig. 2 Correlation analyses of five fine structural features of chickadee song with changes in absolute acoustic frequency for high-ranking and low-ranking males. The *points* shown represent the original data points (46 birds \times 9 songs each), and the *best-fit lines* are calculated using randomisation procedures

Table 1 Correlation analyses of five fine structural features of black-capped chickadee (*Poecile atricapillus*) song with changes in absolute acoustic frequency by age of singer. Correlation coefficients (r) and probability values for five measures against the acoustic frequency of song performance for 12 second year (SY) males (young) and 34 after second year (ASY) males (older)

Age Feature	SY		ASY	
	observed r	P	observed r	P
Song length	-0.3500	<0.0001	-0.2105	<0.0001
<i>Fee</i> length	-0.1729	<0.0001	-0.2844	<0.0001
Relative <i>fee</i> loudness	-0.0509	0.1456	-0.2770	<0.0001
Glissando ratio	0.0354	0.2296	-0.0115	0.5950
Interval ratio	-0.4432	<0.0001	0.0836	0.2412

Fig. 3a–c Oscillograms and spectrograms representing songs of three birds from each of the lowest, the middle and the top third of the chickadee frequency range. Plots **a–c** indicate individual birds. Bird **a** is a high-ranking ASY male; bird **b** is a low-ranking ASY male; and bird **c** is a low-ranking SY male



negative correlation with acoustic frequency while the songs of older males did not. However, our measure of relative *fee* loudness, which showed a significant negative correlation with acoustic frequency for songs of ASY birds, did not appear to change with pitch for younger SY birds. This result is unexpected and may be a result of our small sample size in this age category and a corresponding lack of statistical power to discriminate a correlation for this measure in the case where one exists (power = $1 - \beta = 0.54$, or only a little more than a 50% chance of correctly rejecting the null hypothesis for this small sample of birds).

Meanwhile, the statistical power to detect frequency-related variation in the glissando ratio and the interval ratio (variation at least as large as variation for these measures due to other factors) was moderate for our sample of 46 birds (0.65 and 0.64, respectively). Our statistical power for our correlation analyses of the song measures of high-ranking and low-ranking males was somewhat less (high-rank: 0.61 for glissando ratio and 0.61 for interval ratio; low-rank: 0.60 and 0.59, respectively). The statistical power for ASY age category correlation analysis was 0.64 for glissando ratio and 0.62 for interval ratio, but statistical power for our examination of SY birds was smaller at 0.57 for glissando ratio and 0.57 for interval ratio.

Fig. 3 shows examples of spectrograms and oscillograms chosen from songs from the bottom, middle and top third of the frequency range for three representative

males (bird **a** is a high-ranking ASY male; bird **b** is a low-ranking ASY male; and bird **c** is a low-ranking SY male). These songs illustrate some of the distinctive differences between songs of different frequencies within an individual male's dawn chorus, including differences in the relative loudness of the *fee* and *bee* notes. One intriguing feature is an amplitude break in the *fee* note that appears in some songs performed in the middle or upper frequencies of the species range (an amplitude break in the *bee* note appeared in songs of all birds regardless of acoustic frequency). For instance, of the 30 birds in our sample that sang songs in the lower third of the species frequency range, none of these sang a complete amplitude break in the *fee* note. Meanwhile, 9 of 43 birds showed this complete break in the top two thirds of the frequency range (e.g. the 3,060–3,360 Hz songs for Fig. 3 bird **b** and the 3,360–3,630 Hz songs for all birds in Fig. 3).

Discussion

Outside of the context of frequency-matched counter singing between territorial males, song pitch shifting in passerines has not been carefully studied. The presence of this behaviour during the solo dawn chorus of male black-capped chickadees strongly suggests it is important in intersexual communication and may play a role encoding information about a singer's relative quality as a potential sexual partner. While we found no difference between

high-ranking and low-ranking males in dawn chorus pitch shifting behaviour per se, we found high-ranking males maintained stereotypy in a key song parameter, the interval ratio, when singing at different acoustic pitches. For low-ranking birds, however, the interval ratio changed with shifts in pitch, diminishing by almost 1.7% from the low end of the frequency range to the highest. While this does not seem to be a large number, it may be an important contributor to the <2% continent-wide variation in this song measure for this species (Kroodsma et al. 1999). We found a similar pattern between songs of older (ASY) males and younger males (SY), reflecting the correlation between age and rank in black-capped chickadees (Smith 1991). Since social rank in chickadees corresponds with longevity and reproductive success, our results suggest females may use dawn chorus pitch shifting and the performance of this song measure as a reliable indicator of relative male quality when assessing mating opportunities to improve reproductive success or the genetic viability of their young (e.g. Hasselquist et al. 1996; Forstmeier et al. 2002).

Relative acoustic frequency measures (expressed as frequency ratios) in animal sounds often remain imperious to transposed changes in absolute pitch and are perceived as the same or similar (perceptually invariant) by listeners (see review in Hulse et al. 1992). For example, the ability to generalise relative pitch discrimination to songs of different frequency has been shown in starlings (*Sturnus vulgaris*; Hulse and Cynx 1985) and chickadees (Weisman and Ratcliffe 1989). These perceptually invariant frequency ratios have been implicated in conspecific song recognition in a small number of songbirds, including white-throated sparrows (*Zonotrichia albicollis*; Hurly et al. 1990, 1992), veeries (*Catharus fuscescens*; Weary et al. 1991), and black-capped chickadees (Weisman and Ratcliffe 1989). In the case of chickadees, the playback response of both territorial males (Shackleton et al. 1992) and sexually primed females (Ratcliffe and Otter 1996) was found to be significantly affected when the glissando was flattened (the glissando ratio reduced to almost 1). Our finding that the glissando ratio remains unchanged despite shifts in absolute pitch (for both high and low-ranking males) is consistent with the view that this ratio may be a critical species-typical cue, important for both the territorial defence and mate attraction functions of the chickadee dawn chorus and thus under stabilising selection that ensures its consistency (Ryan and Rand 1993).

The interval ratio, on the other hand, may play a somewhat different role. Previous research suggests this ratio is not attended to by territorial males (Ratcliffe and Weisman 1992; Shackleton et al. 1992; Ratcliffe and Otter 1996; but see Weisman and Ratcliffe 1989), but is important to the sexual response of females (Ratcliffe and Otter 1996). Our results suggests a possible explanation for this: the interval ratio, when combined with changes in pitch, is a reliable intersexual cue to singer quality for females assessing males based on their dawn chorus song. For instance, singing this ratio at different absolute

pitches might provide an honest indicator of quality if it is difficult to perform for all but males who are energetically, physiologically or developmentally equipped for it (e.g. Lambrechts 1996, Podos 1996). The sound production demands of song fine structure have been implicated as a preferred trait by female canaries (*Serinus flaviventris*; Vallet et al. 1998) and correlated with longevity and extra-pair paternity in dusky warblers (*Phylloscopus fuscatu*s; Forstmeier et al. 2002). Our findings suggest the interval ratios sung by low-ranking males (i.e. lower quality males) differ most from the consistent ratios of high-ranking males at lower absolute frequencies. Small birds like chickadees may be constrained when performing at lower pitches by the frequency limitations imposed by their small syrinx size (Ryan and Brenowitz 1985) or by their vocal tract configuration (Podos 2001). Meanwhile, song-learning experiments with hand-reared chickadees suggests birds tutored with songs at low absolute frequencies nevertheless did not readily sing low songs (Shackleton and Ratcliffe 1993). The same experiments also indicate that the interval ratio is among the most difficult elements of the chickadee song to learn or learn with any consistency, and half the tutored chickadees did not change frequency between the two notes at all. Thus, the development or performance of the interval ratio in this species may be restricted by limits on sound production, and the ability to overcome these motor constraints by singing accurately at lower frequencies may provide an honest indicator of singer quality (Podos 1996).

We also found that pitch shifts in chickadee dawn chorus songs were correlated with significant corresponding changes in other fine structural features; changes reflected in the songs of both high-ranking males and their low-ranking flock mates. In particular, songs performed at the lower end of the absolute frequency range for chickadee songs were longer, with relatively longer, louder *fee* notes, than songs performed at higher absolute frequencies. These differences, while continuous across the frequency range, accounted for as much as 8% of the variation in song length as well as 8% and 6% of the difference in length and loudness of the *fee* note, respectively. Furthermore, songs performed in the upper part of the chickadee frequency range were also more likely to exhibit a measurable amplitude break in the early part of the *fee* note (e.g. *fe-ee*). None of this is surprising since correlations between continuous variation in song structure (such as temporal or relative frequency features) and absolute frequency have been recognised in other species and associated with the motor constraints of sound production (Lambrechts 1996; Suthers and Goller 1997; Suthers et al. 1999). But the results nevertheless reveal previously unrecognised, consistent variation in a song that has long been considered among the most simple and stereotyped of learned bird songs (Hailman 1989; Kroodsma et al. 1999). These findings could shed new light on reported geographic variation in black-capped chickadee song, such as the appearance of a “broken *fee*” note in the high frequency songs of chickadee populations

in Massachusetts (Kroodsma et al. 1999) which appears to be a shared characteristic of mid and upper frequency songs by some birds in our Ontario population, and on the interpretation of results in several earlier playback and song perception experiments that have assumed song parameters remained constant with absolute pitch (e.g. Weisman and Ratcliffe 1989; Shackleton et al. 1992; Shackleton and Ratcliffe 1994; Fotheringham and Ratcliffe 1995; Ratcliffe and Otter 1996; Mennill et al. 2002; Otter et al. 2002).

Black-capped chickadees provided one of the first examples of the ability of a songbird to transpose its single song type up and down a continuous frequency range (Horn et al. 1992). This species was also among the first to show relative pitch perception in animals (Weisman and Ratcliffe 1989). The evolutionary importance of each of these features has been considered separately and within the context of male-male territorial disputes (Horn et al. 1992; Shackleton et al. 1992; Shackleton and Ratcliffe 1994). The present study demonstrates that these features could also play a role in intersexual communication during the solo performances of the chickadee dawn chorus. Females assessing mating opportunities from dawn chorus song could use the consistency of the interval ratio across different absolute pitches to discriminate high-ranking and low-ranking males. The presence of this cue to quality may also help explain the evolutionary relevance of pitch shifting during the dawn chorus.

However, the presence of statistically discernible cues in bird song does not mean that these cues are necessarily useful or even meaningful to listeners (Horn and Falls 1996). Evidence suggests chickadees are capable of discerning alterations to the interval ratio (Weisman and Ratcliffe 1989), but it remains to be examined how these birds may be using this cue to measure male quality and whether pitch shifting is required to reveal the information encoded in this relative pitch parameter. Further research is required to test whether combined changes to absolute and relative pitch in a song series may influence female sexual responsiveness or mate selection.

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