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# FUNCTION OF FREQUENCY-SHIFTED SONGS OF BLACK-CAPPED CHICKADEES[1]

BRAD G. HILL AND M. ROSS LEIN[2]
*Department of Biology, University of Calgary, Calgary, Alberta T2N 1N4, Canada*

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Both Saunders (1935) and Odum (1942) noted that Black-capped Chickadees (*Parus atricapillus*) sometimes sing two versions of their *fee bee* song, with one version being shifted downward in frequency. Saunders stated that chickadees, which will sing in response to a whistled imitation of their song, could "be induced to change the pitch if the imitator first does so." This suggests that shifted songs might occur naturally during interactions between singing birds. Recently, Ratcliffe and Weisman (1985) have described the phenomenon quantitatively in captive birds, but they were uncertain about the functional significance of such "shifted" songs. They found that captive birds sang shifted songs more frequently during playback of recorded song than they did in a solo context, but this difference was not statistically significant.

During a study of interspecific relationships between Black-capped Chickadees and Mountain Chickadees (*P. gambeli*) in southwestern Alberta, we recorded the use of shifted songs by free-living Black-capped Chickadees during both natural interactions and playback experiments. Although these observations were made incidentally to other work, they permit us to describe the use of shifted songs, and to suggest the significance of this unusual type of intra-individual song variation.

## METHODS

Our study area was in the Sheep River valley, about 70 km SW of Calgary, Alberta. The two species of chickadees occupy overlapping territories in mixed forest dominated by lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*), and white spruce (*Picea glauca*). Observations were made between May 1982 and August 1984. Most records of shifted songs were obtained from color-banded individuals during continuous observations made for the purpose of delimiting territories. Some were obtained, however, during song playback experiments at nesting cavities. A few of the records come from more casual observations. In almost all cases the sex and identity of the singing bird, its recent history, and the behavioral context were known.

One tape recording of a male singing shifted songs was made during casual observations using a Nagra 4.2 recorder and a Gibson P-650 parabolic microphone. Three other males were recorded during playback experiments using a Sony TC-142 cassette recorder and a Sennheiser MKE 883 "shotgun" microphone. Frequency measurements were made using a Calcomp 9000 digitizing tablet from spectrograms prepared with a Kay Elemetrics Model 7800 Digital Sona-Graph using a narrow band (45 Hz) filter. Both notes of *fee bee* songs are pure whistles, showing very little change in frequency over their duration (see fig. 1g in Ficken et al. 1978). However, because some individuals show a slight and continuous decrease in frequency over the course of a note, we arbitrarily measured frequencies at the temporal midpoints of notes.

## RESULTS

The shifted songs of birds from our population showed frequency characteristics similar to those of birds from Ontario described by Ratcliffe and Weisman (1985) (Table 1). Both the *fee* and *bee* notes of shifted songs were lower in frequency than in "normal" songs (mean frequency shift ± SE = −0.48 ± 0.02 kHz for *fee*; −0.33 ± 0.2 kHz for *bee*). In addition, the mean frequency difference between the *fee* and *bee* notes was less in shifted songs (0.40 ± 0.01 kHz) than in normal songs (0.56 ± 0.001 kHz). Both shifted and normal songs exhibited a high degree of individual stereotypy as indicated by the low standard error values for frequency measurements (Table 1).

Shifted songs were not common in our study population. Of the 167 naturally-occurring bouts of song which we observed, only 14 (8.4%) contained shifted songs. In two instances both members of a pair of counter-singing males used shifted songs. Three additional bouts of shifted songs were recorded during a total of 17 playback experiments.

Shifted songs usually occurred during directed interactions. Ten of 14 naturally-occurring bouts (71%) were given by counter-singing males. In comparison, only 16 of 153 bouts (10%) of normal songs involved counter-singing. In six of the 10 bouts of counter-singing, a male switched from singing normal songs to shifted songs after a movement toward the other bird, usually to within 10 m. In three of the 10 cases the bird switched back to normal songs after moving away from its opponent. Of the four remaining naturally-occurring bouts, two involved males who had been singing normal songs but then switched to shifted songs when approached closely by their mates. We have occasionally observed males attacking their mates when approached while singing, suggesting that these two cases might also involve situations of potential aggres-

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[2] Author to whom reprint requests should be sent.

sion. One bout was given by a female who was mated but alone at the time, and one was given in an unknown context by an unidentified bird (probably a male).

The bouts of shifted songs given by males during playback experiments followed a pattern similar to that observed in natural bouts. In all three cases shifted songs began when the singer was closer to the speaker (2 to 4 m) than he had been when normal songs began (10 to 15 m). Shifted songs also began much later after the beginning of playback (81 to 174 sec) than did normal songs (2 to 22 sec). In addition, at the end of the playback period, birds which had sung shifted songs always switched to normal songs prior to complete cessation of singing.

## DISCUSSION

One of the functions of song in the Black-capped Chickadee is territorial advertisement (Ficken 1981). We suggest that the shifted song plays a role in territorial advertisement as well, but that it is a more aggressive signal than normal song. That is, it carries a message that the singer has a higher probability of performing agonistic behavior than when singing normal songs. Although the shifted song was used in a number of different situations, almost all of them were clearly agonistic. Ficken et al. (1978) argued that the *gargle* vocalization of Black-capped Chickadees represents a higher level of aggression than does song, and that males switch to that vocalization as the probability of agonism increases. It is possible that shifted song represents a higher probability of agonistic behavior than does normal song, but a lower probability than does the *gargle*.

This interpretation is consistent with the suggestion that males will shift frequency in response to hearing conspecifics. While Ratcliffe and Weisman (1985) found no conclusive evidence to support this suggestion in their experiments with captive chickadees, we feel that the stimulus level used by these authors (playback of 16 songs over >21 min) may have been too low to elicit the frequency shifts effectively. Our experiments used a playback rate of 24 songs in 3 min and, even then, those birds which did respond with shifted songs did so with a considerable latency. Also suggestive of a threshold effect is the fact that the free-living birds which we observed sang shifted songs in continuous bouts, while the captives studied by Ratcliffe and Weisman "tended to intersperse single, shifted songs between bouts of normal song."

Morton (1977) proposed a series of relationships between the physical structure of vocalizations and the motivation of the signaller. One of his motivation-structural (M.-S.) rules is that calls of low frequency indicate higher aggressiveness than do calls of higher frequency. Although proposed originally for vocalizations which function over only a short distance, the M.-S. rules may also influence the structure of some long-distance vocalizations (Hope 1980). If our interpretation, that the shifted song is a vocalization indicating increased probability of aggression, is correct, then the lower frequency would appear to conform to Morton's (1977) ideas.

TABLE 1. Frequency characteristics (kHz) of normal and shifted *fee bee* songs of Black-capped Chickadees.

| Male | | Normal song | | Shifted song | |
|---|---|---|---|---|---|
| | | *Fee* | *Bee* | *Fee* | *Bee* |
| 1 | $\bar{x}$ | 3.87 | 3.31 | 3.28 | 2.89 |
| | SE | 0.01 | 0.01 | 0.02 | 0.03 |
| | $n$* | 6 | 6 | 5 | 5 |
| 2 | $\bar{x}$ | 3.90 | 3.34 | 3.42 | 3.00 |
| | SE | 0.04 | 0.03 | 0.02 | 0.02 |
| | $n$ | 5 | 5 | 5 | 5 |
| 3 | $\bar{x}$ | 3.73 | 3.18 | 3.30 | 2.92 |
| | SE | 0.04 | 0.01 | 0.01 | 0.01 |
| | $n$ | 4 | 4 | 5 | 5 |
| 4 | $\bar{x}$ | 3.74 | 3.19 | 3.32 | 2.88 |
| | SE | 0.01 | 0.01 | 0.01 | 0.01 |
| | $n$ | 5 | 5 | 5 | 5 |

* $n$ = Number of songs measured.

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