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USE OF SONG TYPES BY MOUNTAIN CHICKADEES (*POECILE GAMBELI*)

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ABSTRACT.—We investigated the composition and function of individual song repertoires in Mountain Chickadees (*Poecile gambeli*) in Alberta, Canada. Individual males had repertoires of 4–7 song types, but three types made up 90% of all songs. We tested and rejected the hypothesis that all song types convey the same behavioral messages. Different song types were associated with different behavioral situations. Males used 3-note songs predominantly during undisturbed singing and 2-note songs predominantly during non-aggressive activity. Three-note songs with each successive note lower pitched were associated with male–male interactions. We suggest that different song types convey messages indicating different levels of aggression by the singer. The function of individual repertoires in Mountain Chickadees appears to be similar to that of other North American chickadees and titmice, with different song types having different communicative functions. *Received 7 Aug. 1998, accepted 11 Feb. 1999.*

Although individuals of some species of songbirds sing only one type of song (Searcy 1983), males of many species possess repertoires comprising a number of discrete categories of songs, or song types (Dodson and Lemon 1975). The significance of song repertoires has been the subject of much research and speculation (reviewed by Krebs and Kroodsma 1980, Kroodsma 1982, Kroodsma and Byers 1991, MacDougall-Shackleton 1998).

Most species of the genera *Parus, Poecile,* and *Baeolophus* have individual song repertoires (Hailman 1989), although the role of repertoires appears to differ among species [these closely-related genera were formerly lumped as *Parus* (American Ornithologists' Union 1997)]. Individual male Great Tits (*Parus major*) may use different song types in sequence with no apparent change in the external situation (Hinde 1952), suggesting that all song types convey the same messages. Consequently, Great Tits have been used to test many of the hypotheses that suggest that overall repertoire size is important (e.g., Krebs 1976, 1977; McGregor et al. 1981; Baker et al. 1986; Lambrechts and Dhondt 1988). In contrast, other species, such as the Blue Tit (*Parus caeruleus*), the North American titmice (*Baeolophus*), and some of the North American chickadees (*Poecile*), seem to possess song types that convey different messages (Smith 1972, Dixon and Martin 1979, Gaddis 1983, Schroeder and Wiley 1983, Bijnens and Dhondt 1984, Johnson 1987).

We examine the role of individual repertoires of Mountain Chickadees (*Poecile gambeli*). Mountain Chickadees sing relatively simple songs consisting of 2–6 whistled notes, with any number of these notes shifted to frequencies lower than the others (Hill 1987). Song types are defined easily by variation in number and pitch of notes; individual repertoires consist of 3–5 song types (Hill and Lein 1989). Although no studies have investigated whether Mountain Chickadees can differentiate among song types, this seems probable because closely related Black-capped Chickadees (*Poecile atricapillus*) distinguish among songs varying in note number and pitch (Ratcliffe and Weisman 1986; Weisman and Ratcliffe 1989).

We documented song variation and singing behavior of male Mountain Chickadees during the breeding season. Our null hypothesis was that all song types of the Mountain Chickadee convey the same behavioral messages, and thus the song type that a male sings would be independent of the situation in which it is used. The alternate hypothesis was that song types convey different messages and thus certain song types would have a higher probability of being sung in specific situations.

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METHODS

The study was conducted at the Barrier Lake site (51° 00′ N, 115° 00′ W) of the University of Calgary's Kananaskis Field Stations in the Kananaskis Valley of the Rocky Mountains of southwestern Alberta. The forest inhabited by Mountain Chickadees is dominated by trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and lodgepole pine (*Pinus contorta*). Mountain Chickadees are secondary cavity-nesters, using pre-existing cavities such as natural crevices or deserted nests of other cavity-nesting birds (Hill 1987, pers. obs.). In southwestern Alberta, Mountain Chickadees start to search for suitable nesting cavities during April (Hill 1987, pers. obs.). Nest-building occurs in early May. Incubation starts near the end of May and lasts about 14 days. The nestling period generally lasts 18–21 days (Dahlsten and Copper 1979) but may be as short as 14 days (pers. obs.). Nestlings fledge during the last week in June and early July.

Mountain Chickadee songs, and information on the situations of song use, were recorded from April to July 1993. Data were collected from 11 males, of which 7 were marked with a unique combination of colored plastic leg bands. We could identify unbanded males because males in adjacent territories were banded; we also used territorial location, use of favorite singing sites, or association with a particular nest cavity to identify unbanded males. All males except one foraged frequently with one other Mountain Chickadee and therefore were presumed to be mated. Because Mountain Chickadees defend their entire home range (Hill 1987), we determined the extent of a male's territory by noting areas in which he was found regularly. Observations of aggressive interactions between males helped to confirm the locations of territorial boundaries.

It was impossible to sample songs of all individuals in one day, but usually each individual was observed at least once in a three-day period. Observations occurred between 04:00 and 12:00 (MST), the period when chickadees are most active. An observation period began when a male started to sing and lasted from a few minutes to over an hour, depending on how long the individual sang. Songs and verbal descriptions of the different elements of the situation during singing were recorded onto Sony C-90HF cassette tapes using AKG D190E or Sony ECM-33P microphones, Sony PBR-330 parabolic reflectors, and Sony TCM-5000 or Sony TCM-5000EV tape recorders.

All recordings were made by either MOW or a field assistant. Before working independently, the field assistant accompanied MOW during 15 observation periods to ensure that both observers were making comparable observations. We did not notice chickadees engaging in behaviors directed at the observer during any of the observation periods, so we believe that the effect of our presence was minimal.

We recorded three elements of the situation while males were singing. (1) Behavior of the singer: a. undisturbed (i.e., singing while stationary and not engaged in other activities); b. engaged in non-aggressive activities (e.g., foraging, preening, feeding nestlings, etc.); c. engaged in aggressive activities (i.e. counter-singing with or chasing territorial neighbors). (2) Position on territory: a. within 50 m of the nest site; b. away from the nest site. (3) Location of mate: a. present in the vicinity of the singer; b. absent from the vicinity. Each song was assigned to a particular situation. If the situation changed while the male was singing, then songs recorded before the change were assigned to the first situation, and songs recorded after the change assigned to the second situation. Nests of six pairs were found, allowing us to also assign songs for these males to particular breeding stages (nest search/build, egg-laying, incubation, or nestling).

Mountain Chickadees often were out of sight when in the tops of coniferous trees. We assumed that songs given during such intervals were in the same situation as the last song given prior to disappearance. However, if a subject was out of sight for more than 5 minutes, we recorded its behavior for that interval as unknown.

We categorized different song types by variation in number of notes and relative pitch of notes within a song. These two features showed the most obvious variation among songs and were relatively easy to distinguish by ear. We confirmed these classifications by examining audiospectrographs of many songs using SIGNAL bioacoustical analysis software (Engineering Design, Belmont, Massachusetts). Transcriptions of recordings were made using OBSERVER software (Noldus Information Technology, Wageningen, The Netherlands).

We examined separately the relative importance of number of notes in a song and the pitch of notes within a song. To determine the influence of number of notes, we combined all song types with the same number of notes regardless of the pitch of the notes within the song. Statistical tests were performed only for 2-note and 3-note songs because sample sizes for songs with 1 note and 4 notes or more were too small. To examine the influence of pitch, statistical tests were performed only for "common 3-note songs" and "descending 3-note songs" (see descriptions in Results). Sample sizes of other song types with variations in pitch were too small for statistical testing.

If different song types are not used in different situations, one would predict that a particular song type should occur in a specific situation at the frequency expected if song types are used at random. To examine the influence of note number in songs, we calculated χ^2 values for 2 × 2 contingency tables of either the relative number of 2-note songs and all other song types compared between specific situations of use, or the relative number of 3-note songs and all other song types compared between specific situations of use. To examine the influence of pitch in songs, we calculated χ^2 values for 2 × 2 contingency tables of the number of common 3-note songs and descending 3-note songs compared between specific situations of use. The independent event in all contingency tables was a single song.

We conducted a separate contingency analysis for each individual for every situation of use. We were not able to record all individuals in different situations. Consequently, the number of individuals used in each comparison varied from four to seven. We combined the results of individual contingency analyses using a test described by Cochran (1971:151). This test accounts for differences in direction of response among individuals and can be used even if there is a wide range of sample sizes and probabilities among individuals. The test calculates a z-value that can be compared to the normal distribution to determine significance, with non-significant results indicating that the song types are independent of the situation of use. The sign of the z-value indicates the direction of deviation from the expected.

Most statistical tests were performed using STATISTIX 3.5 for Windows (Analytical Software, St. Paul, Minnesota). Differences at an $\alpha \leq 0.05$ were considered to be significant.

RESULTS

Composition of song repertoires.—We recorded an average of 1,501 songs (± 435 SE; range = 222–4,372) from each of the 11 focal males, with an individual male being recorded an average of 15.1 days (± 2.2; range = 6–28). Average total repertoire size was 7.4 song types (± 0.3; range = 6–9). However, song types used rarely by an individual may have been "accidental" productions rather than regular elements in the repertoire. Excluding song types that represented less than 1% of the total songs for an individual, the average repertoire size was 5.1 song types (± 0.3; range = 4–7). There was no relationship between the number of songs recorded from an individual and the estimated size of his repertoire (all song types: Spearman $r = 0.36$, $P > 0.05$, $n = 11$; song types > 1%: Spearman $r = -0.27$, $P > 0.05$, $n = 11$), indicating that all repertoires were sampled adequately.

"Common 3-note songs" (3-note songs with the last two notes lower in pitch than the first note, Fig. 1A), "common 2-note songs" (2-note songs with the second note lower-pitched, Fig. 1B), and "descending 3-note songs" (3-note songs with each successive note at least 200 Hz lower in pitch than the previous note, Fig. 1C) were the prevalent song types. The most-frequent song type was common 2-note song for 5 of the 11 focal males, common 3-note song for 4 males, and descending 3-note song for 2 males. All males sang these three song types, but for three individuals < 4% of total songs recorded were descending 3-note songs. All other variants had frequencies of < 12% of an individual's repertoire, including 2-note and 3-note songs with all notes of the same pitch (i.e., within 200 Hz of one another; Figs. 1D, 1E) and songs with four or more notes (Fig. 1F). Wiebe (1995) gives details of frequencies of use of song types by each focal male and the use of 2-note songs, common 3-note songs and descending 3-note songs, in different situations by individual males. These data are summarized in the following sections.

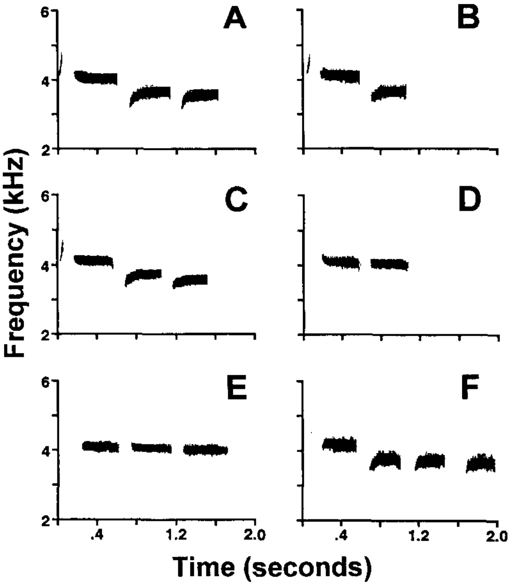

FIG. 1. Audiospectrograms of song types most commonly used by Mountain Chickadees on the study area. A. Common 3-note song. B. Common 2-note song. C. Descending 3-note song. D. 2-note song with both notes the same pitch. E. Three-note song with all notes the same pitch. F. Typical 4-note song. All high-quality recordings of songs had the short, upswept note at the beginning of the song that is present in the common 3-note, the common 2-note song, and the descending 3-note song shown in this figure.

Variation in song use among breeding stages.—Two-note and 3-note songs were not used at random during many breeding stages, although there was much individual variation in the relative use of these song types within all stages (Tables 1, 2). Likewise, common and descending 3-note songs were not used at random during different stages and there was also much individual variation (Table 3).

TABLE 1. The use of 2-note songs by male Mountain Chickadees in various situations, compared to all other song types. Columns headed "All males" refer to combined analysis of contingency tables for individual males. Columns headed "Individual males" indicate numbers of contingency tables for individual males with significant departures from expectations.

	All males				Individual males Preferred song type		
Situation	*n*	Preferred song[a]	*z*-value	*P*	2-note	Other	None
Nest searching/building stage	5	Other	−6.77	<0.01	2	3	0
Egg-laying stage	6		+1.86	0.06	3	1	2
Incubation stage	6	2-note	+5.99	<0.01	3	1	2
Nestling stage	4	Other	−2.30	0.02	1	1	2
Near nest	6	2-note	+3.94	<0.01	4	0	2
Mate present	7	Other	−2.45	0.01	1	3	3
Undisturbed singing	7	Other	−9.11	<0.01	0	5	2
Male-male interaction	6		−0.22	0.83	0	0	6

[a] Indicates that 2-note songs were used significantly more frequently (2-note) or less frequently (Other) than expected in that situation. A blank indicates no significant deviation from expected frequencies.

Variation in song use among behavioral situations.—When singing near the nest site, males used 2-note songs significantly more frequently (Table 1) and 3-note songs significantly less frequently (Table 2) than expected. This pattern also is reflected in the song types used preferentially by individuals. Common 3-note songs were less frequent than expected (and descending 3-note songs more frequent) when males were singing near the nest, although there was much individual variation (Table 3).

Males sang 2-note songs significantly less frequently than expected in the presence of their mates, as indicated by the combined analysis and by the preferred song types of individuals (Table 1). Common 3-note songs were used significantly more frequently than expected in this situation, with five of seven individuals using common 3-note songs preferentially (Table 3).

When engaged in undisturbed singing, in comparison to singing while engaged in another non-aggressive activity such as foraging, 2-note songs were used significantly less frequently (Table 1), and 3-note songs significantly more frequently (Table 2) than expected. Song type preferences of individuals are entirely concordant with this overall pattern. Frequencies of common and descending 3-note songs did not differ from expectations during undisturbed singing (Table 3).

During male–male interactions, common 3-note songs were used significantly less frequently, and descending 3-note songs significantly more frequently, than expected (Table 3). Three of five males showed significant preferential use of descending 3-note songs

TABLE 2. The use of 3-note songs by male Mountain Chickadees in various situations, compared to all other song types. See Table 1 for an explanation of the format.

	All males				Individual males Preferred song type		
Situation	*n*	Preferred song[a]	*z*-value	*P*	3-note	Other	None
Nest searching/building stage	5	3-note	+5.71	<0.01	3	2	0
Egg-laying stage	6		−0.76	0.45	1	3	2
Incubation stage	6	Other	−5.55	<0.01	0	3	3
Nestling stage	4		+1.55	0.12	1	1	2
Near nest	6	Other	−4.82	<0.01	0	4	2
Mate present	7		+1.48	0.14	3	2	2
Undisturbed singing	7	3-note	+10.34	<0.01	5	0	2
Male-male interaction	6		+0.59	0.56	0	1	5

[a] Indicates that 3-note songs were used significantly more frequently (3-note) or less frequently (Other) than expected in that situation. A blank indicates no significant deviation from expected frequencies.

TABLE 3. The use of common 3-note songs by male Mountain Chickadees compared to the use of descending 3-note songs in various situations. See Table 1 for an explanation of the format.

	All males					Individual males Preferred song type		
Situation	*n*	Preferred song[a]	*z*-value	*P*	Common 3-note	Descending 3-note	None
Nest searching/building stage	4	Common	+8.73	<0.01	3	1	0
Egg-laying stage	6	Common	+8.36	<0.01	3	2	1
Incubation stage	5	Descending	−10.73	<0.01	2	3	0
Nestling stage	4	Descending	−5.65	<0.01	1	2	1
Near nest	6	Descending	−4.35	<0.01	3	2	1
Mate present	7	Common	−6.56	<0.01	5	1	1
Undisturbed singing	4		+0.94	0.35	2	1	1
Male-male interaction	5	Descending	−6.72	<0.01	0	3	2

[a] Indicates the 3-note song type that was used significantly more frequently than expected in that situation. A blank indicates no significant deviation from expected frequencies.

during this situation whereas none used common 3-note songs preferentially.

DISCUSSION

Individual song repertoires.—Excluding infrequent song types, males had individual repertoires of 4–7 song types. Hill and Lein (1989) estimated a slightly smaller repertoire size of 3–5 song types. However, they sampled songs less intensively and may not have recorded enough songs to obtain complete song repertoires for all individuals.

Other researchers imply that the most common song type of Mountain Chickadees is a 3-note song with all notes of the same pitch (Gaddis 1985, Hailman 1989, Hill and Lein 1989). In contrast, we found that males in our study rarely sang songs of this type. We are unable to explain this difference, but it may support Gaddis' (1985) suggestion of geographical variation in Mountain Chickadee songs.

Use of song types in different situations.—Our analyses of song length grouped different song types with the same numbers of notes into a single category, possibly obscuring some patterns in the use of different song types. However, because almost all 2-note songs recorded were common 2-note songs, the results from analyses of all 2-note songs would be almost identical to results using only common 2-note songs. Almost all 3-note songs recorded were either common or descending 3-note songs. Any differences between these song types that were obscured in the song length analyses should be revealed in the song pitch analyses.

Different song types had significant associations with different breeding stages. However, there was also much individual variation in all stages, with different males using different songs preferentially during the same breeding stage. This suggests that although the z-values were significant statistically, the results may not be meaningful biologically. Different song types are probably not signaling messages about the breeding stage of the singer. Instead, different breeding stages may be associated with other situations that are more relevant biologically to the messages of the song type.

The number of notes in songs of Mountain Chickadees was associated significantly with location relative to the singer's nest. All individuals showing significant preferences either used more 2-note songs near the nest than away from it, or more 3-notes away from the nest than near it. Some other studies on songbirds also have found that males sang different song types depending on their territorial location (e.g., Lein 1978, Weary et al. 1994). Although pitch of the last note in 3-note songs was associated with location relative to the nest, this association is weak because of the large degree of individual variation.

In Mountain Chickadees, the tendency to sing 2-note songs near the nest and 3-note songs away from the nest may be influenced by factors other than just the singer's location. Males were more likely to engage in non-aggressive activities while singing near the nest than when singing away from the nest, suggesting that location relative to the nest and male behavior were related. Although note number may communicate some information about the singer's location, these factors may be related only indirectly and the association between male behavior and note number may be more important biologically.

Different song types were associated with the presence or absence of the singer's mate. Other researchers (e.g., Temrin 1986, Staicer 1989) have claimed that song types used preferentially in the presence of females have a greater intersexual function. One methodological problem in our study is that a female may have been recorded as absent when she actually was nearby in the nest hole, but not visible to the observer. Two-note songs and descending 3-note songs, which were positively associated with the absence of the female, were also positively associated with the nest site. Furthermore, in most cases singers did not seem to be directing song specifically at females. Males sometimes sang low-volume, "quiet" songs, usually of 1 or 2 notes, when approaching nests to feed incubating mates. Although such songs may be directed specifically at females, we never observed normal volume songs used in this manner. Therefore, we are hesitant, without further experimental study, to suggest that common 3-note songs have a greater intersexual function than do 2-note songs and descending 3-note songs.

The behavior of singing males was associated with the number of notes in the song, but not with pitch. Two-note songs were positively associated with singing while engaged in non-aggressive activity and 3-note songs were positively associated with undisturbed singing. Although not all males had individual results that were significant, all males showed this trend.

We suggest that 3-note songs signal a higher motivation level of the singer to sing than do 2-note songs. If so, 3-note songs might indicate that the singer is more willing to engage in some of the agonistic actions associated with singing in Mountain Chickadees, such as countersinging bouts or interacting with other males at the edge of the territory to confirm boundaries. Thus, 3-note songs could convey more aggressive messages than 2-note songs.

Male–male interactions in Mountain Chickadees were associated with changes in pitch of notes in the song. Because most males were more likely to sing common 3-note songs when apparently unprovoked by another bird's activities than during interactions with rival males, this song type may function in spontaneous advertisement of the territory. Descending 3-note songs were associated with male-male interactions and it is probable that lowering the pitch of the last note in 3-note songs may convey some message to the rival. Other researchers have suggested that song types associated with male–male interactions probably convey more aggressive messages than do other song types (e.g., Nelson and Croner 1991). Interactions between males are situations of high levels of agonistic stimulation for Mountain Chickadees and so they may be more likely to use songs that convey stronger aggressive tendencies at this time. Thus, descending 3-note songs may convey more aggressive messages than common 3-note songs.

Comparison to closely-related species.— Our findings suggest that the function of individual repertoires in Mountain Chickadees is similar to that of other North American chickadees and titmice, with different song types used in different situations and appearing to have different communicative functions. Three species of North American titmice have certain song types that are used predominantly in male–male interactions (Gaddis 1983, Schroeder and Wiley 1983, Johnson 1987). These are probably similar in function to the descending 3-note song of the Mountain Chickadee, which is also used in male–male interactions. The Bridled Titmouse (*Baeolophus wollweberi*) has one song type used predominantly in spontaneous advertisement of territory (Gaddis 1983), and we found that the common 3-note song of the Mountain Chickadee is used predominantly in undisturbed singing. Schroeder and Wiley (1983) suggested that different song types of the Tufted Titmouse (*B. bicolor*) convey different levels of aggression by the singer. This corresponds to our suggestion that, in Mountain Chickadees, descending 3-note songs, common 3-note songs, and 2-note songs indicate high, intermediate, and low levels of aggression, respectively.

There are also some differences in the manner in which titmice and Mountain Chickadees use songs. For instance, the Bridled Titmouse has a song type used predominantly in long-distance countersinging (Gaddis 1983). We did not find any song type in Mountain Chickadees that was used in this manner, although it is possible that some songs that we categorized as "undisturbed" singing may have actually been in response to far away song that was inaudible to the observer. Johnson (1987) noted that the Plain Titmouse (*Baeolophus inornatus*) was more likely to use some song types in situations related to nesting activities. Although 2-note songs were associated with close proximity to the nest, there was no indication that Mountain Chickadees were using these songs in any way that was related specifically to nesting activity.

Carolina Chickadees (*Poecile carolinensis*) have one song type associated with countersinging that is thought to be a more aggressive song type (Smith 1972). This song type could be similar in function to descending 3-note songs given by Mountain Chickadees during male–male interactions. However, Smith (1972) also observed that Carolina Chickadees were more likely to use this aggressive song type while patrolling territorial boundaries whereas we did not note any strong association between descending 3-note songs and territorial boundaries.

Pitch may be an important cue in coding information in the songs of both Mountain and Black-capped chickadees, but the two species differ in how they vary the pitch of their songs. Unlike Black-capped Chickadees, which shift the entire song downward in pitch, Mountain Chickadees shift individual notes in a song to a lower pitch. Black-capped Chickadee songs shifted downward in pitch were observed during countersinging between males in the field and in response to playback in both wild and captive birds (Ratcliffe and Weisman 1985, Hill and Lein 1987). Mountain Chickadees 3-note songs, with the last note lower in pitch (descending 3-note songs), were associated with male–male interactions whereas 3-note songs with the last two notes of the same pitch (common 3-note songs) were associated with the less-aggressive situation of territorial advertisement. In both species, pitch seems to be lowered during more aggressive situations. Morton (1977) suggested that calls of low pitch indicate higher aggressiveness by the signaler than do calls of higher pitch. This idea seems to be applicable to song in Mountain Chickadees and Black-capped chickadees.

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