

ACOUSTIC SIGNALS IN THE MATING OF MOUNTAIN AND BLACK-CAPPED CHICKADEES

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FEW accounts of mating in chickadees are on record, and in none have the associated sound signals been analyzed spectrographically. This dearth of information derives from several factors, including the short seasonal span of these events, the relative inconspicuousness of the birds at this time, and frequently, screening by vegetation. In the course of field studies of color-banded individuals we observed mating several times in two species and analyzed the accompanying vocalizations.

METHODS

Sounds were recorded on a Nagra III BH recorder at 15 inches per second, using an Altec 633A microphone mounted in a 24-inch parabolic reflector. A Kay Electric Co. Sona-graph with wide bandpass filter and FL-1 setting was employed. To facilitate analysis of the form of the sounds, tapes were played back at one-half speed in the preparation of spectrograms.

RESULTS

Mountain Chickadee, *Parus gambeli*.—The mating performance of this species was witnessed by Folks on 29 May and 1 June, and by Dixon and Folks on 3 June, all in 1965, at the Beaver Mountain Ski Area, 7,400 feet elevation, Cache County, Utah. The last two incidents involved the same pair, and the sequence on 3 June was tape-recorded after the participants had been followed for 1 hour and 50 minutes. The female of that pair was unmarked, but the male had been banded in the vicinity on 15 May. The members of the pair observed on 29 May had been banded 2 weeks earlier.

The female on 3 June uttered intermittently a chatter associated with begging (Figure 1A) as she foraged with her mate, but no courtship feeding was noted during this interval. Once she gathered some fur and evidently visited the nest (subsequently found nearby), accompanied by her mate. The male initiated squealing solicitation notes 46, 11, and 8 minutes before copulation took place. None of these flurries exceeded 15 seconds. At 09:33 the male resumed this calling from a pine about 10 yards from the fir in which the female was perched. The male intensified his solicitation calls (upper horizontal bars, Figure 1B) after 40 seconds, when the female flew to perch in a leafless aspen in direct view. After having called for 1½ minutes the male began wing shivering and flew toward the female in three successive flights. When he was about 5 feet distant, she began wing shivering and initiated calls that were lower

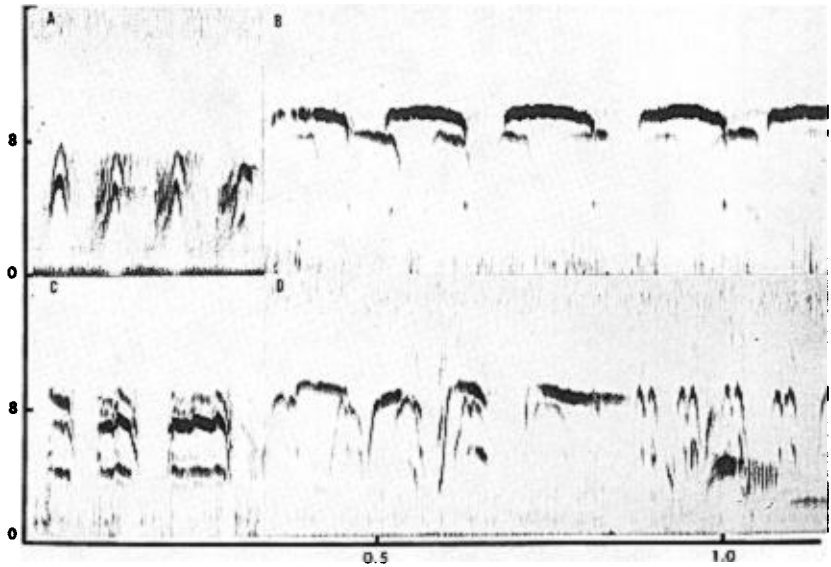


Figure 1. Sound spectrograms of calls of chickadees played at one-half speed. (Vertical axis, frequency in kilocycles per second; horizontal, time in seconds.) A begging call of female Mountain Chickadee. B, solicitation calls of male (upper bars) and female Mountain Chickadees. C, begging call of female Black-capped Chickadee. D, solicitation calls of Black-capped Chickadees; male precopulatory call at lower right.

pitched and sharper than those of the male (Figure 1B). The male mounted with wings whirring, and some 4 seconds later a call characteristic of close-quarters aggressive situations was uttered. This guttural call (Figure 2A) resembles the song of the House Wren (*Troglodytes aedon*) in quality and rapidity of delivery. Presumably copulation was completed before this call was delivered. The male's solicitation notes were resumed immediately (Figure 2A), followed by five staccato notes of undetermined significance. Both individuals flew to perches nearby and foraged. Neither courtship feeding nor additional aggressive acts occurred in the ensuing few minutes.

The aggressive call evidently was uttered by the male, as the sequence of male solicitation notes was interrupted, and the energy output of the aggressive notes resembled that of the stronger male sounds (Figure 2A). John D. Gilbert (pers. comm.) reported hearing a similar call prior to mounting on 30 May 1962.

In each incident witnessed, the male made extended and forceful vocal solicitations. In the last two episodes the male did not begin wing shivering

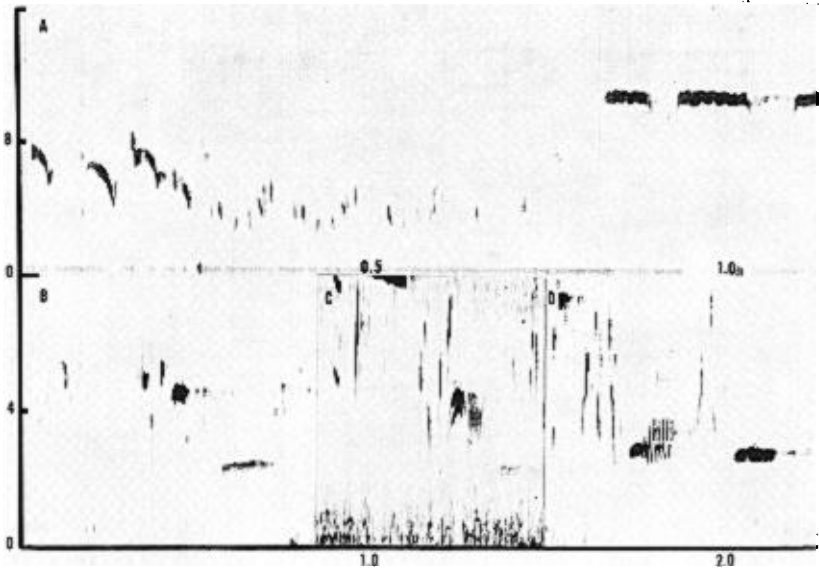


Figure 2. A, sound spectrogram of aggressive call of Mountain Chickadee, followed by male solicitation notes (upper right). B, C, precopulatory calls of male Black-capped Chickadee. D, a supplanting call of the same species. (B, C, and D processed at normal tape speed; A at one-half speed.)

until the female appeared in full view. The female did not respond with wing vibration or solicitation notes until the male was in close proximity. An aggressive call was heard at the termination of coition on 1 June also, but was not noted with the other pair on 29 May. In all three episodes the terminal solicitation and coition occurred in leafless aspens interspersed among the conifers. None of the incidents was preceded or followed by courtship feeding, and singing was not associated with any of the episodes except preceding the one Gilbert witnessed on 30 May, 1962.

Black-capped Chickadee, *Parus atricapillus*.—Observations of at least portions of 10 mating sequences were made at the Malibu-Guinavah Forest Camp, 5,000 feet elevation, 7 miles east of Logan, Utah, in each of several years. Dixon tape-recorded a sequence that was nearly complete on 24 May 1967. The individuals were unbanded, but presumably had occupied the area for several weeks. As their brood fledged on 29 June, incubation probably began on 25 May. The pair was followed for 1½ hours prior to copulation, and courtship feeding was seen five times in the last 40 minutes of this interval.

The begging notes of the female (Figure 1C) were delivered in bursts

of several seconds' duration and at irregular intervals. Both members of the pair began solicitation calls almost simultaneously, without preliminaries. The notes the female uttered were of short duration, exhibited two "peaks," and were repeated at regular intervals (best seen at the right in Figure 1D). The sonograms show that these continued uninterrupted throughout the mounting.

The male's solicitation notes were prolonged and higher pitched, reflecting greater and more consistent output of energy. The last of these notes was extended, grading into the first "sleh-poór" call (Figures 1D, 2C) that was uttered immediately before mounting. A series of notes of gradually increasing frequency followed, the later ones protracted into typical male solicitation notes. The male emitted a second "sleh-poór" identical to the first, and subsequently resumed the solicitation notes that continued after those of the female ended.

It is not clear which individual initiated the solicitation in the episode described above. On two occasions (12 and 14 May 1965) Stefanski watched copulations initiated by the female. The male involved in the second of these incidents solicited first in another mating seen later on 14 May (the day the first egg was laid) and twice on 17 May 1965. Thus it appears that solicitation may be started by either member of the pair.

The melodious "sleh-poór" call was uttered by the male *prior to* mounting on four other occasions on which a complete sequence was witnessed or full details recorded on 11 May 1961 and on 12, 14, and 17 May 1965. Each of the three incidents in 1965 involved a different color-banded male. This bell-like sequence was not heard in an incident on 17 May 1965, in which Dixon heard the introductory note shrilly prolonged but the subsequent notes apparently absent. Possibly the episode was well advanced when the observer arrived. This male had uttered the "sleh-poór" call on 12 May. On 15 May 1966 Dixon tape-recorded a sequence in which four "sleh-poór" calls were delivered in 8 seconds. The context could not be ascertained as the birds were screened from view.

Copulation in Black-capped Chickadees was notable for the suddenness of its onset. In no case was solicitation begun longer than 1 minute prior to mounting, and often the interval was much shorter.

DISCUSSION

The vocalizations discussed above occur in a span of only a few days and are critical to the success of reproduction. Hence natural selection would favor little variability in the form of the signals. We are confident of the stereotyped nature of the signals themselves, and the agreement in the details of the several incidents suggests that they represent normal sequences. Therefore a few inferences seem warranted.

Comments on courtship.—The solicitation notes of the male and the female are distinctive in both species as is shown in Figure 1. In *P. atricapillus* therefore, the mating call category of Odum (1942) must be subdivided, as both male and female utter the twitter.

The occurrence of the male precopulatory call (“sleh-poór”) of the Black-capped Chickadee prior to mounting in nearly all the episodes witnessed indicates that it is a normal pattern. This vocalization appears to be a temporally compressed derivative of a rather distinctive utterance that accompanies supplanting attacks in winter fighting and in territorial disputes (Figure 2D). This striking similarity supports Brewer’s (1961) report of a dominance note preceding mounting in the closely related *P. carolinensis*. Stokes (1960) detected no hostile elements in copulation in either male or female Blue Tits (*P. caeruleus*); he concludes that aggressive tendencies in that species are subordinate to stronger ones for escape and sex. Morley (1949) reports the male Marsh Tit (*P. palustris*) replaces the solicitation calls with a unique “song-note” at the time he settles on his mate’s back. Although the circumstances and timing are similar to those in the Black-capped Chickadee, the derivation and motivation are obscure.

The male solicitation calls of the Mountain Chickadee may be adaptive in attracting the attention of the mate in dense foliage of conifers. However the prolonged bouts of solicitation and the apparent absence of a male precopulatory call suggest a different balance of attack, escape, and sexual tendencies between the sexes in this species as contrasted to the Black-capped Chickadee. This inference is supported by the more pugnacious temperament of the latter species as seen in both intra- and interspecific encounters (Minock and Dixon, MS).

Ethological isolation.—We do not wish to imply that *gambeli* shares an immediate common ancestry with the closely knit trio of *atricapillus*, *carolinensis*, and *sclateri* (see Snow, 1956), although all four should be assigned to the same species group. Suchetet (1897: 300) cites a presumed hybrid (*gambeli* × *atricapillus*) reported to him by Robert Ridgway as being exactly intermediate in every respect. The account refers to a specimen in the U. S. National Museum that Richard C. Banks located recently and judges (Banks, 1970) to be an individual of *P. atricapillus*, aberrant only in having “traces of white superciliary stripes.” Although there is no evidence of hybridization between *gambeli* and *atricapillus*, Gray (1958: 192–193) reports well-documented cases of hybridization involving four other species combinations that are more disparate than the two in question. Hence the mechanisms that serve to maintain the integrity of these species warrant attention.

Although most populations of the two chickadees occupy markedly different habitats and are separated altitudinally (Dixon, 1961), there are localities, such as Beaver Mountain, where individuals are in contact during the breeding season. Orians and Willson (1964) mention interspecific territorial dispersion of these chickadees in eastern Washington. Specific differences in plumage characters are especially notable in the facial region, and such visual cues must be of paramount importance in species that form dominance-subordination hierarchies. These chickadees are equivalent in size, and they utilize the habitat in similar ways. Their vocalizations are recognizably distinct, the calls of *gambeli* being raspier and more slowly uttered, and the terminal note of the song not lower in pitch. Despite these contrasts, individuals of one species occasionally respond to songs or calls of birds of the other species.

Conceivably a mismatch might occur where populations are thinly distributed and thresholds for selection of an appropriate mate lowered (Mayr, 1963: 103; Gompertz, 1968). Even so, the process of nesting is prolonged, and timing is especially critical at higher elevations. Thus the chances for successful hybrid nestings are reduced.

The sound signals associated with the intimate relations of the pair are distinctive. The begging calls of the female, which are not persistent until the incubation stage in *atricapillus* (Odum, 1941: 323), are dissimilar (Figures 1A, 1C). The solicitation notes of the male in *gambeli* are more prolonged and higher pitched than in *atricapillus*, and *gambeli* seems to lack a unique precopulatory call in the male. These differences contribute to the constellation of ethological differences that serves to keep the gene pools distinct. The extent to which they reflect fundamental differences in courtship motivation is a field for further study.

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SUMMARY

Spectrograms of the begging calls of females and of the solicitation calls (mating twitter) of *Parus gambeli* and *P. atricapillus* illustrates the distinctiveness of these signals in each species and sex. The incidence of a unique precopulatory vocalization in the latter species is described, and the derivation of this signal from an aggressive call postulated. This signal and the abbreviated solicitation of either sex in *atricapillus* stand in contrast to the relatively prolonged solicitation in the male of

gambeli, and suggest means by which the integrity of these species is maintained.

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