VOCAL REPERTOIRE OF THE BLACK-CAPPED CHICKADEE

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ABSTRACT.—Describes the physical characteristics, usages, and probable functions of 11 vocalizations of adult Black-capped Chickadees and 2 of the young. Some modifications of the vocal repertoire as compared with other passerines are associated with sociality and hole-nesting. The Fee-bee, usually considered the song of this chickadee, is less complex than some call notes and also has some differences in function compared to the songs of other passerines. The two most complex calls (Chick-a-dee and Gargle) are associated with social activities. Vocal signals tend toward sexual segregation, which may be important in a monomorphic species. The vocalizations of this species are compared with those of other parids, and selection pressures acting on the structure of vocalizations are discussed. The more complex vocalizations of this species are being studied extensively as mentioned in the accounts below, and are only generally described in this paper.—*Department of Zoology, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin 53201. Present address of third author: Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706.* Accepted 21 June 1976.

THE Black-capped Chickadee (*Parus atricapillus*) is a particularly interesting species for the study of vocal communication for at least two reasons. It lives in small flocks during the winter and hence may have more elaborate or different vocal repertoires than less social species. Furthermore it nests in holes, a habit sometimes associated with modifications of display repertoires (von Haartman 1958).

Black-capped Chickadee vocalizations have been examined by several workers. Odum (1941) provided a phonetically based classification of the vocalizations as part of a larger study of their behavior and ecology. Song was discussed by Dixon and Stefanski (1970) and precopulatory vocalizations by Dixon et al. (1970). The closely related Carolina Chickadee (*P. carolinensis*) was the subject of a message-meaning analysis by Smith (1972).

METHODS

We conducted this study at the University of Wisconsin—Milwaukee Field Station, Saukville (Ozaukee Co.), Wisconsin, from September 1970 to December 1974. This population of chickadees was color banded for individual recognition by Charles Weise, who made available data on age, sex, and winter and breeding locations for most individuals. It was not always possible to identify color bands when birds were in dense vegetation, so some unidentified birds were used. We studied a total of approximately 30 birds. For any specific vocalization the sample size was often smaller, particularly during the reproductive period when we concentrated on four pairs, although additional records were made of some other pairs. From November through April observations were made mainly at feeders, with the microphone placed within 1–3 m of the feeder. Two perches about 25 cm apart on each feeder enabled two birds to be on a feeder at the same time and encouraged interactions. We positioned ourselves about 10 m from the feeder and used 10 × 40 binoculars. From April to July birds were studied on territories in the 20-ha beech-maple forest. We followed individuals around their territories, but once the nest cavity was excavated we concentrated our activities near the nest hole. At that time, we often placed a microphone within 5–8 m of the nest hole. From August to October we followed flocks, and recorded their vocalizations.

Most of the recordings were made with a Nagra III tape recorder at 7.5 ips and Sennheiser MKH 104 omnidirectional or 405 cardioid microphones, but we occasionally used a Uher 4000L tape recorder and Electrovoice 644 Soundspot microphone. While studying the birds, data on individual identity, behavior of the caller prior to and following the call, general context, and behavior of other birds in the vicinity prior to and following the vocalization were spoken into the microphone. Sonagrams were made using a Kay Sound Spectrograph 6061-B on intermediate (150 Hz) band setting.

Classification and naming of displays poses some problems of when to split and when to lump. As

TABLE 1
CHARACTERISTICS OF FEE-BEES AND FAINT FEE-BEES

Individual		Frequency[1] of note 1	Frequency[1] of note 2	Duration[2] Note 1	Interval[2]	Duration[2] Note 2
Fee-bees of individual males						
CPAO	x̄	3.48	3.10	0.371	0.135	0.386
	SD	0.05	0	0.021	0.018	0.017
	N	4	4	6	6	6
	C.V.	0.014	0	0.057	0.135	0.044
AOPR	x̄	3.50	3.17	0.367	0.131	0.367
	SD	0	0.048	0.018	0.030	0.033
	N	10	10	10	10	8
	C.V.	0	0.015	0.048	0.227	0.90
GOAR	x̄	4.10	3.64	0.310	0.144	0.384
	SD	0	0.05	0.021	0.012	0.023
	N 1	6	5	5	5	5
	C.V.	0	0.014	0.068	0.081	0.059
UN	x̄	4.00	3.52	0.318	0.133	0.349
	SD	0	0.045	0.016	0.012	0.020
	N	5	5	5	5	5
	C.V.	0	0.013	0.050	0.091	0.058
SOAC	x̄	3.48	3.13	0.315	0.137	0.371
	SD	0.05	0.05	0.019	0.031	0.032
	N	4	4	4	4	4
	C.V.	0.014	0.016	0.059	0.227	0.086
Faint Fee-bees of female						
	x̄	3.76	3.19	0.263	0.092	0.347
	SD	0.025	0.053	0.039	0.029	0.015
	N	6	6	6	6	6
	C.V.	0.007	0.017	0.147	0.319	0.043
Fee-bees of different individual males						
	x̄	3.71	3.30	0.340	0.135	0.373
	SD	0.28	0.22	0.032	0.022	0.013
	N	30	29	33	32	23
	C.V.	0.075	0.068	0.095	0.163	0.106

[1] Midpoint frequency in kHz. Measurements made to the nearest 0.1 kHz.
[2] Duration in seconds.

Altmann (1967) indicates, the best method is to observe the animal's use of the display and split according to natural categories of usage. Particular problems are introduced by graded displays (e.g. Rowell and Hinde 1962) where the two extremes might be of quite different form and usage but are linked by intermediates. Here we have attempted to indicate where grading occurs. When a vocalization is similar in general structure (although there may be differences in pitch and temporal patterning) to a display of *P. carolinensis* we employ the terminology of Smith (1972) for what is apparently a homologous display, but when the vocalization differs significantly in its characteristics and usage we use our own designations.

RESULTS

Fee-bee.—The Fee-bee, produced as far as we know only by males, typically consists of two whistled notes, the first higher pitched than the second (Fig. 1g). The two tones are separated by an interval of 0.1–0.15 sec. The second tone is often separated into 2 components by a silent period of about 0.05 sec, while the first tone is rarely subdivided. In late summer some Fee-bees of young birds had only a single note, and such vocalizations occur rarely at other times of the year. Of the hundreds of Fee-bees we heard, those with three distinct notes were heard only three times. Table 1 indicates frequency and temporal measurements of Fee-bees for five males. These data indicate relatively little inter-individual variation in this population and considerable overlap among individuals in Fee-bee characteristics, but the coeffi-

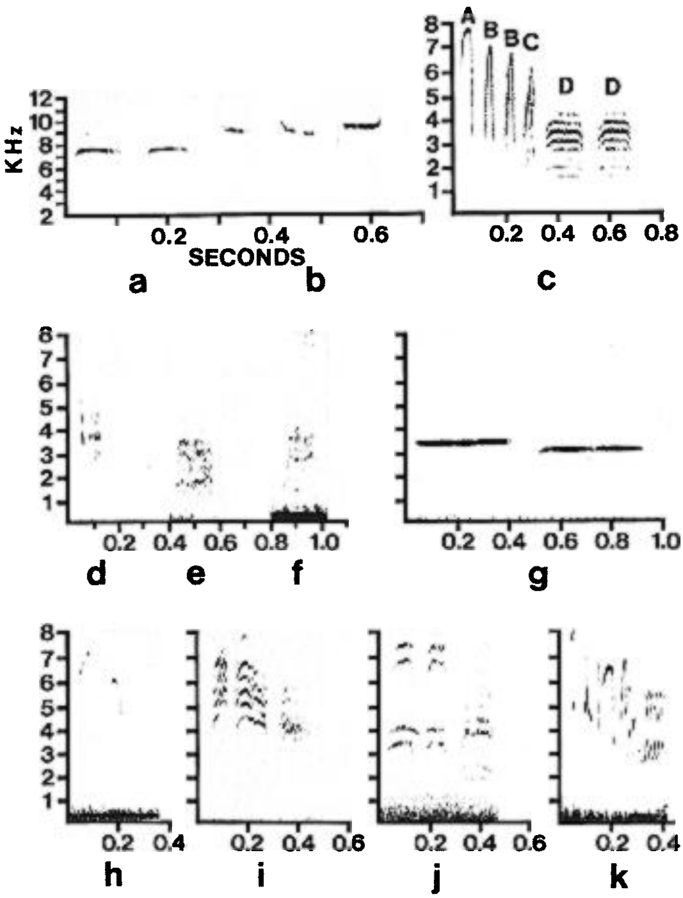

Fig. 1. Sonagrams of Black-capped Chickadee vocalizations. a) High Zees; b) Variable Sees; c) Chick-a-dee call showing A, B, C, and D syllables; d) Twitter; e) Hiss; f) Snarl; g) Fee-bee; h) Tseets; i) Begging Dee; j) Broken Dee; k) Gargle.

cients of variation are larger for grouped songs than those of individuals. Geographic variation occurs in songs of *P. carolinensis* (Ward 1966), but this aspect has never been systematically examined in *P. atricapillus*.

Fee-bee calling begins in late December or early January and continues into November, though sporadically in the fall. The period of most intense vocalizing is April–July. When a male that is within a winter flock calls, he first isolates himself temporarily from group members, and we never saw a male utter these vocalizations while in close proximity to others. During the breeding season males engage in short bouts of calling as they move around their territories, but we feel that they call much less frequently than do territorial males of other species. We never saw a male utter these notes within 10 m of his mate; thus as in winter flocks males do not call unless they are at some distance from a conspecific. As Dixon and Stefanski (1970) pointed out, almost all territorial boundary encounters were initiated when one male came close to a territorial boundary and gave Fee-bees. Once boundary encounters, consisting of short chases and supplantings, were initiated, Fee-bees were no longer given until the males again separated. On 12 occasions while watching late summer flocks, we saw a bird of unknown sex fly about 50 m to a new location and then utter several Fee-bees, after which the other flock members immediately joined it. Dixon and Stefanski (1970) reported similar behavior.

Smith (1972) indicated that in *P. carolinensis* song encodes the message of a readiness to perform agonistic and bond-limited behavior.

Faint Fee-bees.—Faint Fee-bees seem to have the same frequency characteristics as Fee-bees, but both notes and the interval between them tend to be shorter (Table 1), although this analysis was based on the songs of only one female. Faint Fee-bees occur at much lower amplitude than Fee-bees, and their usages are different, as Smith (1972) also indicates for Faint Song in *P. carolinensis*.

Both sexes use Faint Fee-bees, in contrast to Fee-bees which we heard only from males. The male feeds the female near the nest during incubation. The female sometimes comes out of the nest cavity when the male is not nearby. On 11 occasions, she gave Faint Fee-bees, in 12 other Broken Dees (p. 38). Her call usually immediately attracted the male, who then fed her. The male often comes to the nest with food during incubation or for the young while the female is out of sight in the nest cavity. Of 25 observations of this situation, he approached and gave Faint Fee-bees near the nest cavity 80% of the time and other calls 20%. The female usually emerged from the nest hole shortly after the male began vocalizing. More rarely, the male simply flew away after calling for several minutes when the female did not appear. Thus Faint Fee-bees are a mechanism for attracting the mate when it is not visible, resulting in coordination of the feeding activities of the pair at the nest hole. Faint Fee-bees may also be used between parents and young (Dixon and Stefanski 1970). Selection has probably acted to reduce the amplitude of notes that serve primarily as close range signals.

Gargle.—This is the most complex call of the chickadee, each call consisting of a series of two to nine short notes separated by short intervals (Fig. 1k). We distinguished 14 note types in our population. Because of its structural complexity we are treating ordering and note composition separately. The call is most frequently given when two birds are in close proximity at feeders, in flocks during violations of individual distance, and during territorial encounters. Of 145 Gargles recorded only 6 were given by females. If the recipient does not leave after the call is uttered, the caller usually follows with a lunge or supplanting attack. In general Gargles seem to occur when the caller has a high probability of attacking. The Gargle is one of the most effective threat displays of this species. However, Gargles uttered in sexual contexts, which are often of a special type, were never followed by aggression.

Subsong.—The vocalizations that we term "subsong" were recorded on only two occasions, both in July and from what were presumably young birds (sex unknown). The vocalization is of long duration (2–6 sec) and is given at very low amplitude. It consists of a variety of notes of different types, with a wide frequency range (2–8 kHz). Some notes are given simultaneously. In Fig. 2b the subsong consists of many short-duration transients similar to those found in Gargles, but has traces of elements similar to Fee-bees. The other example (Fig. 2a), contains Fee-bee fragments, some elements similar to those found in the Begging Dee of the young and Gargle elements.

Thorpe and Pilcher (1958) report that subsong differs from true song as follows: (1) the main fundamental frequency of the notes is lower than in true song, (2) the frequency range of the subsong as a whole and of the individual notes tends to be greater, (3) the amplitude is lower, (4) the overall pattern of notes comprising the vocalization is very different, (5) the length of the phrases of the song tends to be

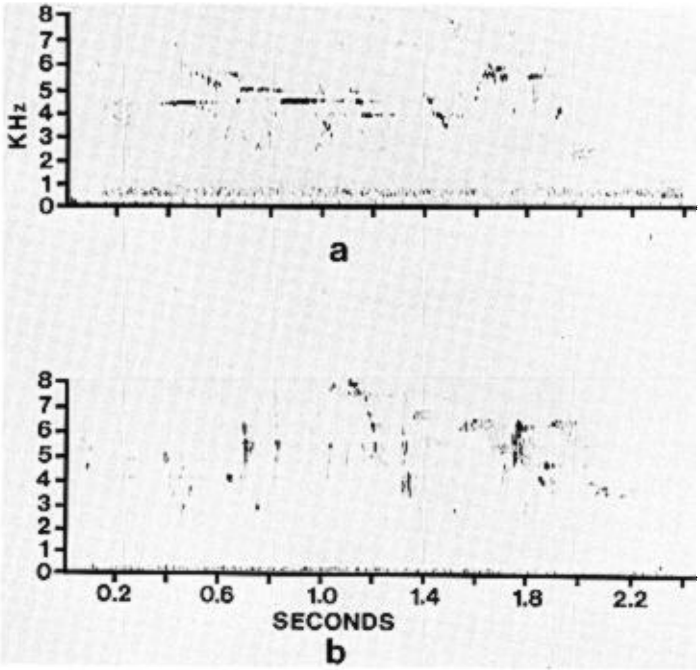

Fig. 2. Sonagrams of subsong of young. a) This example has a preponderance of Fee-bee elements; b) Gargle elements predominate.

longer, (6) subsong is characteristic of lower sexual motivation and is generally produced earlier in the breeding season, and (7) it may be practice for "true" songs. Of the 12 species whose vocalizations they studied, only 3 had all these characteristics. Chickadee subsong seems to have characteristics 2, 3, 4, 5, and possibly 6 and 7. While subsongs of some other species have call notes incorporated in them as well as incipient song elements, the chickadee may be unusual in the preponderance of call notes, especially Gargle elements in subsong. Thus subsong may not only be important as the basis for the crystallization of Fee-bees, but especially so for the more complex Gargle.

Begging Dee.—The call of a young a few days before fledging is illustrated in Fig. 1i. This call, characterized by its complex harmonic structure, evidently serves to elicit feeding by the parents, and may also serve as a location note.

Chick-a-dee call complex.—This call complex given by both sexes consists of one to four notes (A, B, C, and D in Fig. 1c), each of which can be repeated a variable number of times in the same call. Also the four notes can be arranged in various combinations, e.g. AB, ABC, AD, BCD, etc. (Ficken and Hailman, MS). According to their note composition, the various calls are given in situations of mild alarm, as contact calls for the pair and flock and in coordinating group movements. They are more common during the nonbreeding season, and their complexity seems to be related to a variety of social functions.

Broken Dee.—Broken Dees (Smith 1972) resemble the Begging Dees of the young (Fig. 1j). To a lesser degree they are similar to the typical "D" syllable of the Chick-a-dee call (Fig. 1c), but Broken Dees cover a wider frequency range (3.5–7.5 kHz) and the harmonics are more irregular, ascending and descending in pitch rather than

TABLE 2

COMPARISON OF CHARACTERISTICS OF VARIABLE SEES AND HIGH ZEES

		Frequency in kHz	Duration in sec	Inter-note interval in sec
Variable See	x̄	8.97	0.082	0.048
(4 individuals)	SD	0.405	0.015	0.004
	N	12	9	11
	C.V.	0.045	0.353	0.084
High Zees	x̄	7.94	0.10	0.078
(8 individuals)	SD	0.557		0.049
	N	111		12
	C.V.	0.070		0.628

remaining approximately on the same pitch. The calls occur in groups of one to seven repetitions of similar syllables (x̄ = 3.70), which is also similar to the calls of the young (x̄ = 3.55).

Broken Dees are given only by females during a restricted part of the breeding season; their onset is correlated with completion of excavation of the nest cavity, and they are given most frequently from that time through early incubation, when they gradually become less frequent, although they may still be given occasionally when the young are out of the nest.

During incubation the calls tend to grade into typical adult "D" syllables; although the first few syllables of a call may still be of the Begging Dee type, subsequent syllables resemble the adult Dee. If the male is nearby, the calls are often accompanied by Wing Quivering.

After excavation is completed and during egg laying, the pair often forage within 1–5 m of each other, the female calling continually as she follows her mate (although she also gives these calls while foraging along). The male and female may Bill Touch briefly, each Wing Quivering. No food appears to be transferred at this stage, although the male feeds the female during incubation. When the female leaves the nest during incubation she immediately gives Broken Dees or Faint Fee-bees and the male either approaches and feeds her, or in his absence, she forages along. In this case Broken Dees seem to attract the male.

During courtship, calls and postures that are similar to the begging calls of young are common in many female passerines (Andrew 1961) and may serve to elicit an appropriate nonaggressive response from the mate. Broken Dees may or may not elicit feeding by the male, depending on the female's reproductive state. This vocalization and its accompanying behavior seem an important part of courtship, setting the stage for copulation by accustoming the pair to being in close proximity. The response of the mate seems to be to approach and stay with the calling bird. Smith (1972) suggests the message for the comparable call in *P. carolinensis* is that the caller is prepared to engage in bond-limited activities.

Variable See.—Variable See consists of rapidly repeated high-pitched syllables, usually chevron-shaped, and often ending with a Gargle (Fig. 1b). Table 2 indicates frequency and temporal characteristics. Variable Sees are often uttered in strings lasting as long as 6 sec. We heard only females give this call, which was usually accompanied by Wing Quivering. The calls were most common after completion of the nest through early incubation, although we recorded them once when young were in the nest and twice before completion of the nest. In six out of seven instances the call was first given when the female left the nest hole and the male was not present, and in all cases he soon approached and the Variable Sees continued. In 5 out of 7 instances the calls were associated with copulation (in the 2 other cases the pair was not sufficiently visible to see what happened). In the usual copulatory sequence, the female uttered these calls, the male approached within a few centimeters, giving a particular Gargle type, the female continued calling and Wing Quivering. The male then mounted. In a few cases Bill Touching occurred just prior to copulation.

In *P. carolinensis* this call is not restricted to sexual contexts (Smith 1972), and although we noted it most frequently in such situations, in *P. atricapillus* it also sometimes occurs before and after the copulatory period. In the sexual contexts it is likely that the female is experiencing a motivational conflict between engaging in sexual activity and fleeing when the call is uttered in the male's presence just prior to copulation. As the call does occur in other situations, it is unlikely that its message is primarily a sexual one. Smith (1972) suggests for the comparable call in *P. carolinensis* that the overall message of Variable See is probably that the caller is experiencing a conflict between escape and some bond-limited activity. The recipient behaves as if the caller poses no threat to further bond-limited activities. The call probably has important functions in decreasing the distance between members of a pair, preparing the way for copulation. During the period when it is associated with sexual activity, it seems to be an important way of attracting the male and signaling readiness to engage in sexual activity.

Hiss and Snarl.—These two calls seem to form a graded series and thus they would not be considered as two different calls except that their usage seems to differ somewhat. Hisses resemble white noise (Fig. 1e), cover a wide frequency range (1.8–5.0 kHz), and are of variable duration ($\bar{x}$ = 0.159 sec, SD = 0.072). Some calls show traces of a very irregular harmonic structure. The Snarl (Fig. 1f) resembles the Hiss in its noisy structure, and our one sonagram of a Snarl is rather poor, but indicates the call may occur over a somewhat wider frequency range than the Hiss, which it otherwise resembles.

A female chickadee that had been placed in a sock for weighing emitted Hisses when the sock was shaken gently. The only time that we heard this call in the field was when one member of a pair (sex unknown) uttered it as the mate was at the nest entrance when the female suddenly emerged.

As the call may be given by a trapped bird and is probably often directed at potential predators, it probably indicates that the caller is experiencing thwarted escape, with the possible activation of the attack tendency as well, as Smith (1972) suggests for the comparable display of *P. carolinensis*. The Hiss may be the only call in the Chickadee's repertoire whose function is primarily interspecific.

Fights are rare and were observed only three times; all took place when a strange male was within 10 m of a nest cavity. The resident male immediately flew at the intruder and, during the ensuing fights, a snarling noise was heard on two occasions. The situations in which the Snarl occurs may be similar to those of the Hiss, but we think it may be uttered when the attack tendency is relatively stronger.

Twitter.—While resembling the Hiss in its noisy structure and in covering a wide frequency range (1.5–6.7 kHz), this call differs in consisting of a series of regularly spaced transients producing a twittering sound (Fig. 1d). This call was only recorded five times; in four cases a female gave it as she suddenly exited from the nest hole and met the male at the entrance (apparently it was a sudden, unexpected confrontation because members of a pair usually show little aggression or fear toward each other). In another instance it was given when one bird was trapped in a feeder and another bird tried to get in. Its occurrence may be similar to that of the Hiss in occurring in situations of thwarted escape. Because of their rarity we were unable to detect major differences between Snarls, Hisses, and Twitters. All appear to be distance-increasing (Tinbergen 1959). In *P. carolinensis* as well, Smith (1972) noted a graded series of displays encoding messages of thwarted escape, at least some of which are similar to those of *P. atricapillus*.

Tseets.—Tseets are roughly chevron-shaped notes that are variable in pitch (Fig. 1h). They are of short duration and tend not to be repeated in series, usually only one or two being given. Possibly some of the variants are different displays. These calls were often uttered when two birds perched on a feeder less than 0.5 m apart or as one supplanted another, but it was usually impossible to determine if they were given by both birds or by the aggressor or recipient of attacks. Smith (1972) in interpreting similar signals of *P. carolinensis* suggests that they are produced by a conflict between a weak escape tendency and any other category of behavior.

High Zees.—The characteristics of this call are shown in Table 2 and Fig. 1a. Ficken and Witkin (1977) describe the situations in which they occur and selection pressures shaping their characteristics. In brief, this call, more commonly uttered by males in response to a variety of avian and mammalian predators, probably occurs when the birds are in a state of extreme fear. The response of others is to become immobile. Similar calls occur in *P. carolinensis* (Smith 1972).

Discussion

Our observations agree with those of Smith (1972) that in chickadees vocal communication is more important than visual communication, except possibly when the birds are very close together (<5 m). In *P. carolinensis*, visual displays seem to be redundant to the vocalizations that often accompany them (Smith 1972). Vocal displays are probably particularly effective in birds such as chickadees that live in quite dense vegetation during the reproductive season and are often out of sight of each other even during the winter flocking period.

We have described and interpreted 13 major types of vocalizations, 2 given only by young. Table 3 summarizes the usages of adult vocalizations. Of these 11, 4 are apparently uttered only by females or at least are much more commonly given by females, while 3 are only or much more commonly uttered by males. Thus a relatively large number of vocalizations are given exclusively, or nearly exclusively by one sex. Such sexual segregation of calls may be especially important in a monomorphic species, particularly during the reproductive period, in facilitating appropriate responses to the mate. Agonistic encounters between mates are rare during the reproductive season, and some may be cases of mistaken identity as when a female exits quickly from the nest cavity and meets her mate at the entrance. We never saw any other types of agonistic interactions between mates during the breeding season and, compared with other passerines, this seems to be an unusual situation that is at least in part brought about by a very effective communication system and individual recognition of the mate.

Most aspects of social behavior are subject to multiple and often conflicting selection pressures and the resulting behavior is often a compromise between these (Wilson 1975). In order to understand selection pressures affecting chickadee vocalizations, we would have to understand all aspects of their informational content and usage as well as the complex social system of the species. In addition, ethologists

TABLE 3

Usages of Vocalizations of Adults

Vocalization	Context	Distance[1] between signaller & recipient	Sex[2]	Probable function
Fee-bee	On territory or some distance from others during nonbreeding season	L	♂	Territorial advertisement? Stimulates female? Leads flock
Faint Fee-bee	Caller is separated from mate	S, M	♂, ♀	Feeding interactions at nest hole; parent-young
Broken Dee	Reproductive period only	S, M	♀	Cements pair bond; may elicit feeding
Variable See	Reproductive period only, often precopulatory	S, M	♀	Attracts mate; may facilitate copulation
Hiss	Surprised at nest hole (usually by predator)	S	♀	Deters predation
Snarl	Fights	S	♂	Increases distance between caller and recipient
Twitter	Bird is startled, often at nest hole by mate	S	♀	Probably same as above; may also inhibit an attack
Tseets	Agonistic encounters	S	?	?
High Zees	Predator present	S, M	♂	Alerts group members and induces immobility
Gargles	Territorial encounters, agonistic encounters during flocking	S, M	♂	Increases distance between caller and recipient in agonistic situation, but not in sexual situation
Chick-a-dee call complex	Composition of call varies according to context; given in a variety of situations	M, L	♂, ♀	Alert group members; attract male or flock; coordinate group movements

[1] S = <5 m, M = 5–20 m, L = >20 m.

[2] Indicated as one sex if >90% of calls recorded from one sex.

have long emphasized the value of comparative studies of closely related species in clarifying the evolution of displays (Lorenz 1950). The genus *Parus* would seem ideal for comparative studies because of its large number of species and their ecological diversity. While greater knowledge of Black-capped Chickadee vocalizations and their social contexts is needed, and comparative material on many other members of the genus is scanty, we will try to make a preliminary analysis of selection pressures shaping chickadee vocalizations. Smith (1972) compared the vocalizations of *P. carolinensis* and *P. atricapillus*, Tufted Titmouse (*P. bicolor*), and Plain Titmouse (*P. inornatus*), but sonagrams were not available for the latter three species, and we encountered difficulties in relying on onomatopoetic descriptions of calls in the literature. Consequently we use only those calls of other parids for which there are sonagrams or unambiguous descriptions.

"Songs" in parids.—Dixon and Stefanski (1970) suggested that Fee-bees in the Black-capped Chickadee differ from the songs of many other passerines in several respects; they are simpler in structure, not used in territorial advertisement and

defense, and not confined to the breeding season. First, song in most birds is their most complex vocalization, and complexity is one of the features that distinguishes song from call notes (Thorpe 1961), but the physical structure of the Fee-bee is simpler than that of some of the other vocalizations, such as Gargles and the Chick-a-dee complex.

Second, Dixon and Stefanski (1970) view Fee-bees as not serving as a distant territorial threat to other males, but rather as a means of "locating the rival, challenging and beckoning him to a meeting site rather than as a means of repelling him from a fixed boundary." One of the reasons that Dixon and Stefanski (1970) doubted the role of Fee-bees in territorial proclamation is that they are not used once males come into proximity near the boundary and engage in boundary disputes. We have noted that song is rare during territorial encounters in several species of warblers we have studied, although occasionally these species may give secondary song during encounters. Chaffinches (*Fringilla coelebs*) sing before and after but not during territorial encounters (Marler 1956). The pure tone characteristics of Fee-bees are what one would predict for a long distance signal in a forest species (Morton 1975), and it would be difficult to explain the presence of this characteristic if Fee-bees were not used as a long distance signal. Fee-bees may not be as important in pair formation in this species as song is in other passerines because pair formation occurs in flocks in late fall or early winter before Fee-bee calling becomes frequent. Fee-bees may stimulate the female once pairing has occurred, and may also play some role in delineating territories. The latter possibility should be studied more carefully, possibly through playback experiments. Therefore Fee-bees may have some functions associated with songs of other passerines (territorial advertisement), have reduced importance of others (pair formation), and have new functions not found in song (leading flock movements). Although complexity and usages differ from songs of other passerines, we will continue to use the designation "song" in comparing Fee-bees with similar vocalizations of other parids.

While Fee-bees seem to be very simple and stereotyped in *P. atricapillus*, this is not the case with comparable vocalizations of other parids. For example, in *P. carolinensis* number of notes in the song is variable as is the relationship of high (H) and low (L) notes that may occur in varied combinations, e.g. HHLL, HHLLL, HLLH (Smith 1972). Each individual Coal Tit (*P. ater*) may have 6 song types (Thielcke 1973); individual Great Tits (*P. major*) have 4 to 7 songs (Gompertz 1961).

The North American assemblage shows some tendency for the loss of song. Reports on the Boreal Chickadee (*P. hudsonicus*) are ambiguous; one worker indicated a "warbling song of three or four notes," but others state that despite familiarity with the species they have never heard it sing, and Bent (1946) concludes that if song occurs in this species, it is very rare. Song is absent in the Chestnut-backed Chickadee (*P. rufescens*) and Bridled Titmouse (*P. wollweberi*) (Dixon 1961).

Song is primarily a long distance signal, so selection pressures will be different than for short range signals. Ability to penetrate vegetation without significant distortion is probably very important for such a signal. The characteristics of the songs of North American parids are those that would be predicated on the basis of the physical characteristics that best penetrate forest habitats. Forest bird songs are often pure tones and do not vary much in frequency when compared with songs of birds from other habitats, and this is probably related to some as yet poorly understood selection pressures relating to the physical environment (Morton 1975). The songs of European parids (Thielcke 1969), which exhibit more frequency modulation, would seem less well adapted for such an environment, but it is possible that European species inhabit a greater diversity of habitats with a corresponding shift of selection pressures. Also European parids show greater sympatry than North American members of the genus (Lack 1969), and this may have led to increased selection for specific distinctiveness in their songs.

Some of the features of the Black-capped Chickadee song are difficult to explain. Songs of this species are characterized by a narrow frequency range, moderate pitch with each note varying little in pitch, and no sharp onsets or terminations. Marler (1955) states that all these characteristics make a signal difficult to localize. In fact, song is rather similar to High Zees, the call given in response to predators, except for the higher pitch and shorter duration in the latter call. If Marler is correct, song in this chickadee would be rather difficult to localize, and localizability would seem a desirable feature of songs used in territorial proclamation.

Usages of song in various species of *Parus* are probably related primarily to several aspects of the social system: the involvement of song in territorial defense, whether pair formation takes place within the winter flock (as in *P. atricapillus*) or later in the spring (*P. major*, Hinde 1952), and possibly degree of sociality (some species may remain on territories as pairs during the winter, Hinde 1952). Song is greatly reduced or absent in several North American species, possibly related to some changes in their social system as compared with other parids. Another important factor may be the small degree of sympatry of North American species, reducing selection for a specific distinctive vocalization involved in pair formation. *Parus atricapillus* seems to represent an intermediate condition in loss of song. Song is relatively infrequent in this species, probably related to the loss or reduction of a role in pair formation. Infrequent singing may subject song characteristics to different selection pressures than more frequent singing. *Parus major* is a frequent singer during the reproductive period and Gompertz (1961) suggested that the variability of their songs is related to the antimonotony principle (Hartshorne 1956); that an infrequent singer such as *P. atricapillus* should have a stereotyped song would not be unexpected. A second cause for variation in songs of individual *P. major* is the tendency for territorial males to "match" their neighbor's songs when counter singing (Gompertz 1961). The simple, stereotyped song of *P. atricapillus* requires no such matching by neighbors.

Call notes.—Different selection pressures have probably acted on song and call notes. In the case of call notes selection for specific distinctiveness is probably greatly reduced. Selection pressures of importance vary for different call notes according to the distance they must be transmitted, the types of information they convey, predator pressure, and their functions related to a particular type of social system.

Broken Dees, the call given by females during the reproductive season, are very similar in *P. carolinensis* and *P. atricapillus*, and possibly in other parids as well. The characteristics of the call are those that make it easily localizable: harmonics and covering a wide frequency range, sudden starts and stops (Marler 1959). These characteristics are probably not very important in usage of the call when the pair is foraging close together, but the call also seems to serve as an attractant when members of the pair are some distance apart.

Variable Sees, also associated with reproductive behavior, are the highest pitched calls of the chickadee, about 1 kHz above the call given in response to predators, High Zees. The two calls are rather similar in duration and internote interval, but Variable Sees typically have a transient, a feature usually absent in High Zees. Both calls cover only a narrow frequency range. The similarity of the two calls is puzzling, because their usages are very different, and they would be expected to be subjected to different selection pressures. High Zees have features that Marler (1955) indicates make the call difficult to localize. Variable Sees may be more easily localizable than High Zees because of the presence of transients. Localizability is probably important for this call because it is often given when the mate is absent and serves as an attractant. Witkin (MS) noted an inverse correlation between the pitch of chickadee calls above 4 kHz and amplitude. Variable Sees seem to be of low amplitude, which may be associated with their use as short and moderate distance signals. Perhaps the high pitch of Variable Sees is due to selection to avoid masking by other sounds in the environment, which would usually be of much lower pitch. As high frequency sounds are subjected to greater attenuation by vegetation than those of lower pitch (Marler 1955) it is not surprising that both High Zees and Variable Sees are used in short or moderate range communication.

A hiss-like call given to nest predators has been reported for 13 species of parids (Thielcke 1968). The call sometimes accompanies swaying movements in the nest hole and Sibley (1955) suggests that this is a snake mimicry that probably deters predators. Hissing seems to be a special adaptation for hole-nesting, as it is performed at the nest hole entrance, and open-nesting passerines do not seem to have similar displays. The primary selection pressure acting on this call seems to be its resemblance to a snake's hiss, but related to this may be the explosive quality of the call which may have a startling effect on the recipient. The Hiss is probably only employed as a very close range signal.

As Snarls were noted only a few times, it is probably premature to generalize about the relationships between their structure and function, but they are very close range signals (<1 m) with probably little need for features making them easily localizable. Although they cover a wide frequency range, they lack the harmonic structure of some other chickadee calls. Their function seems to be to increase the distance between the caller and a recipient, and some aspects of the call may be related to their function in that the call seems explosive and harsh and perhaps has a momentarily startling effect. Twitters seem to have a similar function, although they are probably given more often by females than are Snarls and are indicative of a lesser readiness to attack if the recipient does not move off. Smith (1972) reported a vocalization similar to the Twitter of *P. atricapillus* in *P. carolinensis*, and a sonagram of a call of *P. ater* (Löhrl and Thielcke 1973) looks identical to that of *P. atricapillus.*

Tseets are similar in *P. carolinensis* (Smith 1972) and *P. atricapillus*. They seem to lack features making them easily localizable and are of low amplitude; both characteristics are probably related to their use only at close range.

The complex vocalizations that we have called the "Gargle" are also found in *P. carolinensis* and are termed Slink Rasp, Rasp Slink, and Click Rasps by Smith (1972). Some of the notes are very similar to those of *P. atricapillus*, although others differ. The Gargle consists of an array of notes with varying temporal and frequency characteristics. The structure of the call seems to be particularly adapted for some of the types of information it may convey—individual and possibly group identity, the coding of which requires complex arrangements of notes.

"Chick-a-dee" type calls are widespread in both the European (Thielcke 1968) and North American members of the genus (Smith 1972). The Old World Species for which Thielcke (1968) furnished sonagrams are quite similar to each other in having D syllables of very short duration, except for *P. varius* and *P. montanus*. The calls of *P. montanus* appear very similar to those of the longer duration D notes of the North

American group (sonagrams of *P. atricapillus, P. hudsonicus, P. carolinensis, P. gambeli* in Thielcke 1968). As this call complex functions primarily in flocking, and sociality during the nonreproductive period is widespread in the genus, the distribution of this call is not surprising. In *P. atricapillus* the marked transients in the A, B, and C notes, and the harmonic structure of the D note probably facilitate localization, which would be particularly important for this call, which together with song are the signals most likely to be involved in long distance communication. Similarities in the calls of sympatric species, particularly in Europe, may facilitate interspecific flocking, which occurs in some members of the genus (Hinde 1952).

All major call categories that we distinguish in *P. atricapillus* have counterparts in the other North American member of the genus that has been analyzed sonagraphically (*P. carolinensis*, Smith 1972), but comparing the frequency and temporal characteristic of their calls is difficult as Smith (1972) does not give measurements of sonagrams. Their usages also seem similar. The only detailed sonagraphic analysis of a European parid is that of Gompertz (1961) for *P. major*. Most of the vocalizations appear so different in structure, that few homologies were apparent with calls of *P. atricapillus*. It would be especially interesting to be able to compare the calls of *P. atricapillus* with those of *P. montanus* to which it is supposedly so closely related (Mayr and Short 1970). As there has probably been little selection for specific distinctiveness in call notes, and the social systems are probably rather similar, calls probably furnish better indications of phylogenetic relationships than song, which has probably been subjected to selection for specific distinctiveness and the particular habitat in which each species lives.

Some vocalizations of *P. atricapillus* do not seem different in usage from vocalizations of other passerines given in similar situations, but the snakelike Hiss is probably an adaptation for hole-nesting, as is the use of Faint Fee-bees mediating interactions between the pair at the nest hole when one bird is out of view. Other vocalizations show differences in complexity and/or usage from those of more solitary passerines. Fee-bees differ in complexity and usage from what we usually consider characteristic of song. Calls related to social functions include the Gargle and Chick-a-dee call, both of which are more complex than the call notes of most other passerines.

Most calls of the chickadee are discrete and distinct when compared to other calls in the species' repertoire. Only the Hiss, Snarl, and possibly Twitter seem part of a graded series. In general, in this species calls associated with courtship appear discrete, while those primarily associated with thwarted escape or attack-escape conflicts are graded. Many other social species, e.g. Common Crow (*Corvus brachyrhynchos*) (Chamberlain and Cornwell 1971), Chicken (*Gallus gallus*) (Konishi 1963) and Village Weaverbird (*Textor cucullatus*) (Collias 1963), seem to have a vocal repertoire with more extensive grading than the chickadee, and such grading of vocalizations is common in the social primates (Marler 1965).

Gompertz (1961) identified as many as 40 vocalizations in *P. major*. In *P. major*, as in *P. atricapillus* in the Chickadee call and Gargle, notes are often combined to generate new variations. Problems in classification arise, particularly when to split and when to lump such call variations. We have identified only 11 vocalizations in adult Black-capped Chickadees, but one category (Chick-a-dee calls) comprises a whole complex of vocalizations, variations of which may transmit slightly different information. Thus this chickadee, as a result of selection pressures relating to increasing the number of messages associated with sociality, has not proliferated major new categories of discrete calls, or generated extensive graded signals, but rather has elaborated the variations of note combinations.

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