

potheses. The group of owls in regions without mammalian predators includes those restricted to smaller and more remote islands, since larger islands and continents have or recently had mammalian predators. Full species on islands include 7 tufted forms and 12 forms with tufts that are inconspicuous or lacking. These data weaken the hypothesis of predator mimicry, which predicts that owls of small and remote islands should lack ear tufts. Of the island species, 7 of 19 (37%) are tufted, while on continents 41 of 113 (36%) species are tufted. Thus, islands and continents have similar proportions of tufted owl species.

These results support the camouflage and species recognition theories but not the predator mimicry hypothesis. The evidence also points to a problem with the species recognition hypothesis, i.e., its assumed mechanism may fail to operate. All species with ear tufts are nocturnal and inhabit forest or brushland. For two such owls to approach each other close enough to see silhouettes, they first must communicate in the dark, usually amidst vegetation. This prerequisite long-distance link surely must occur by voice and not by sight. It seems likely that species identification is established during the vocal encounter. If so, the only proposal concerning the function of ear tufts that finds support from my tests is that of camouflage. However, the camouflage hypothesis does not fully explain the occurrence of tufts either, since more than half of the nocturnal, forest-dwelling owls lack tufts, despite the advantage these structures presumably confer. A firmer conclusion awaits field observations of perching and

roosting behavior of owls, including site preferences and postures. Such studies should be carried out in part at the vegetation heights at which owls sit, since it is at these heights that owls are seen by most other animals, including other owls.

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## WHAT IS THE SONG OF THE BLACK-CAPPED CHICKADEE?

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For most species of songbird, song and call notes are readily distinguishable in structure, usage and function (i.e., Thorpe 1961). Songs are usually complex, species-specific vocalizations given during the reproductive period, often showing individual differences, and sometimes dialect patterns. They usually function in pair formation and territorial advertisement. Call notes are usually simple vocalizations given throughout the year.

The whistled "Fee Bee" vocalization of the Black-capped Chickadee (*Parus atricapillus*) is generally considered to be the bird's song, but this vocalization differs in several respects from songs of other oscines (Dixon and Stefanski 1970, Ficken et al. 1978). Another vocalization, the "Gargle" (Ficken et al. 1978) shows some song-like characteristics. Thus, what vocalization or vocalizations in this species correspond to song in other oscines? Here I compare Gargle and Fee Bee vocalizations and explore their relationships to song. Since Dixon and Stefanski (1970) and Ficken et al. (1978) discussed the Fee Bee vocalization in detail, I will refer to Fee Bees mainly in comparison to Gargles.

#### METHODS

I recorded chickadee vocalizations at the University of Wisconsin-Milwaukee Field Station, Saukville, Ozaukee Co., Wisconsin from 1969 to 1980. Most chickadees

were individually color-banded by C. M. Weise. For several years I recorded vocalizations throughout the year, but since 1975 have concentrated on recordings near feeders in winter. Most recordings were made with a Nagra 4.2 tape recorder using a Sennheiser 104 microphone. They were analyzed with a Kay 6061 B Sona-graph using an intermediate band setting (150 kHz). I recorded several hundred Fee Bees from at least 11 different males and over 4,000 Gargles from at least 100 individuals.

#### RESULTS

*Structure of the vocalizations.* The Fee Bee is a pure tone whistle (Fig. 1A), showing little frequency modulation, with the first note higher than the second. A Gargle (Fig. 1B) consists of a series of syllables composed of transients and often with terminal trills. Both vocalizations exhibit specific distinctiveness as compared to similar vocalizations of other members of the genus and are clearly homologous with the vocalizations of the closely related Carolina Chickadee (*P. carolinensis*; Smith 1972, Ficken et al. 1978).

Occasionally a male gave a Fee Bee consisting of only the first note and even more rarely included a third note. However, over 95% of the Fee Bees (N = 111) consisted of only two notes in my study population. Measurements of sonograms are given in Ficken et al. (1978) and different males have similar vocalizations. Thus, in this study area at least, the song was quite stereotyped among individuals.

The Gargle, on the other hand, is very complex, usually consisting of 2 to 12 different syllables that can be variously combined. Each unique combination of syllables is referred to as a type. Any individual may utter several types of Gargles. For example, in 1978

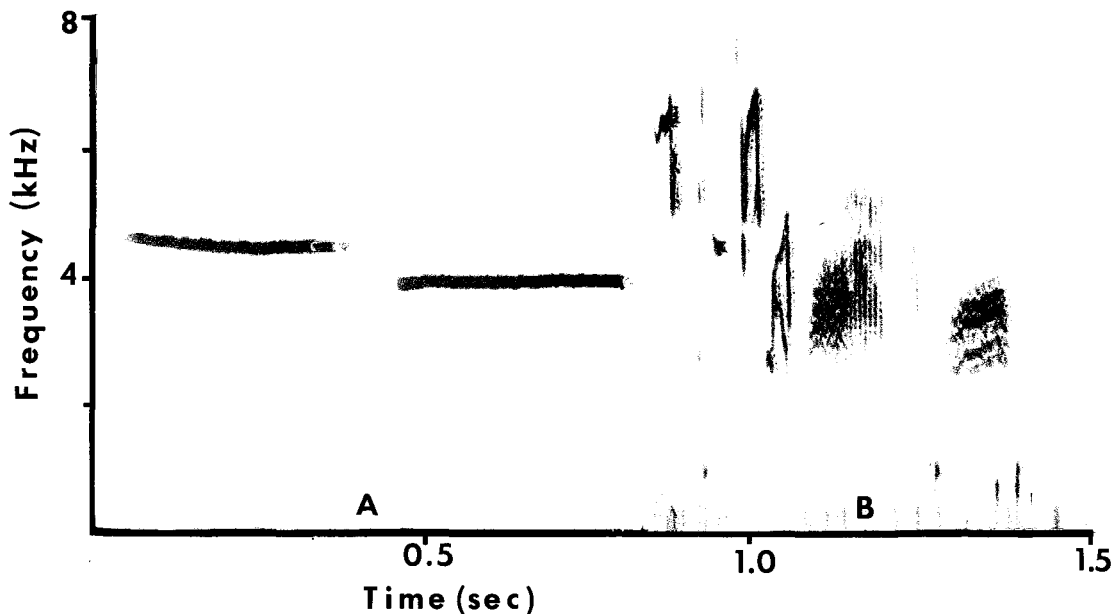


FIGURE 1. Sonograms of Black-capped Chickadee vocalizations: A. Fee Bee. B. Gargle.

my colleagues and I recorded 55 Gargles given by one male in agonistic situations at a winter feeder. Three types of Gargle were each given more than 10 times, with 17 others being given 1 to 3 times. In addition, males in different flocks in the same locality shared some Gargle types, but not all. Dialects occurred, showing some different syllables between populations as close as 3 km. Thus, Gargles showed greater possibilities for individual and dialect differences than Fee Bees. No dialects have been reported in Fee Bees, although there may be some geographic variation.

*Ontogeny.* Some preliminary observations suggest that learning is important in the development of Gargles. Four chickadees were hand-reared by K. Apel from the age of about 15 days and subsequently were never exposed to chickadee vocalizations other than their own. As adults, their Gargles were aberrant, lacking well-defined syllables. The adults never uttered Fee Bees, possibly owing to some deficiency of the rearing experience other than auditory isolation, or the lack of the proper stimuli for eliciting the vocalization in a small cage.

#### DISCUSSION

Two vocalizations of the Black-capped Chickadee have some song-like characteristics and functions. Table 1 summarizes some characteristics of Fee Bees and Gargles and indicates whether these correspond to what is generally considered to be typical of song.

Both vocalizations are given primarily by males (Ficken et al. 1978). Fee Bees differ from song in most birds in that although uttered more often during the breeding season, they are also given during the non-breeding season (Dixon and Stefanski 1970). When giving Fee Bees in a winter flock, a chickadee usually moves away from the flock before delivering them. Gargles, however, are often given when close to another bird (usually within 1 m). Gargles are given throughout the year. Even during the breeding season, chickadees deliver Fee Bees less frequently than most birds sing (Dixon and Stefanski 1970; pers. observ.),

although at times, particularly at dawn, the vocalizations may be given in bouts. Gargles are uttered throughout the day, but their occurrence seems to depend on particular circumstances, e.g., approach of another bird. Gargles are sometimes given in bouts by lone birds.

Both vocalizations are given in territorial defense. However, Fee Bees seem to be involved only in territorial advertisement. These calls are frequently produced by males while approaching a territorial boundary, and they seem to serve a "beckoning" function in that the adjacent territory holder then approaches and boundary conflicts often ensue (Dixon and Stefanski 1970; pers. observ.). Once in the boundary zone, neither male gives Fee Bees, but Gargles are frequent as the males perch within 1–2 m of each other and indulge in short chases.

Odum (1942) referred to Gargles as "dominance" calls, and certainly these vocalizations appear to be involved mainly in close range agonistic encounters concerned with dominance.

The role of the two vocalizations in pair formation is uncertain. Pair formation is completed in winter during a period when Fee Bees are given. Although males sometimes Gargle at females during this period, I know of no evidence that their function in this context is other than agonistic. As the mates are so close together during this period, there may not have been selection for involvement of a strong vocal component in pair formation. The function of nearly year-round Fee Bee production is unclear. However, we suggested that, in late summer at least, they are used by a male to lead the flock to new feeding areas (Ficken et al. 1978).

The territorial functions appear to depend, at least partly, on transmission distance. The Gargle is used as a signal at less than 10 m (Ficken et al. 1978) while the Fee Bee is used over greater distances. It may be difficult to evolve a single signal that is well adapted for both circumstances. For example, the pure tones of Fee Bees are probably well adapted for long distance

TABLE 1. A comparison of two vocalizations of the Black-capped Chickadee according to the properties of typical oscine song.

Characteristics of song*	Gargles	Fee Bees
Complex structure	X	0
Primarily by males	X	X
Species specific	X	X
More than one type/individual (often)	X	0
Dialects (often)	X	0
Breeding season only	0	0
Given in prolonged bouts on territory	0	Occasionally
Territorial advertisement	0	X
Territorial boundary encounters (some species)	X	0
Pair formation	?	?
Acquired by learning	X	?
Long transmission distance	0	X

\* Thorpe, 1961.

transmission, while the transients and trills of Gargles would not carry well in a forest environment because of attenuation by vegetation (Morton 1975).

In considering "What is the song of the Black-capped Chickadee?" note that there is not a single vocalization that corresponds well in structure and function to song. Some of the characteristics of song in other oscines are found in two different vocalizations. However, both of these vocalizations by chickadees also have other usages that do not correspond to song.

Ficken et al. (1978) compared data on some parid vocalizations and found that songs tend to be more complex in European than North American species of *Parus*. Three North American species lack a whistled song: Chestnut-backed Chickadee (*P. rufescens*; Bent 1946), Boreal Chickadee (*P. hudsonicus*; McLaren 1976), and the Mexican Chickadee (*P. sclateri*; Dixon and Martin 1979). In the Mexican Chickadee, the vocalizations that appear similar to Gargles function both to attract a rival to a territorial boundary and in "reiterating boundaries from a distance" (Dixon and Martin 1979). The latter authors viewed this vocaliza-

tion as the song of the Mexican Chickadee. The Boreal Chickadee lacks a vocalization involved in territorial advertisement, although its repertoire includes a vocalization similar to a Gargle and also a "musical call" (McLaren 1976).

The whistled "song" of the Black-capped Chickadee appears to be in a transitional stage. Although the Fee Bee seems to be involved in territorial advertisement, this whistled "song" appears to be less important than the song of other oscines. This chickadee is probably evolving less reliance on a Fee Bee "song," which I predict will eventually be lost, as appears to have been the case in some other parids.

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