

A COMPARATIVE ANALYSIS OF THE VOCAL COMMUNICATION SYSTEMS  
OF THE CAROLINA CHICKADEE AND THE TUFTED TITMOUSE

BY

PHILIP GADDIS

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By

Philip Gaddis

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Chairman: John H. Kaufmann  
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Repertoires of the vocal communication signals of two interspecifically social species, *Parus carolinensis* and *P. bicolor*, are described and compared according to acoustic structure and behavioral function. Calls of both species were placed in four major subsystems on the basis of similarities in acoustic structure. The subsystems that corresponded in function between the two species were compared and their similarities evaluated. The extent of structural similarities in these subsystems correlated with the extent of interspecific relevance of their communicative functions. Calls used for close-range contact were very similar between the two species. Calls used for mid-range contact and contact under changing conditions differed in details of acoustic structure between the two species but were basically similar, and call subunits were arranged by the two species according to similar rules of syntax. I interpret this as a maintenance of sufficient similarity to facilitate interspecific flocking while allowing sufficient divergence to enable intraspecific group cohesion within the mixed flock. Calls used in aggressive encounters, which were primarily intraspecific, were completely

different between the two species, although both subsystems were derived from the mid-range contact calls of their respective species. Calls used for long-range contact and territorial advertisement were also completely different.

## INTRODUCTION

The Carolina chickadee (*Parus carolinensis*) and the tufted titmouse (*P. bicolor*) flock together throughout most of the year where their ranges overlap. Even in the breeding season, when flocking is less common, the two species nevertheless spend much of their time together. When the mixed flocks do form, from late summer to early spring, many other species are associated with the flocks, but the vocalizations of the two parid species are unmistakably predominant in the flocks' acoustic output. Some of the vocalizations of the chickadees are humanly indistinguishable from those of the titmice, some are similar, some bear vague resemblance in certain aspects, and some are quite different. This study was undertaken to evaluate more precisely these similarities in vocalization structure, to study relations between structural and functional similarities, and ultimately to describe the extent of interspecific language.

Peter Marler (1957) described the extent of similarities in vocalizations of several sympatric, British bird species and formulated expectations for similarities in communication signals. These expectations were confirmed in studies on two sympatric and interspecifically social species of *Cercopithecus* monkeys (Marler, 1973). My study of the two sympatric and interspecifically social species of *Parus* closely parallels this work on the monkeys and further confirms Marler's predictions.

## BACKGROUND ON THE SPECIES STUDIED

The genus *Parus* is a relatively distinctive group that comprises 44 of the 46 species of the family, Paridae (Snow, 1967). No pre-pleistocene fossils are known for the genus (Brodkorb, 1978), and thus very little can be said with certainty regarding its history. However, this genus reaches its greatest diversity in Eurasia, especially in the eastern Himalayas and mountains of western China where 14 species occur (Lack, 1971), and it seems likely that the genus arose there. The genus can be subdivided into ten subgenera based on the classification of Hellmayr (1903). Five or more species may coexist in many areas of Eurasia, but, with only a few exceptions, coexisting species are from different subgenera (Lack, 1971). The exceptions are *P. palustris* and *P. montana*, which coexist over much of temperate Eurasia including England and Japan, and *P. atricapillus* and *P. rufescens*, which coexist in the Pacific northwest of the United States (Smith, S. M., 1967). Both species pairs are from the subgenus *Poecile*, the largest of the subgenera. Coexisting forms are usually well separated by habitat, or by food and microhabitat preferences (Lack, 1971). Only one subgenus (*Melaniparus*) occurs in Africa south of the Sahara, and, although ten species exist, overlap between them is rare (Lack, 1971).

Two subgenera occur in North America. The subgenus *Poecile* consists of six North American and six Eurasian species, one of which, *P. cinetus*, occurs in Alaska as well as Eurasia from Scandinavia to Siberia. All of the species of the subgenus *Poecile* are very similar

in appearance, with only *P. superciliosus* of the mountains of western China, and *P. gambeli* of the mountains of western U.S. deviating from the general pattern by having a white superciliary line. The other North American species can be divided further into brown-capped and black-capped groups (Lack, 1971: superspecies). The brown-capped group consists of *P. cinctus*, *P. hudsonicus*, and *P. rufescens*, the latter two of which were considered sibling species by Grinnell (1904). The black-capped group consists of *P. sclateri*, *P. atricapillus*, and *P. carolinensis*, the latter two of which were considered sibling species by Brewer (1963), and were thought to have diverged during the Illinoian glaciation in the eastern U.S. *Parus carolinensis* presently occupies the southeastern U.S. from the Atlantic ocean to central Missouri, Kansas, Oklahoma, and Texas and from southern Pennsylvania, Ohio, Indiana, and Illinois south to the Gulf of Mexico. *Parus carolinensis* is subdivided into four subspecies (Snow, 1967; five subspecies in A.O.U. Checklist, 1957) based on subtleties of plumage coloration and on measurements of wings and tails, with the larger subspecies in the north.

The subgenus *Baeolophus* is considered to be a uniquely North American group (Lack, 1971; Dixon, 1961) although *P. wollweberi* was considered by Hellmayr (1903) to be more closely related to the subgenus *Lophophanes* of Eurasia. Besides *P. wollweberi*, *Baeolophus* consists of only two other species. *Parus inornatus* occurs in southwestern U.S. north to southern Oregon and east to the Rocky Mountains. *Parus bicolor* is distributed from southern New England, extreme southern Ontario, and southeastern Nebraska south to northern Hidalgo and Veracruz, Mexico. The subspecies of *P. bicolor* occupying the eastern United States,

*P. b. bicolor*, is relatively distinct from the other four subspecies, and was recognized as a species by the A.O.U. until 1976 (A.O.U. Checklist, Thirty-third Supplement, 1967). *Parus b. bicolor* averages around 30% heavier than its neighboring subspecies, *P. b. semeti* (Dixon, 1961), and bears distinctive crest markings, but the two subspecies interbreed where their ranges meet (Dixon, 1955) and so have been considered one species.

The range of *P. carolinensis* is virtually contained within the range of *P. b. bicolor*. *Parus b. bicolor*, however, extends into the range of *P. atricapillus* several hundred miles along its (*P. b. bicolor*'s) northern and northwestern boundaries. The ranges of both *P. carolinensis* and *P. b. bicolor* are advancing northward (Brewer, 1963; Pielou, 1957).

In general, members of the genus *Parus* are present wherever forest or savanna occurs in Eurasia, Africa, or North America. They have also taken well to areas of human habitations, and persist in gardens and hedgerows. They are broadly omnivorous in their food preferences. They are partial to caterpillars, but also take many other arthropods as well as acorns and the seeds of many other trees and plants. Their ability to exploit plant resources no doubt enables them to spend the winter in cold temperate climates. The genus is basically non-migratory but some of the far northern species make regular migrations southward in the winter (Havlin and Jurlov, 1977; Hilden, 1977).

Except during the breeding season, species of the genus *Parus* are nearly always associated with mixed species flocks. *Parus lugubris* of southeastern Europe and the northern part of the mideast, and *P. inornatus* of southwestern U.S., however, show little flocking behavior

(Hinde, 1952; Dixon, 1949). Mixed species flocks appear to be a nearly universal phenomenon in forest habitats throughout the world. Wherever parids occur they are nuclear species in the mixed flocks in that the flocks tend to form around them. Throughout Eurasia and North America, the most regular flocking associates of the parids are nuthatches, Sittidae, treecreepers, Certhiidae, and various species of Sylviidae. In Eurasia, muscicapid flycatchers are regular associates (Hinde, 1952; Macdonald and Henderson, 1977; Filonov, 1960). In southern and south-eastern Asia, many species of babblers, Timaliidae, are associated with the mixed flocks (Ali, 1977). In North America, various species of the family Parulidae are regular associates (Morse, 1970). The distribution ranges of the Paridae, Sittidae, Certhiidae, and Sylviidae in North America are largely coincident.

Throughout the fall, winter and early spring in central Florida and probably wherever else they co-occur, *P. carolinensis* and *P. bicolor* spend virtually all of their time in each other's company. In my study area, the two species tended to roost colonially in tree holes and also in piles of Spanish moss, *Tillandsia usneoides*, in the case of the titmouse. The birds went to roost together one half to one hour before sunset and emerged together at 3/4 to one hour after sunrise, staying in longer in cold weather. The birds often gathered at traditional centers following morning emergence, as well as at other times during the day, with a great deal of calling. The mixed flock would then leave all together or in smaller mixed groups in separate directions.

The most regular attendant species in my study area were the black and white warbler, *Mniotilta varia*, yellow-throated warbler, *Dendroica*

*dominica*, and brown creeper, *Certhia familiaris*, all of which occurred at a density of only one individual per flock and were only rarely seen away from flocks. The solitary vireo, *Vireo solitarius*, downy woodpecker, *Picoides pubescens*, red-bellied woodpecker, *Melanerpes carolinensis*, pine warbler, *Dendroica pinus*, and orange-crowned warbler, *Vermivora celata*, were also regular attendant species. They occurred at one to three individuals per flock and were frequently seen away from the flocks. The yellow-rumped warbler, *Dendroica coronata*, American goldfinch, *Carduelis tristis*, and ruby crowned kinglet, *Regulus calendula*, occurred irregularly with the flocks in groups of four or more to more than thirty (more than fifty in the case of the yellow-rumped warbler) per flock. The brown headed nuthatch, *Sitta pusilla*, did not occur on my study area probably due to the small size of the pine "island" but, in more extensive areas of pine in the southeast, it regularly occurs with the parids in mixed flocks (Morse, 1970; pers. obs.).

While the parids were feeding on long leaf pine seeds during the fall and early winter, the flocks moved slowly ( $< 2$  km/hr), were often widely dispersed, and often became fragmented. When the pine seeds ran out in early winter, and especially in cold weather, the flocks were more cohesive and moved faster through the woods (2-5 km/hr). The flocks were most active during early morning and late afternoon. When pine seeds were available, and during warm weather when insects were apparently more available, the flocks' activity declined during mid-day and the birds would perch quietly together and preen. During periods of cold weather in mid-winter, the flocks continued to forage actively throughout the day.

The flocks were exposed to predator pressure at a rate of around two attacks or flybys per day by the sharp-shinned hawk, *Accipiter striatus*, and occasionally the Cooper's hawk, *Accipiter cooperii*, from November to March.

Supplanting attacks and attempts at food piracy were rare when pine seeds were available but became frequent later in the winter. These were usually directed against members of the same species but titmice were occasionally supplanted by red-bellied woodpeckers, chickadees by titmice, warblers by chickadees and titmice, and yellow-throated warblers by all other species, especially the pine warblers (cf. Ficken *et al.*, 1968). The vulnerability of chickadees and titmice to piracy is due to their habit of taking food items that require manipulation by holding the item with the feet while tearing it up with the bill. Although attempts at piracy were at times frequent, no successful attempts were observed. The food item was occasionally dropped in the process and lost. Birds were occasionally displaced from a cone or other foraging site after it had yielded a bit of food.

The flocks defended a winter territory against neighboring flocks. The chickadees and titmice fought only against their own species. Occasionally only the titmice fought, and, after the two factions separated, the chickadees continued on with the opposite group from the one they had originally been traveling with, indicating that the chickadees' flock range spanned more than one titmouse flock range. The groups of four to six titmice defended territories of thirty to forty acres. The groups of 5 to 8 chickadees defended territories that were probably at least twice the size of the titmouse flock territories.

The flocks appeared to disregard flock boundaries and to continue foraging into neighboring territories until discovered and expelled by the neighboring flock.

Pair formation presumably takes place during the winter. Display flights (cf. Tooby, 1948; Smith, S. T., 1972) were observed during January and February. They were seen to be performed on four occasions by titmice and once by a chickadee in the areas where the flocks gathered in the morning and at other times during the day (see above).

When the weather warmed up in March, the dominant pair of the flock carved out a breeding territory from the flock territory and excluded others of its species. The remaining area of the flock territory was then taken over by a second pair from the remaining flock and the others were excluded. The two species nested in tree-holes and raised three to six fledglings. The fledglings were led around the breeding territory for around two weeks for the chickadee and four or five weeks for the titmouse until the parents gradually stopped feeding the young and the flocks began mixing. Border confrontations during this period consisted of fights between parents only. Strife between fledglings within family groups became more and more intense as they got older. Following this period of family group activity, the flocks began mixing and a period of intense and complicated fighting followed, while winter flocks and flock territories were formed. This period lasted from mid-summer to early fall.

This general life history pattern is typical of the genus (cf. Bent, 1946; Hinde, 1952; Löhr, 1964; etc.).

## METHODS

### Study Area

The study area consisted of approximately 50 ha in the center of the 2200 ha San Felasco Hammock State Preserve. The center of the study area is 20 km NW of the University of Florida campus and at least 3 km from the nearest public road.

At the center of the study area is an open stand of long-leaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*). This stand slopes off gradually on three of four sides into denser second growth loblolly pine (*Pinus taeda*) and turkey oak. Much denser second growth woods consisting of sweetgum (*Liquidambar styraciflua*), southern red oak (*Quercus falcata*), mockernut hickory (*Carya tomentosa*), and laurel oak (*Quercus hemisphaerica*) occur on the fourth side. This second growth deciduous woods continues to slope off to a small swamp surrounded by a relatively mature stand of laurel oak, pignut hickory (*Carya glabra*), basket oak (*Quercus michauxii*), and magnolia (*Magnolia grandiflora* and *M. virginiana*).

Around my home in Gainesville, tall laurel oaks are abundant. Many live oaks (*Quercus virginiana*), long leaf, and loblolly pines are also scattered throughout the neighborhood.

### Observational Techniques

Flocks containing Carolina chickadees (*Parus carolinensis*) and/or tufted titmice (*P. bicolor*) were followed in San Felasco Hammock State

Preserve from March, 1977, to December, 1978. The most intensive observations were made between September, 1977, and June, 1978, during which time the flocks were followed on a daily basis. Beginning in December, 1977, attempts were made to mark birds for individual identification. Mist nets were used to catch the birds. The chickadees and titmice were marked with colored plastic leg bands on both legs and with a U.S. Fish and Wildlife Service aluminum leg band on one leg. The birds were extremely difficult to catch; it took nearly four months to catch and mark 12 titmice and six chickadees. Attempts to bait and then trap the birds were unsuccessful in San Felasco Hammock. An additional six titmice and two chickadees were trapped and marked after having been attracted to feeders at my home in a residential neighborhood of Gainesville, three blocks north of the U.F. campus. These birds were not given the systematic attention given the birds at San Felasco Hammock, but many recordings of their vocalizations were made.

After a few weeks of following the flocks regularly, the birds habituated to my presence and I was able to stay in the midst of the flock and observe the birds at close range. Recordings of their vocalizations were made on a Superscope C105 cassette recorder with a Realistic electret condenser microphone and also on a Nagra IINN open reel recorder with a Gibson P200 microphone in a 46 cm parabolic reflector. Approximately 40 hours of tape were recorded and then analyzed on a Kay Electric 7029A Sona-Graph.

Detailed transcripts of the tapes were made and sonograms of representative examples of each call from each bout of its occurrence were made. The resulting sonograms were then sorted and arranged into

categories of calls and then the calls into major subsystems. The calls were given names and then an index of each of these calls was compiled from the tape transcripts. Contextual information, if available, was included with each index entry. This contextual information was summarized for each call and then used in the process of inferring functions and messages of the calls. Tape recordings of all calls have been deposited in the Florida State Museum Bioacoustics Laboratory.

#### Definitions

The process of communication is interpreted in many different ways by its various investigators. It is a complex subject and I find no set of definitions of all relevant variables entirely satisfactory. None of the following definitions are entirely my own but no single work in the literature contains them all.

I use the term function according to Williams (1966) as a consequence of an act or an effect of an organ's activities that enhances the fitness of an individual organism. An adaptation is the evolutionary means of accomplishing a function. Information is anything that stimulates a sense organ of any kind (Smith, W. J., 1977). A signal is a behavioral, physiological, or morphological characteristic adapted for conveying information (Otte, 1974). A message is an abstract quality that defines the packaging of the information made available by a signal (sensu Smith, W. J., 1977). A message is an effect of a signal. The function of a signal is the manipulation of the behavior of another organism (sensu Dawkins and Krebs, 1978). Communication is the process of transmitting messages.

A call is any vocalization. A call type is a class of calls with certain specified similarities. A form is a specific call configuration.

A note is a sound with virtually no frequency inflection. A syllable is a continuous sound with one or more frequency inflections. A phrase is a more or less stereotyped cluster of notes and/or syllables used as a subunit in longer calls. A series is a string of notes, syllables, and/or phrases considered to be one call unit. The notes and phrases of a series are also referred to as call subunits. A bout is an episode of calling. Two sounds are considered to be harmonically related if the frequency difference between them is integral to the absolute frequencies of the two sounds (Roederer, 1975). One sound is a harmonic of another if its frequency is an integral multiple of that other sound. Onset and cutoff arms refer to the vertical components seen in sonograms at the beginning and ending of certain vocalizations.

## RESULTS

### Chickadee Subsystem 1

#### Structure

The calls of this subsystem consist of four basic types (Fig. 1). They all sound like a soft, quick "tseet." Types A and B represent extremes in a continuum in which intermediate forms are expressed with descending onset portions of variable length. Type B consists of those forms without descending onset. The portion of the call that was horizontal or nearly so (as seen in sonograms) varied in length in those cases where unambiguously measurable from 12-30 msec ( $\bar{x} = 20$ ,  $SD = 6.12$ ) for type A and 25-45 msec for types B and C ( $B \bar{x} = 34.7$  msec;  $SD = 5.3$ ;  $C \bar{x} = 32.5$  msec,  $SD = 6$ ). However, most cases were not safely measurable due to differential reverberation at various call amplitudes and in acoustic media of variable structure and density (for a discussion of reverberation, see Wiley and Richards, 1978). Calls of all four types, when given at sufficiently high amplitudes, were followed by an "echo" at much lower amplitude. This "echo" was invariably identical to the original call and followed at a latency of approximately 214-218 msec.

#### Usage and Contexts

Calls of this subsystem were given during virtually all kinds of activities. The calls appeared to be correlated with short hops or

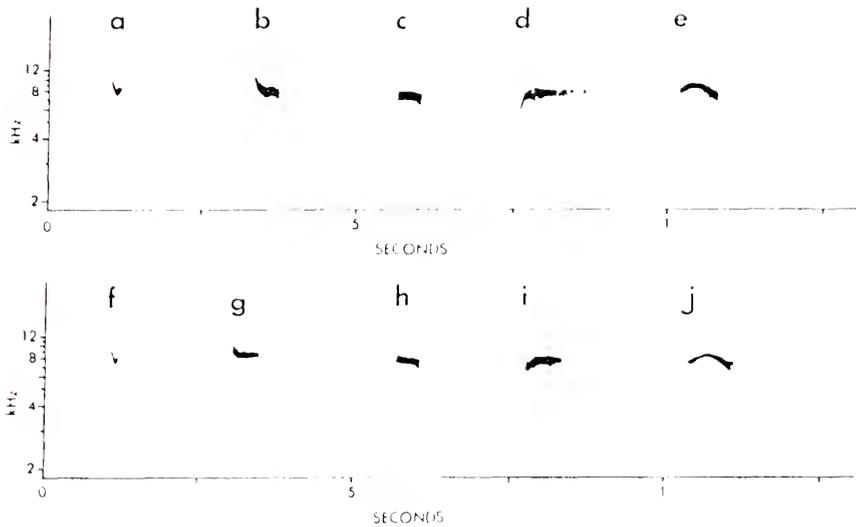


Figure 1. a-e show calls of *P. carolinensis* subsystem I. a shows type A'; b, type A; c, type B; d, type C; e, type D. f-j show calls of *P. bicolor* subsystem I. f shows type A'; g, type A; h, type B; i, type C; j, type D.

other foraging, food manipulating, or preening movements. Those calls for which unambiguous contextual data were available indicated that type A calls were given during active foraging (23 out of 25 cases) whereas type B calls were given more frequently during food manipulation and periods of inactivity (10 out of 18 cases). This difference in usage between types A and B is statistically significant ( $\chi^2 = 11.88$ ;  $df = 1$ ,  $p < .001$ ). Those cases in which type B calls were given during active foraging tended to be later in the day when flock movement rates and individual foraging rates were more relaxed than earlier in the day.

Type C calls were most frequently given during active foraging (10 out of 18 cases) but much less conclusively so than type A calls. Calls of type D were always given during long flights and usually by the first of a group to fly. Calls that appeared to be intermediate between types C and D occurred, and those of type C were associated with a high likelihood of a long flight following their occurrence (.6).

During aggressive confrontations, an extremely shortened form of type A referred to as A' was frequently given. The contexts in which these calls were given constitute the highest level of excitement and activity rate that chickadees experienced. The shortness of A' calls and the prominence of the descending onset fits the pattern of type A and B in that these variables appeared to be correlated with activity rate.

### Chickadee Subsystem IIa

#### Structure

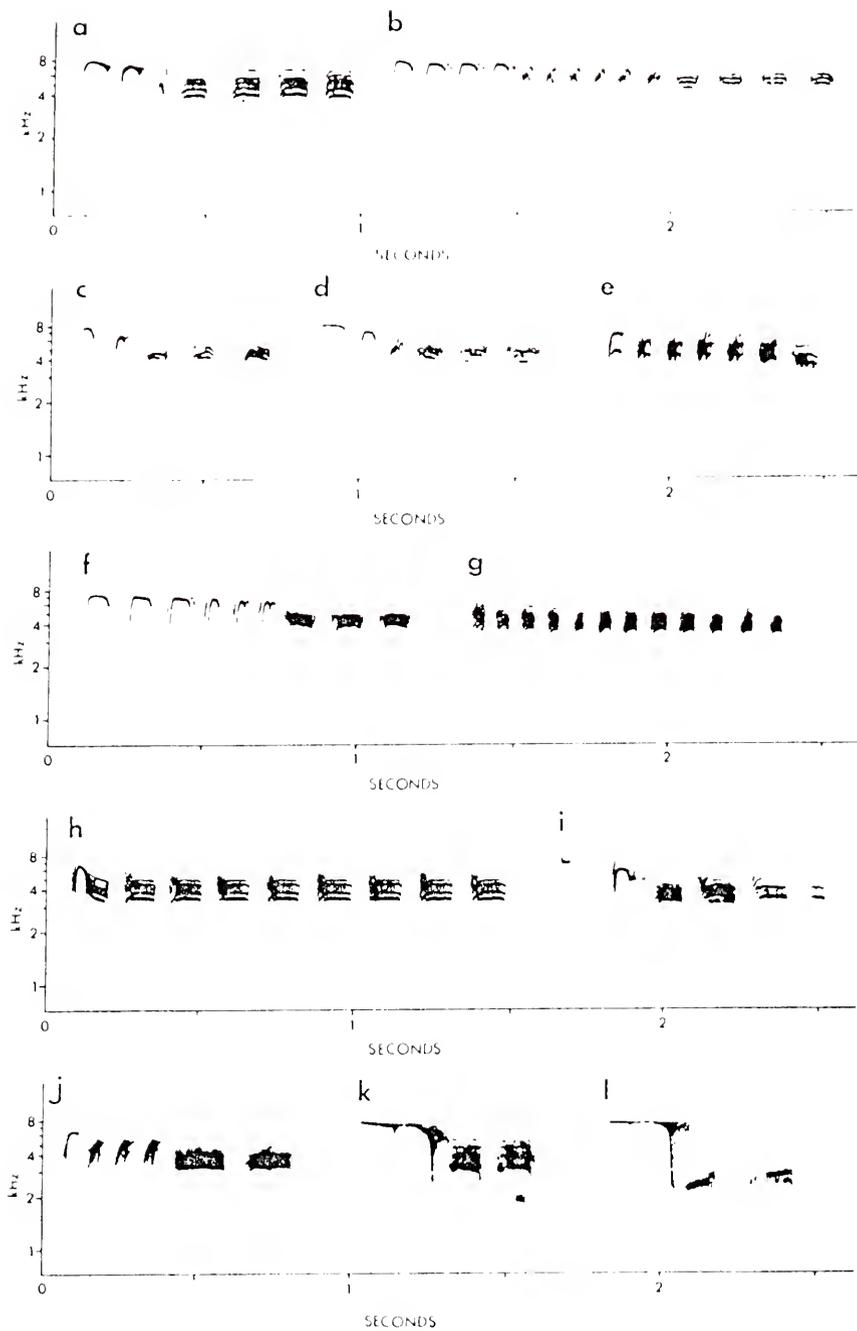
The calls of this subsystem are made up of two to several subunits of three basic types which differ primarily in the magnitude of emphasized

frequency and in the extent of harmonic content (Fig. 2). It is for the calls of this subsystem that the chickadee is named. The subunits of type A occurred in a graded series varying in duration, length of onset and cutoff arms, and maximum frequency. These variables were related in such a way that the high frequency extreme was the longest in duration and had no onset or cutoff arms. Those subunits at lower frequencies had correspondingly shorter durations and greater onset and cutoff arms. The subunits toward the low frequency extreme often carried sound energy at a second frequency associated with the onset arm but these subunits did not carry sound energy at more than two frequencies simultaneously. I recognize six forms that appear to represent modes in a graded series of type A subunits.

Subunits of type B also occurred in a graded series which varied in harmonic complexity. The increase in complexity was associated with an increase in duration. The emphasized frequency remained constant throughout the series. Those subunits at the simplest extreme of the series resembled the shortest, lowest frequency subunits of type A; those at the most complex extreme resembled the subunits of type C but still carried the peaked ending. Thus, the type B series represented a transition from type A to type C. I recognize three forms that appear to represent modes in a graded series of type B subunits.

Subunits of type C were relatively flat stacks (as seen in sonograms) of what appeared to be harmonics of a fundamental at approximately 450 Hz (cf. Greenewalt, 1968). These were the "dee" notes of the "chick-ka-dee" series. Those harmonics between 3 1/2 and 8 kHz were typically represented. The subunits varied in the flatness of these harmonics in a very irregular way and I was unable to recognize a pattern in the

Figure 2. a-k calls of *P. carolinensis* subsystem IIa. a, c, f, h, and i are series containing subunits of types A and C. h shows a call with fused type A and C subunits. i shows a call introduced by a call from subsystem I type A. b, d, e, and j show series containing subunits of types A, B, and C. g shows a series of short type C subunits. This series was given during an interflock border confrontation and is also typical of the calls given during mobbing. l shows a call from titmouse subsystem IIa given in exchange with a chickadee whose call is shown in k. The type A subunits given by the chickadee in k are unlike those given in exchange with other chickadees but are very similar to those of the titmouse. The type C subunits of the titmouse call in l are unusually short and are comparable in length to those of the chickadee in k.



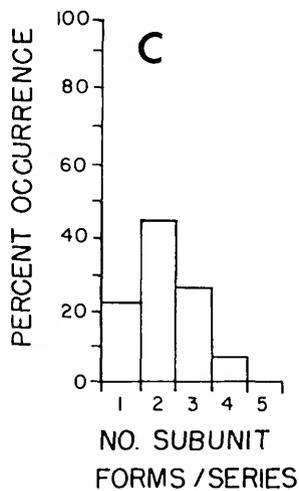
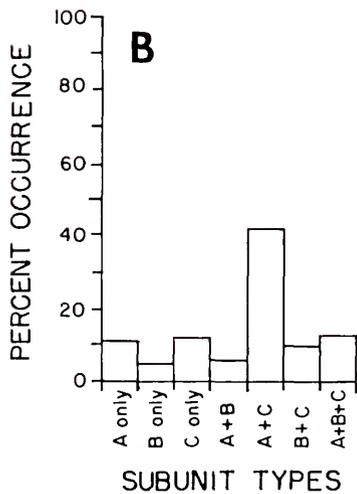
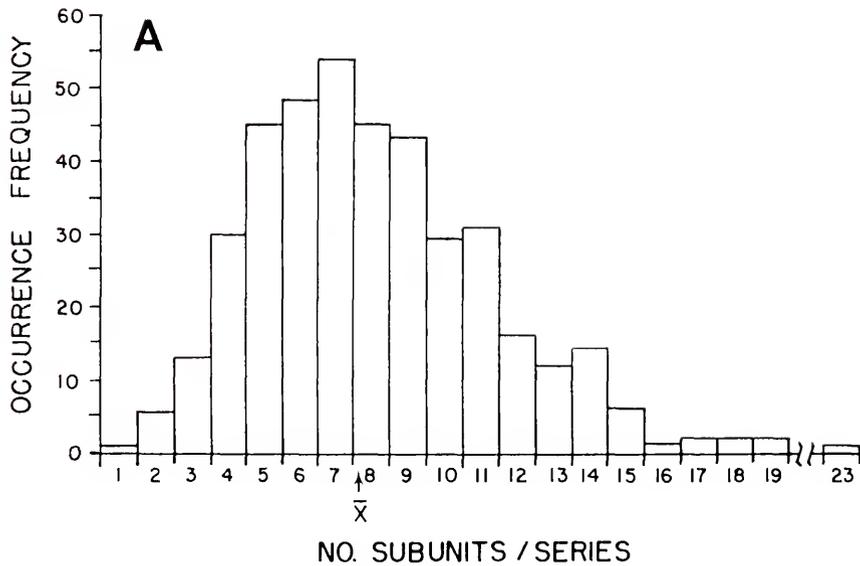
variability. The subunits also varied in duration and I have recognized 3 forms based on this variable.

### Usage

Any of the subunit forms could occur alone and nearly all were combined with other forms in a remarkable variety of combinations, but only according to certain rigidly upheld rules of syntax. The highest frequency form of type A (0 or "high zee" alarm call) if in combination occurred only with the next highest form (A1). Either of the two forms could occur first, but frequency transitions within a series were progressive and no more than one frequency reversal within a series was ever recorded. Any of the other forms could co-occur in the same series. Type A forms always preceded forms of types B and C; forms of type B always preceded those of C. Within type A, the forms with higher frequency and longer duration always preceded those with lower frequency and shorter duration. Within type B, forms with simplest harmonic content preceded the more complex forms. The subunits of type C could occur in any order. They could grade into each other or occur in distinct runs of a single form but no more than one trend reversal or more than three runs of a single form per series were recorded. A series could begin with any subunit form but it was followed only by those forms that did not violate the above rules, *i.e.* by those forms at equal or lower frequency emphasis and equal or greater harmonic complexity.

A sample of 402 series for which sonograms were made averaged 8.02 subunits/series (Fig. 3A) (SD = 3.3, mode = 7, range = 1.23). Of the 295 of these 402 that contained type A subunits, the mean number

- Figure 3. A. Occurrence frequency of *P. carolinensis* sub-system IIa series containing different numbers of subunits per series  $\bar{x} = 8.02$ ,  $N = 402$ .
- B. Percentage occurrence of *P. carolinensis* IIa series with different type compositions.  $N = 402$ .
- C. Percentage occurrence of *P. carolinensis* IIa series with different numbers of subunit forms per series.  $N = 402$ .



of type A subunits/series = 3.2 (SD = 2.5, mode = 1, range = 1-11). Of the 131 containing type B subunits, the mean number of subunits/series = 3.6 (SD = 2.4, no strong mode, range = 1-12). Of the 296 containing type C subunits, the mean number of subunits/series = 6 (SD = 3.3, range = 1-16, no strong mode). An average of 2.2 subunit forms was represented in any call (Fig. 3C) (SD = .86, range = 1-5). Twenty series contained fused subunits of types A and C (Fig. 2h). Two other series contained fused subunits of types B and C. Only one fused pair occurred per series. The distribution of subunit type combinations is shown in Fig. 3B. From this figure, it is clear that the predominant combination is of subunits from types A and C (42.5%). The distribution of the individual subunit forms is shown in Fig. 4.

### Contexts

The calls of subsystem 11a are collectively the most conspicuous aspect of the chickadees' behavior, and it is quite appropriate that the bird should be named after this call. As with the calls of subsystem 1, those of 11a were given during virtually all kinds of behavior. Nevertheless, two general features appeared to be consistently associated with their occurrence. One was an exchange of varying versions by two or more birds over distances from less than 5 to 40 or more meters, and the other was a change in the movement pattern of one caller or as many as all birds in a flock. The calls were given when accelerations (velocity and/or direction changes) or cohesion changes were made by a flock, especially when a flock left an area, arrived at another, or was obstructed in its movement by a vegetational discontinuity. The calls were given when an individual approached and joined other birds, or when an individual left others. When making these movements, the calls were given on landing, or shortly after landing on a flight. The calls were

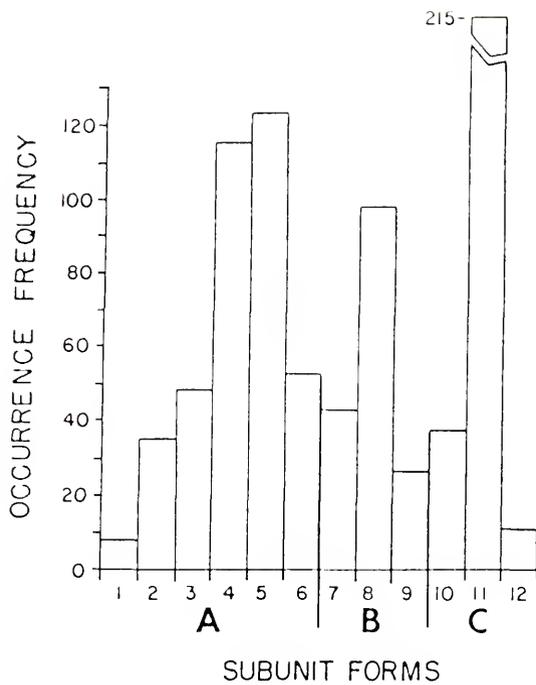


Figure 4. Occurrence frequency of *P. carolinensis* Ila subunit forms in a sample of 402 series.

also given by birds that had been prevented from carrying out an intended activity such as visiting a drinking hole, pine cone, or feeder by the presence there of a dominant bird.

Calls of this subsystem were given during fights and these tended to be series that predominated in one type. Series of type A only were given in the initial stages of fights and whenever a potentially dangerous situation was at hand. Series of type B only were given in later stages of fights and as the birds drew apart and left. Similarly, type A subunits were prominent in combination series when birds arrived at an area or a group of other birds, and type B subunits were prominent in combinations when the birds left an area or group. Series consisting entirely of type C subunits occurred regularly in fights. Series of short type C subunits were given during mobbing as well as during fights.

11a0 and 11aA1 to 11a0 combination series were also heard during fights, but most frequently these calls were given when the birds were exposed to a threat of predation.

#### Chickadee Subsystem 11b

##### Structure, Usage, and Contexts

This call was made up of five to eight very gradually descending subunits bearing a strong resemblance to 11a-C subunits (Fig. 5A). The calls were given by females from very early in the breeding season until the young had hatched. They were given by young chickadees from shortly before fledging until after dispersal from their natal flocks. When given by females they were given at very low amplitude at close distances from their mates who usually responded by feeding them. The calls were

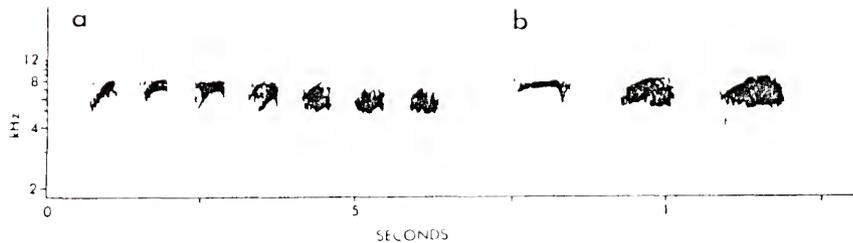


Figure 5. A. Call from *P. carolinensis* subsystem IIb. This call was given by an adult female.

B. Call from *P. bicolor* subsystem IIb. This call was given by a fledgling.

also given prior to copulation. When given by juveniles in their first few weeks following fledging, the calls were much louder than when given by adult females, and became louder on the approach of a parent bird. After the period of fledgling dispersal began, the juveniles continued to give the calls, but they were no longer responded to with feeding. The calls were usually associated with wing quivering when given by females as well as juveniles.

### Chickadee Subsystem IIc

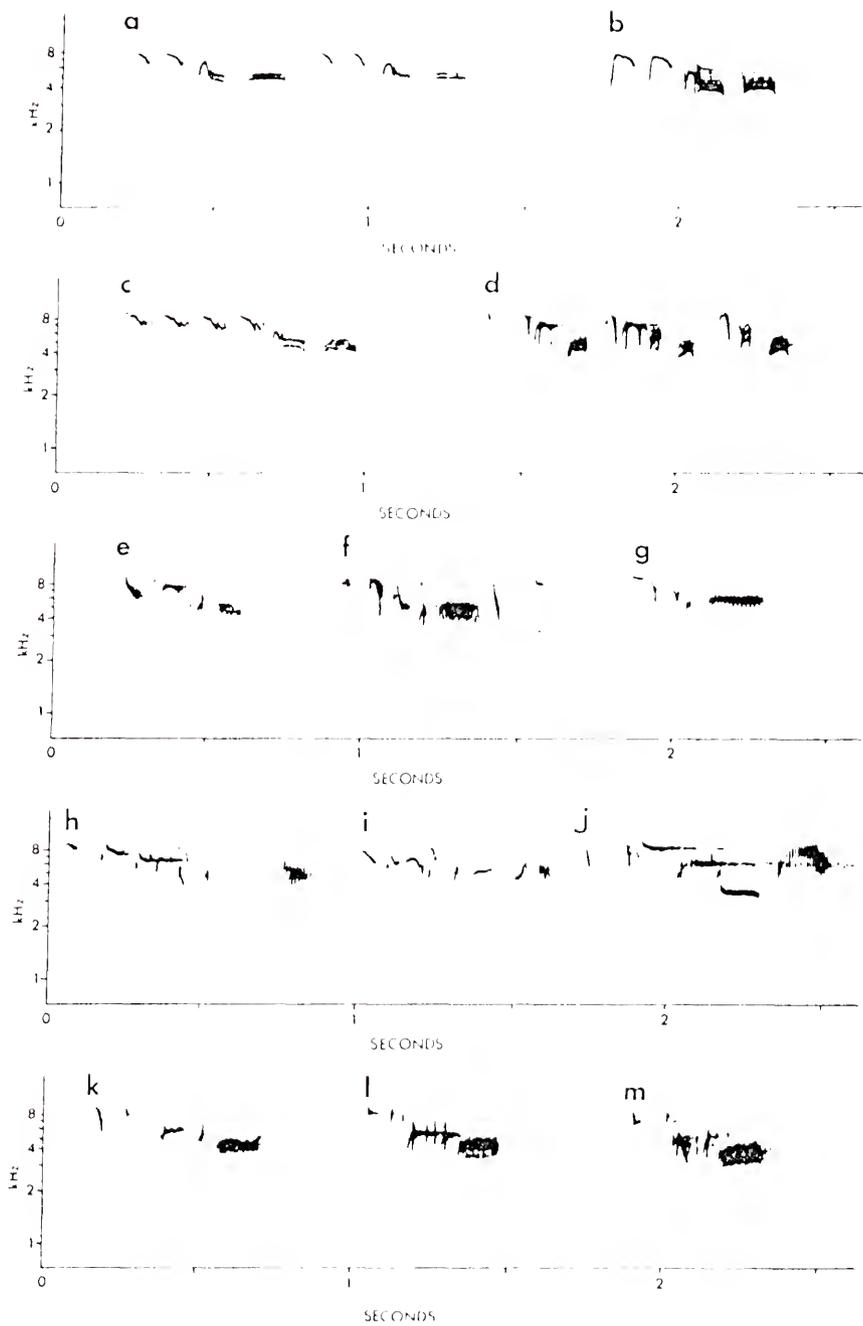
#### Structure

The calls of this subsystem were made up of subunits from subsystem IIa and were arranged in accordance with the same syntax rules with one major exception: the series could be repeated in rapid succession. These calls were also set apart by a high degree of stereotypy. Two basic types of call occurred (Fig. 6). Type 1 consisted of a four-subunit series and two variations that differed from this form in lacking one of the two internal subunits. Type 2 occurred in only one form but it was occasionally extended beyond the basic five-subunit form to include a variable number of introductory or terminal subunits. Only the five-subunit form was repeated in continuous series. The extended, non-repetitive form frequently preceded the repetitive form or was mixed with it.

#### Usage and Contexts

The calls of type 1 occurred in series with one to six units per series. The four-subunit form did not occur more than three times per series. The three forms of type 1 were occasionally mixed in the same

Figure 6. a, b, and c show calls from *P. carolinensis* subsystem IIc type 2. c shows an example of the extended form of this call. d shows a series of IIc type 1 subunit phrases. All three phrase forms are represented in this unusual call. e-m show T R calls of *P. carolinensis* subsystem IIIa. e shows T1aR; f, T1bR; g, T8R; h, T4aR; i, T4cR; j, T6R; k and l, T3aR; m, T3bR.



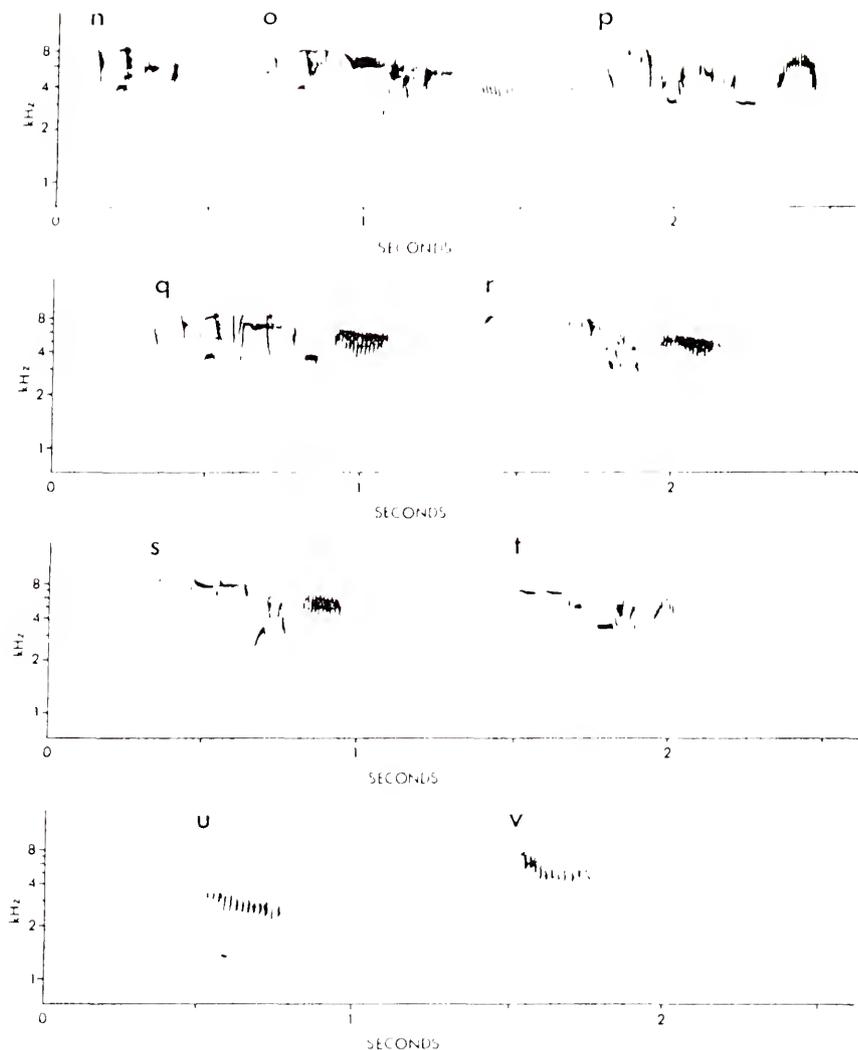


Figure 6. continued. n-t show calls of *P. carolinensis* IIIa containing the X phrase. n shows XT1bR; o, XT7R; p, XT1cR; q, XT4bR; r, XR; s, T2aXR; t, T2bXR. u shows an isolated *P. carolinensis* rasp. v shows a rasp from a *P. bicolor* juvenile.

series. Type 2 occurred at two per series in the majority (70%) of the cases.

Type 1 calls occurred at the end of the interflock or interpair fights as the birds began to leave the area. They were usually exchanged by two or more birds and the calls continued to be given as the birds left. They were usually mixed with series from subsystem IIa A, IIa B, and calls from subsystem III. The calls were given usually during fast retreat, usually under pursuit.

Type 2 calls were also given toward the ends of fights but were not necessarily followed by exchanges or immediate retreat. They were usually well mixed with the variable calls of IIa and especially series of IIa B.

### Chickadee Subsystem IIIa

#### Structure

Calls of this subsystem were stereotyped combinations of two basic phrase types that appeared with or without one of several rasp forms (Fig. 6). These calls had a distinctive fast, liquid, sputtery quality. Fifteen stereotyped combinations were distinguished.

Phrase type X occurred in one basic form only. It was preceded by a prefix of variable length when it preceded a phrase of the other type, type T. It was followed by a suffix when preceded by a T phrase. X very rarely occurred without T, in which case it carried both prefix and suffix. All four recordings of X without T were made in Gainesville.

I distinguish 12 variations of the type T phrase. Of these, six never occurred in combination with X. Of the remaining six forms that

did occur with X, three never occurred without X, and three could occur with or without X. Of the six T forms that occurred with X, four were always preceded by X; the other two forms were always followed by X.

Eleven rasp forms are distinguished (this includes two forms used with calls of IIIb, below). Seven forms occurred with one call form only. Of the remaining four rasp forms, one occurred in six different calls, in each case following a T phrase that appeared to be closely related to T1. One occurred in three combinations that all contained X. Two other rasp forms occurred with two different T phrases, and in each case the two forms were closely related. Thus where the same rasp form occurred in different combinations, the combinations' T phrases bore some structural similarity. Certain T phrases (T1a and T4a) and certain XT combinations (XT1b, XT1c, XT4b) could occasionally occur without the terminal rasp. Very rarely, the rasp occurred alone.

I was able to distinguish the three major categories of these calls (TR, TXR, and XTR) in the field. The specific forms within the major categories, however, could be safely identified only after sonographic analysis.

#### Usage and Contexts

Calls of this subsystem occurred during interflock and inter-individual fights and during territorial boundary advertisement and exchange. In 89 observed fights, at least one call from IIIa was given in each case. A mean of 3.6 calls of all kinds were given in these fights (SD = 1.54, range 1-9). Seventy-one percent of these fights contained only one representation from IIIa, 23% contained 2, and 6% contained 3. Most fights contained calls from only one major category

(TR, TXR, XTR) and this category was usually TR. Combinations of these categories were relatively unusual. Nevertheless, calls of one category were more likely to be mixed with calls of another category than with calls of their own (10% of fights had two different calls from the same category, 19% had calls from two or three categories).

Of 35 pairwise combinations of specific call forms, 23 (66%) occurred only once and another 10 (29%) occurred only twice. The remaining two combinations occurred three and five times, respectively.

The calls occurred during all phases of fights and tended to be most prominent in the initial stages. The likelihood of attack following calls of any major category (TR, XTR, and TXR) was not significantly different from any of the others and ranged from .25-.275. When T and XT were considered separately, however, XT did not prove to be different from the others, but T alone showed a .625 likelihood of being followed by attack. No significant difference was found in the occurrence of these categories in interflock vs. interpair fights ( $\chi^2$ ).

Calls containing X were prominent during territorial border patrolling and/or displacement of one bird by another at a clumped resource (*i.e.*, drinking hole, pine cone, feeder, etc.).

I could determine no consistent pattern from the contextual data on any specific call from subsystem IIIa. Due to the tendency of the chickadees to fight in dense vegetation, I was usually unable to determine the identity of the callers, and it may be that some of the variability in these calls can be explained by individual specificity. However, most of the calls occurred without variation at widely separated localities and many over distances of 20 or more km. I therefore consider it unlikely that individual variation can account for very much of the observed variation in the calls of this subsystem.

## Chickadee Subsystem IIIb

### Structure

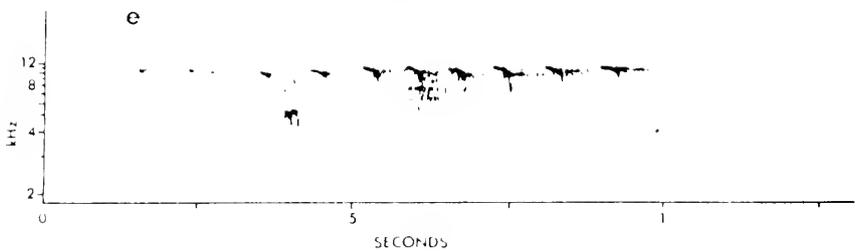
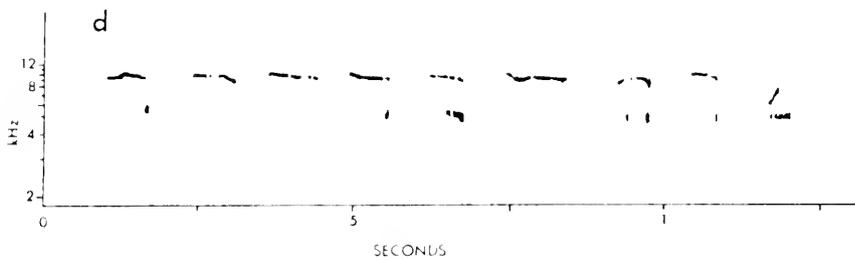
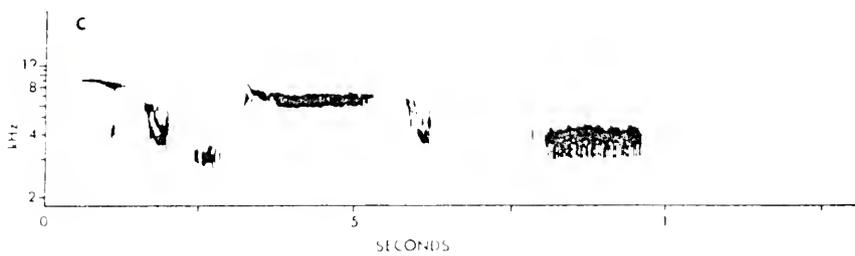
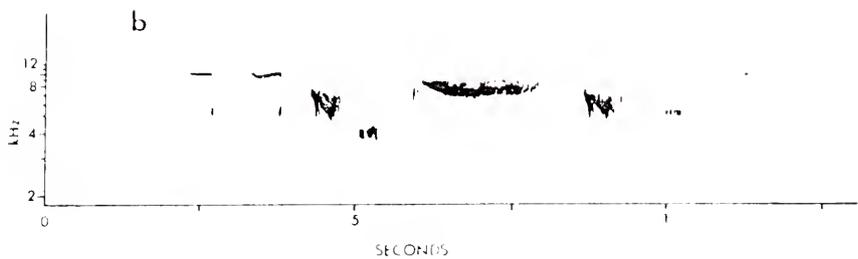
This subsystem contained two calls that were both structurally and functionally distinct from the calls of IIIa although clearly related in basic features of structure (Fig. 7). Type IIIb-1 was unique in subsystem III in that it appeared to contain two T phrases preceding the rasp. The two T phrases were structurally different from each other but both appeared to be related to T4. Type IIIb-2 appeared to be made up of the final two notes of T4 followed by a unique, high frequency rasp. The rasp was often followed immediately by the T4 segment. It was occasionally followed by T3aR, and occasionally by only the rasp of T3aR. The call was always preceded and occasionally followed by long series of high frequency (8-10 kHz) liquid, chattery notes (HSC). Long series of these notes, interspersed with IIIb-2 could continue for several seconds. These high frequency notes were extremely irregular in form and often carried sound energy at two harmonically unrelated frequencies, giving them a distinctive, squeaky quality.

### Usage and Contexts

Type IIIb-1 occurred during interflock fights and was always followed by a departure of one of the flocks. In many cases, it was given by onlookers rather than those directly involved in fighting.

Type IIIb-2 was always given at very close range to another chickadee of the same flock or to a mate (by female). It was never followed by attack by either bird. It occasionally occurred at the beginning of interflock or interpair fights. On three occasions, a chickadee approached me very closely and gave this call.

Figure 7. Calls from *P. carolinensis* subsystem IIIb. a shows type 1; b and c, type 2. c shows both rasp forms associated with this call. Both b and c show HSC introductory notes. d and e show long series of these HSC notes. e shows an unusual series of very irregular notes in series with the more typical HSC notes. These may be homologous with the "broken see" series recorded by Smith (1972) in Pennsylvania.



### Chickadee Subsystem IV

#### Structure

Calls of subsystem IV were made up of two and occasionally three repetitions of one of two basic phrases (Fig. 8). The phrases could be slightly modified within one call. They could be transcribed as "feebee-feebee."

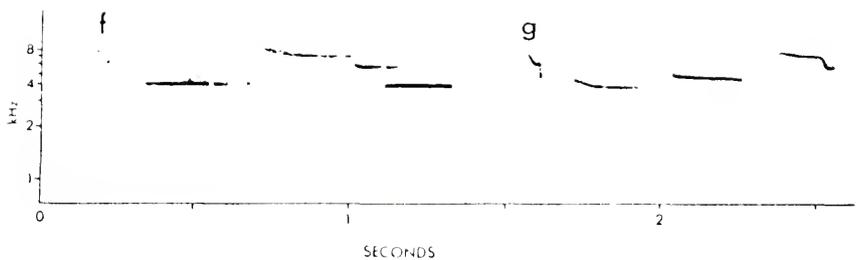
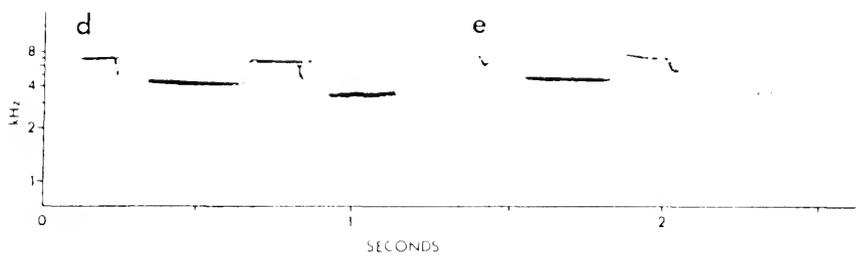
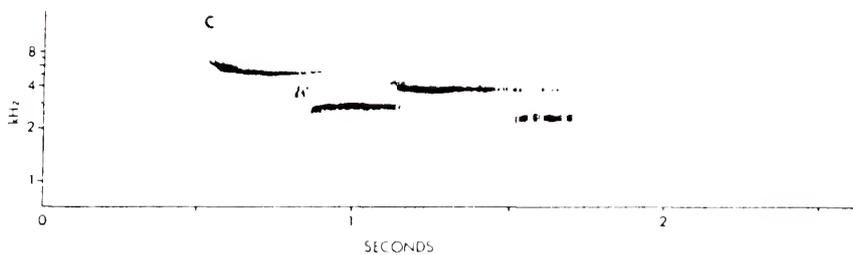
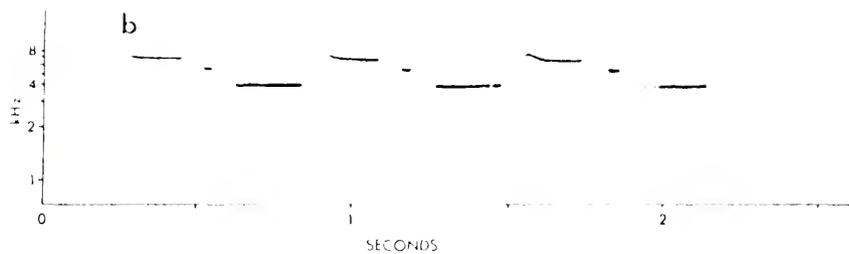
Type 1 consisted of two and rarely three repetitions of a phrase with two long notes and a short note at an intermediate frequency. The phrase could be repeated without variation or with the first note of the second phrase at the frequency of the short intermediate note. The terminal note was frequently deleted. This variation did not occur in a three-phrase form.

Type 2 consisted of a two note phrase whose first note had a long descending cutoff arm. This phrase was repeated at a lower frequency. A second variation of this call occurred with the first note of the phrase reduced to only its descending cutoff arm. The phrase was repeated a second time at a lower frequency, and the phrase could be repeated a third time at still a lower frequency than the second.

#### Usage and Contexts

Calls of this subsystem were most frequently given during patrolling of territory boundaries by males. The calls were given at regular "song posts" in series of up to more than 60 calls that could last many minutes. Three territorial males whose repertoires were thoroughly surveyed expressed both types and both two-phrase variations of types 1 and 2. The singing bird typically sang one type many times, switched

Figure 8. Calls of *P. carolinensis* subsystem IV.  
a, b, and c are type 1 calls. d and e show calls  
of type 2. f and g show irregular versions with  
rearranged subunits.



to another type and repeated it many times. It then switched back to the first type, or moved on to another "song post." If answered, the chickadee exchanged for only a few times before approaching the source of the answer with a variable medley of calls from all three other major subsystems. Calls of subsystem IIIa were also included in territory border calling series in the absence of exchange. These usually contained the X phrase.

The calls were also given from the nest and at any other place in the chickadees' territory while the bird foraged. The calls from the nest were usually of type 2, and were often incomplete and occasionally mixed with call subunits from subsystem IIa A. The calls occasionally contained rearranged phrases and occasionally were totally garbled and unrecognizable. The calls were also given by chickadees that were presumed to be wandering, landless birds that were invading new territory. The calls were also given during the non-breeding season, especially following interflock fights.

#### Titmouse Subsystem I

##### Structure

As with chickadee subsystem I, titmouse subsystem I consisted of four basic types (Fig. 1). Calls of type A were variable in the length of the descending onset and appear to grade into the calls of type B. The portion of the call that was flat or nearly so varied in length in type A from 4 to 38 msec ( $\bar{x}$  = 20.4, SD = 7.9 msec, N = 30), in type B from 17 to 58 msec ( $\bar{x}$  = 37.1 msec, SD = 16.3 msec, N = 10), and in type C from 12.5 to 25 msec ( $\bar{x}$  = 15.9 msec, SD = 5.5 msec, N = 6). Calls of all

four types were occasionally followed by an "echo" at much lower amplitude and at a latency of approximately 214-218 msec.

### Usage and Contexts

The titmice tended to give type A calls while actively foraging (35 of 43 cases) and type B when foraging more slowly, while manipulating food or when otherwise inactive (11 of 20 cases). The distinction is less conclusive for type B, but the difference in usage between types A and B is statistically significant ( $\chi^2 = 9.06$ ,  $p < .01$ ). A very short version of type A, called type A', was given during fights. The cases in which type B calls were given during active foraging tended to occur later in the day or when flock movement was slower. Type C was given rarely by titmice. In three of the six cases, it was given just before flying. In the remaining three cases, the birds were foraging actively. Type D was given during long flights by the first of a group to cross an open space. It was occasionally given by successive birds but not by the last. On one occasion, the call was chorused by four perched and inactive titmice just before they left the area in long flights.

### Titmouse Subsystem IIa

#### Structure

Calls of this subsystem were made up of subunits from two basic types. Those of the first, type A, were clear, whistle-like tones with sound energy at only one frequency at a time. Those of the second, type C, were broad frequency-spectrum harmonic series with a harsh scolding quality (Fig. 9). These calls sounded somewhat like "seejert," "seejower," etc.

Figure 9. Calls of *P. bicolor* subsystem IIa. a shows A1-C1; b, A3-C2; c, A4-C2; d, fused A4-C1 with low frequency emphasis; e, A5-C1; f, A6-C2.

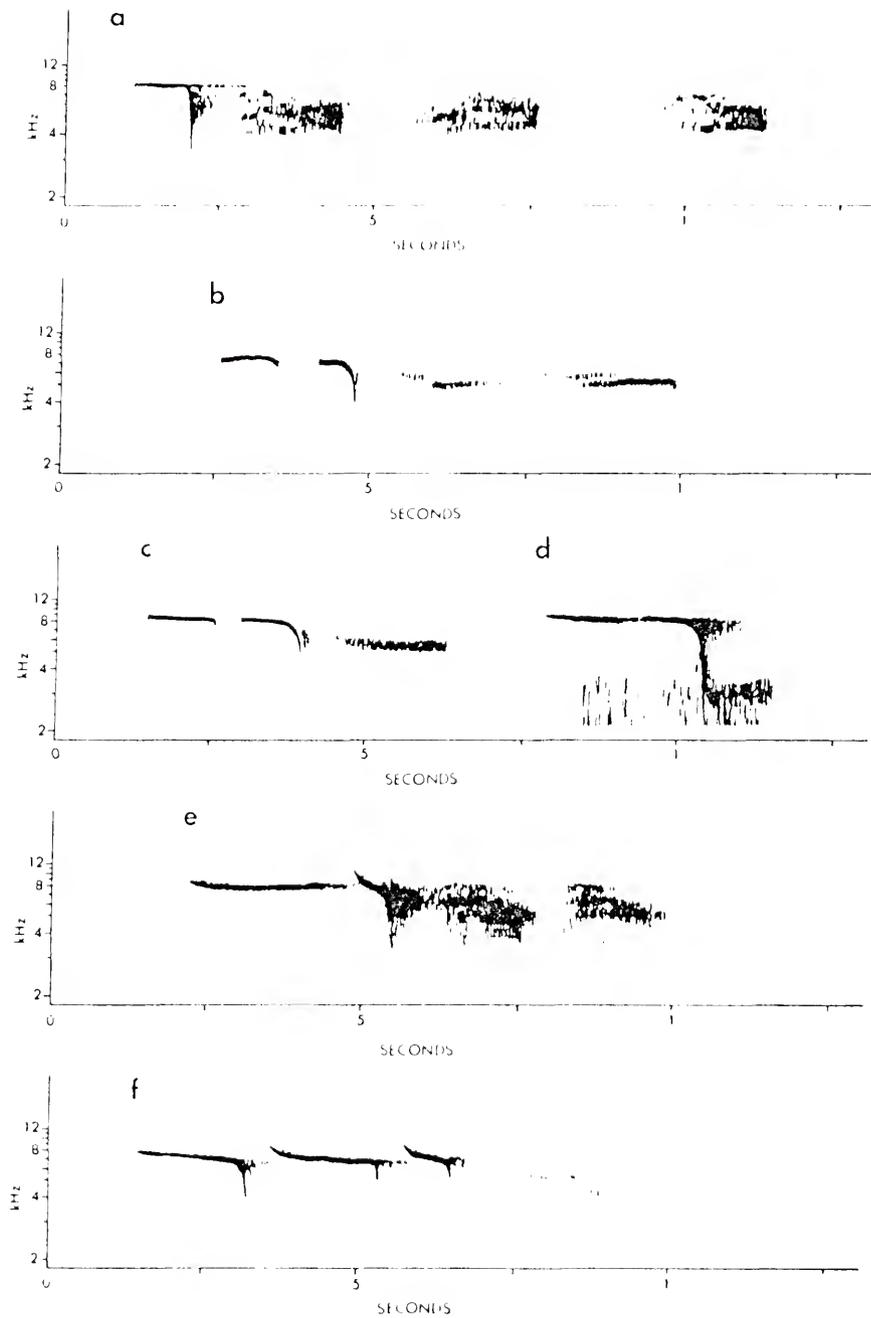
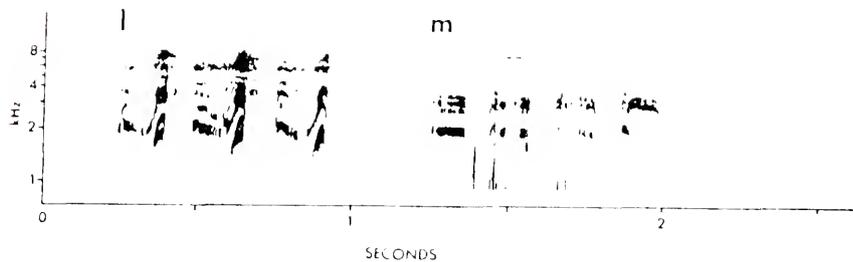
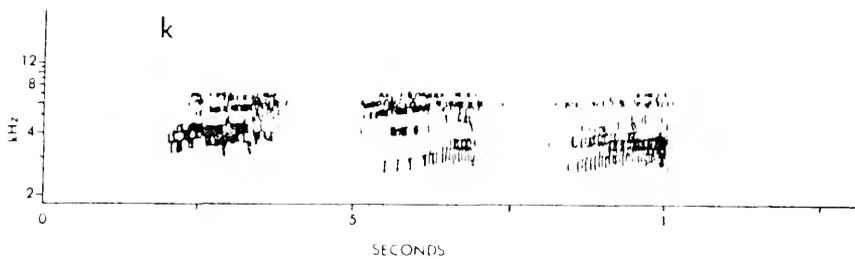
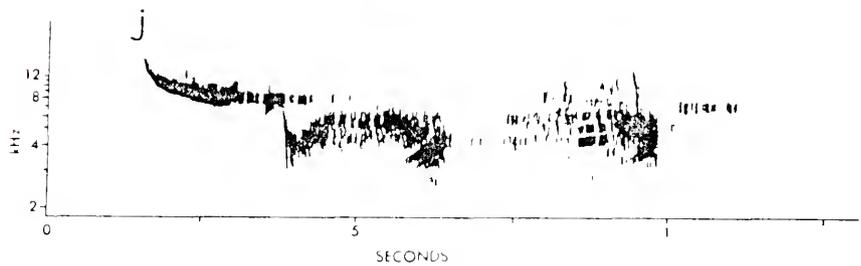
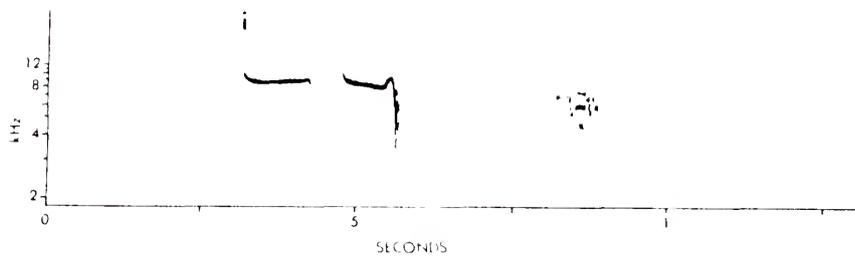
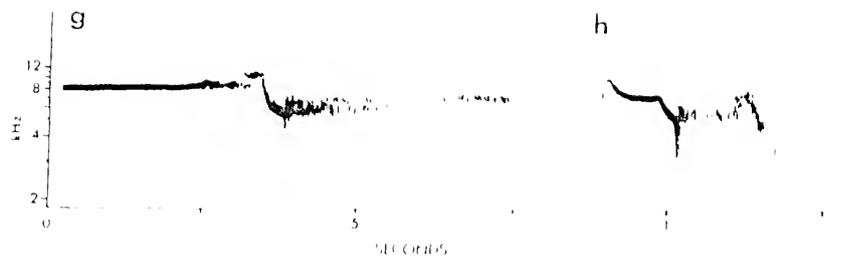


Figure 9. continued. g shows A7-C2; h, A8-C3; i, A9-C3;  
j, A9-C3; k, C3; l, C4; m, C5.



Type A subunits were variable in frequency and ranged from seven to near 10 kHz. Those over 9 kHz were constant in frequency (*i.e.*, flat) and were rarely followed by notes of type C. Those between eight and nine kHz could be constant in frequency or carried a slightly descending onset. They also carried a cutoff arm of variable length. In those subunits that were followed by others of type A, the cutoff arm, if present, was very short. In those that were followed by a subunit from type C, the cutoff arm was always present and covered a frequency range of five + kHz. The cutoff arm could be sharp (A1), broadly rounded (A3-6), or more highly modified (A7-9).

Type C subunits were harmonic series of a fundamental at about 500 Hz. C1 was the most commonly occurring form. It covered a frequency range from 3 to 9 kHz. It could vary in the emphasized frequencies: a high frequency emphasis ( $> 4 \frac{1}{2}$  kHz) and a low frequency emphasis ( $< 4 \frac{1}{2}$  kHz) form occurred. C2 carried only two harmonics with a faint third occasionally present. The harmonics present in this form were between 4 and 6 kHz. Other forms could show frequency inflection patterns: C3 rose evenly in frequency, C4 had a strongly peaked ending, C5 descended in frequency.

Subunits of both types could occur alone but combinations of the two types were more frequently expressed. Whereas the simplest forms of type A, A1 through A6, were most likely to occur alone, it was the more complex forms of type C, C3 through C5, that were most frequently given without introduction from type A. When subunits from the two types were combined, the transition was always from type A to type C. In a sample of 268 calls, the overall number of subunits/call averaged

3.9 (SD = 1.77, range = 1-14, mode = 3 [36%]) (Fig. 10). Type A subunits, when present, averaged two subunits/call (SD = .58, range = 1-4). Type C subunits, when present, averaged 2.4 subunits/call (mode = 1 [46%], range = 1-14). The most frequently occurring combination was two subunits of type A and one of type C. The subunit transition involved was usually A3 to C1. An Introductory subunit of type A was occasionally fused to the first subunit of type C (Fig. 9d). These combinations involved A3 and a C1 form with low frequency emphasis.

#### Usage and Contexts

Calls of this subsystem were extremely common and were the most conspicuous aspect of the titmouse's vocal communication system. The calls were given in a great variety of circumstances, but, in general, they appeared to be correlated with changes in flock movement patterns and with essentially hostile encounters (fights, mobbings, etc.).

A1 and A2 with or without C3 accompanied major changes in flock movement patterns such as when a flock left an area or arrived at a new one. The calls were given from a perch or on landing from a flight, especially when others were following. The calls were given when the previous path of movement was obstructed by vegetational discontinuities or by the presence of danger. In the latter case, high frequency type A calls (9 to 10+ kHz) were given. When this was caused by a human observer, A3-C1 calls were mixed with the high frequency calls. When the flock approached a possible border confrontation with another flock, A1 and A5 through A9 in association with C1 and C2 were given. C3 through C5 also occurred in this context but usually without introduction. C3 was the most common form in these encounters and, when introduced, it

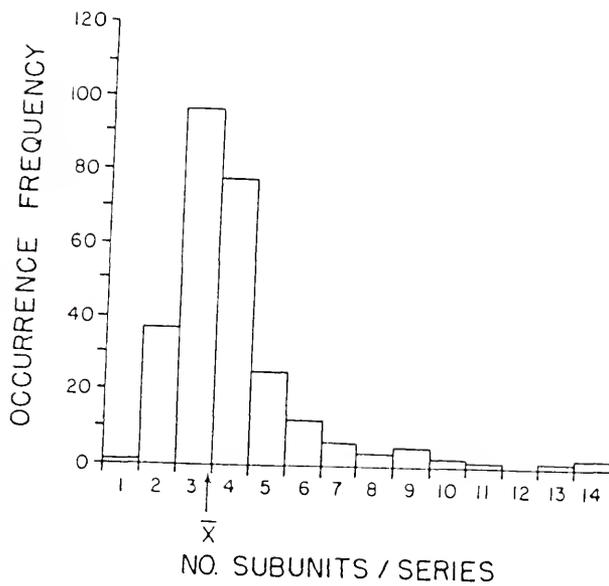


Figure 10. Occurrence frequency of *P. bicolor* 11a series with different numbers of subunits per series.  $\bar{x} = 3.9$ ;  $N = 268$ .

was usually by A1. During mobbing, C3 was the predominant call and occurred in series of 7-11 shortened subunits. C4 occurred at flock borders when no opponent was apparent and also following border fights after the opponent had withdrawn. C5 was a rare call that occurred following border exchanges that did not escalate to actual combat. The call was occasionally chorused by several of the birds.

A5 and A6 were frequently used in interflock and interpair border exchanges. During fights, they were given by onlookers. A7 through A9 were given during and following actual combat. A1 was also given during close confrontation, and the vertical portion was occasionally given alone during intense fighting.

The high frequency forms of type 1 (9 to 10+ kHz) were given during close chases, probably by the fleeing bird. The most frequent context of these forms, however, was during alarm responses, especially when an accipiter appeared. The very high frequency forms (10+ kHz) were then repeated in long series as all birds stopped activity.

#### Titmouse Subsystem IIb

##### Structure, Usage, and Contexts

This call consisted of one descending harmonically simple subunit followed by one or two ascending harmonically rich subunits (Fig. 5b). The introductory subunit had one or two harmonics, one below and one above the predominant frequency. The terminal subunits were much shorter. The two variations (two- and three-subunit series) were alternated irregularly. They were given by females from early in the breeding season until after the eggs had hatched, and by young titmice from shortly before fledging to the period of dispersal. The calls were

accompanied by wing quivering and responded to by mates or parents with feeding. When given by the female, it was at a low amplitude and close to her mate. When given by the juveniles, it was much louder and became still more so on the approach of a parent. When being fed, the juveniles gave many more of the terminal subunits, which were also extended in duration. Parent titmice gradually stopped responding with feeding after four weeks from fledging, at which time juveniles were beginning to disperse.

### Titmouse Subsystem III

#### Structure

This subsystem was made up of six basic call forms (Fig. 11), all given at high frequencies (7 1/2 to 9 kHz). All forms had a strong dip in frequency, and all except III-1 had a sharp vertical component at the onset. This latter feature gave the calls a distinctive quality. These calls could be transcribed as "kwee" or "kchee." Several distinctive variations of III-6 occurred in isolated cases and could have been individual variations.

#### Usage and Contexts

The calls all occurred during fights and hostile border exchanges at close range. They were given following exchanges of other calls from subsystem IIa as the birds prepared for attack, and during attack itself; shortly thereafter, the calls were given by attacking and victorious birds. The calls could occur in series of one to four. More than one form often occurred in the same bout of calling. Forms

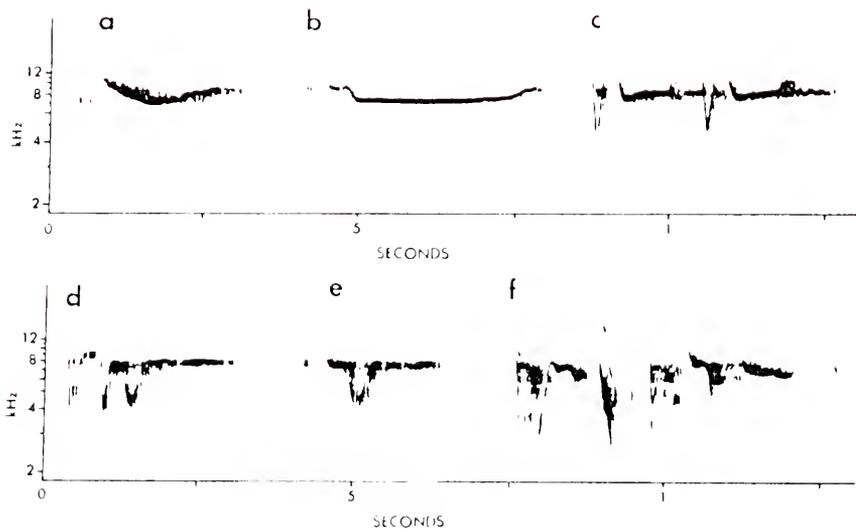


Figure 11. Calls of *P. bicolor* subsystem III. a shows III-1; b, III-2; c, III-4; d, III-6; e, III-5; (d and e were given by the same bird in the relationship shown) f, III-8.

III-4, 5, 6, and 8 were followed immediately by short series of IVb-1 or 6 in 68% of their (calls of subsystem III) occurrence. The IVb calls were always given at a much lower amplitude than the III call, but appeared to be given by the same bird. When combined with the IVb calls, they were given at greater distances from opponent birds than when uncombined, and were associated with much lower likelihood of being followed immediately by attack. The likelihood of attack following a call of III was .67. When the calls were combined with calls of IVb, the likelihood of immediate attack was .06. All forms of III were given in interflock, intraflock, and interpair fights.

The simpler forms of III, namely III-1, 2, 4, and 9 were occasionally followed by and combined with type C calls of IIa. This interchangeability suggests a probable derivation of III from IIa.

#### Titmouse Subsystem IVa

##### Structure

Calls of this subsystem were made up of repetitive series of phrases from three basic types (Fig. 12). All forms sounded somewhat like "peter" or "peto." The phrase types varied in duration, but overall series length for all types was a relatively constant .9 sec (SD = .19, N = 106). Thus phrase length correlated well with number of phrases/series (Fig. 13) ( $r^2 = .912$ ). I have subdivided these phrases into three types based on phrase length and number of phrases/series:

IVaS 1-3/series, 200-325 msec/phrase

IVaM 3-6/series, 100-200 msec/phrase

IVaF 5-10/series, 80-100 msec/phrase

Figure 12. Calls from *P. bicolor* subsystem IVa and IVb. a-h show calls from IVaS. a shows IVaS-1; b, IVaS-2; c, IVaS-3; d, e, and f show IVaS-5 as given by three different males, all of which had common territory borders. g shows IVaS-4; h, IVaS-8. i-l shows calls from IVaM. i shows IVaM-1; j, IVaM-4; k, IVaM-5; l, IVaM-7.

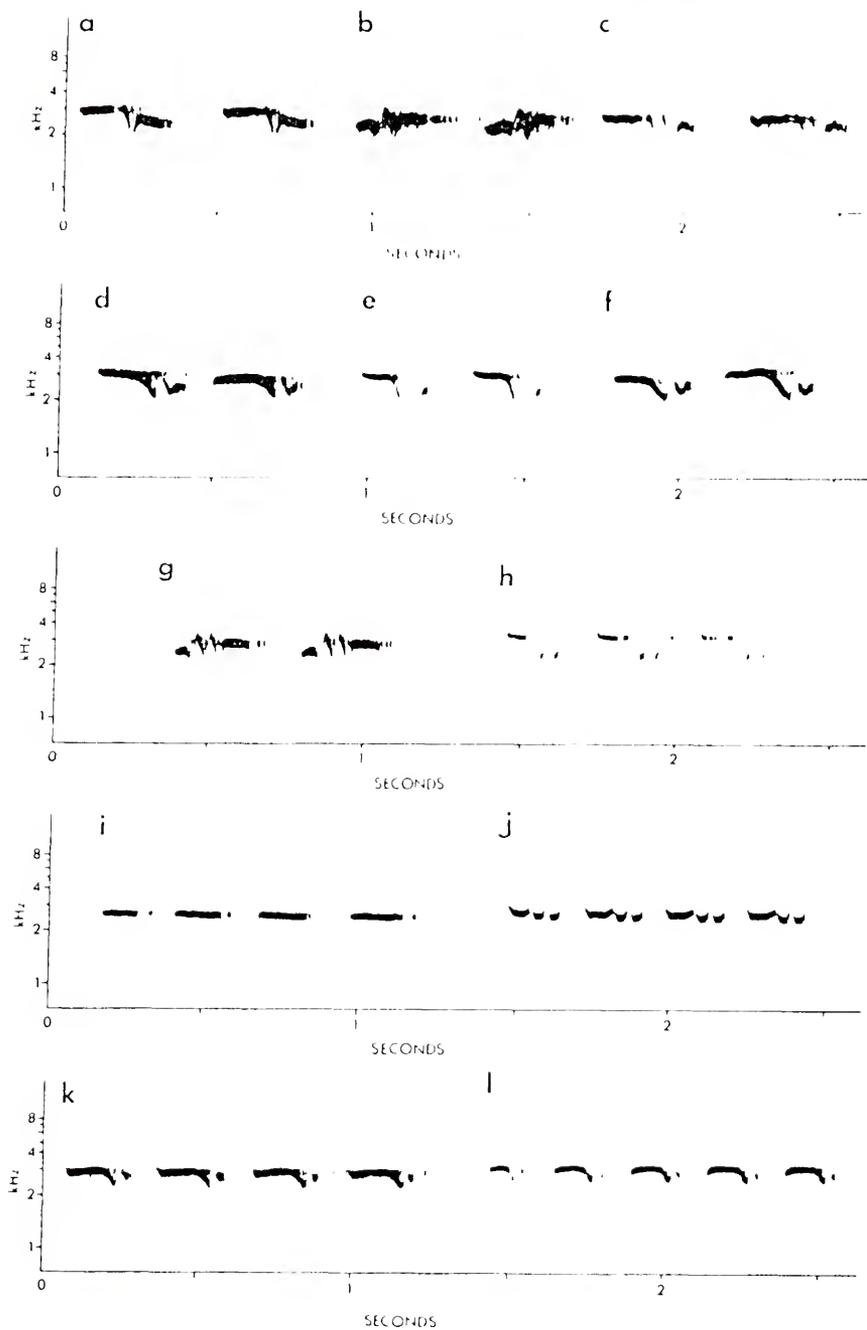
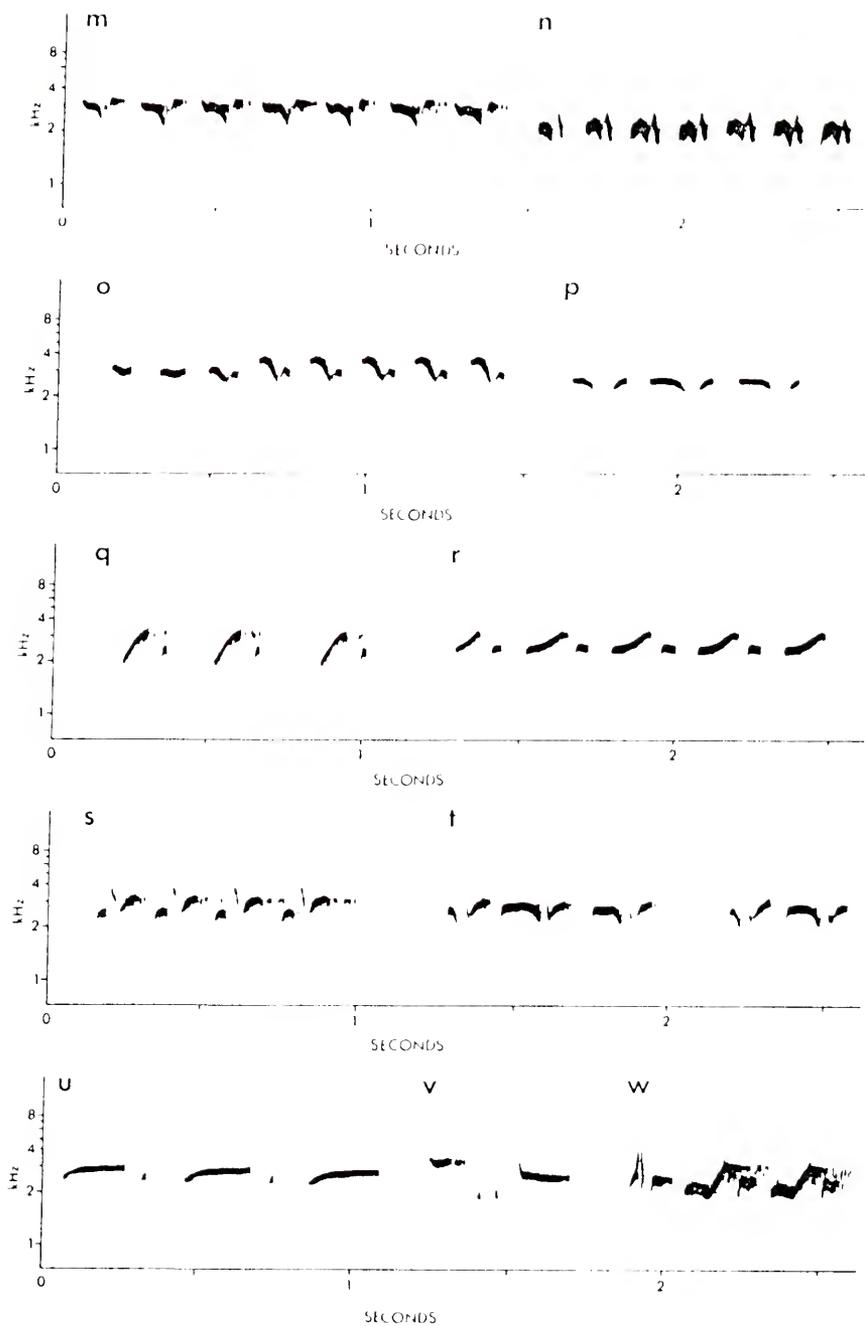


Figure 12. continued. m shows IVaM-6; n, IVaF.  
o shows a series of the female's version of  
IVa. r shows IVaM-8. p, q, and s-w show calls  
of IVb. p shows IVb-6; q, IVb-4; s, IVb-1 as  
given in the San Felasco population; t, IVb-1 as  
given in the Gainesville (home) population; u,  
IVb-3; v, IVb-2; w, IVb-5.



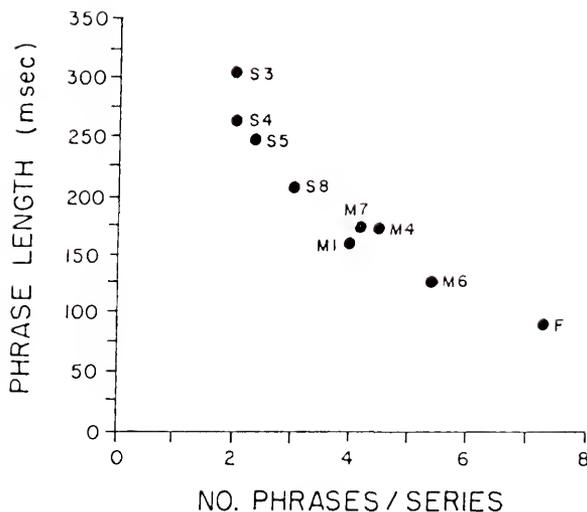


Figure 13. Phrase length of *P. bicolor* IVa calls as a function of number of phrases/series. Only the forms with a sample size greater than five and given by the four most thoroughly surveyed titmice of the San Felasco population were included in this graph. The correlation coefficient ( $r^2$ ) of a linear regression analysis of these points is .912.

The first phrase of a series was usually shorter than the others. This tendency was most pronounced in the IVaM calls. A very irregular form of IVa was given by females during the breeding season. Individual variations occurred in the IVaS calls. For example, three neighboring males gave and often exchanged slightly different versions of IVaS-5 (Fig. 12, d-f). IVaM and IVaF calls were matched by exchanging birds and were virtually indistinguishable.

#### Usage and Contexts

Calls of this subsystem were given by males primarily during territory boundary calling and exchanging. During the winter, the calls were given in border exchanges by the dominant bird in the flock. They were also used by flockmates that had become separated from the flock. IVaM-6 was usually used in this context. IVaM-7 was used by adults in calling to their young when leading them to a new foraging area.

During the breeding season, territorial males gave their calls from prominent and consistent song posts along territory borders. The males usually began calling with IVaM. They frequently continued with the same call for 100 or more repetitions before switching to a new form or leaving the area. Switches in call form were usually to a different call type (*i.e.*, from M to S or F). If these calls were answered, the two birds exchanged the same call for 10-20 repetitions before switching to a different type and approaching each other more closely. Among four adjacent territorial males that were thoroughly surveyed, 12 call forms were used with a mean of eight/bird. Five forms were used by all birds, and four were used by one bird only. Eighteen forms in all were recorded from the San Felasco Hammock

Preserve in general, and still others were recorded elsewhere. Each male tended to have preferred forms from IVaS and M call types, but call forms were always matched in exchanges. The IVaF call type was given predominantly during escalated exchanges after the birds had exchanged IVaM and approached each other more closely. IVaS calls were most frequently given after the birds had appeared to lose interest in the exchange and response latency had increased. The IVaS calls were also given following intraflock squabbles. The female version of IVaM was given as the female left the nest and established contact with the male. The call was given until an answer was received from her mate in a typical IVaM. She then exchanged with her mate using a combination call from IIa as she approached further. The female version was also given as she approached her mate more closely if he was engaged in a border exchange.

#### Titmouse Subsystem IVb

##### Structure

Calls of this subsystem were clearly derived from calls of IVa. IVb calls resembled those of IVa both in phrase structure and, except for IVb-2, in their repetitive nature (Fig. 12). IVb-1 and 4 resembled IVaM forms in structure but both were given at a lower number of repetitions/call and both tended to vary in structure within a given series. IVb-1 occurred in a strongly modified form by the birds at my home (Fig. 12c). IVb-5 appeared to contain two IVb-4 subunits with a third introductory subunit. The call was always repeated without variation in this form. IVb-3 appeared to be made up of one and a

half extended IVb-4 subunits. It occurred as two, two and a half, or three and a half of these subunits. IVb-2 bore no strong resemblance to any other subunit form. It had the general character of a IVaS form when heard. It was never repeated in a continuous series.

All of the calls of IVb could easily be distinguished in the field.

#### Usage and Contexts

IVb-1 was most frequently given in combination with a call from III during fights between flocks or between individual birds. A typical sequence sounded like "kwee-kwee-wadee-wadee." The call was also given by itself usually in series of two or three and as many as six but in the same circumstances and usually in the same bout of calling as the combined form. They were given during all phases of the fights.

IVb-2 was always given in association with III calls but not directly combined as were the IVb-1 calls. The call was rarely used, and no pattern was evident in its usage.

IVb-3 was given following long interflock fights, following interruptions in escalated exchanges between individuals, or temporary separation of opponents. It is perhaps best described as a drawn out "weee-ba-weee...." The call was used by one male in response to IVaM playback after he had approached with answers of the same IVaM call. He then gave IVb-3 as he excitedly circled the area apparently searching for the missing opponent. In other cases, it was given by the dominant bird in flock fights.

IVb-4 was given during interflock and interpair fights by subordinate birds and females that were onlookers to fights. This call was usually associated with calls from subsystem III. In the population at my home, a call very similar to this was given as a IVaM form during territory advertisement (Fig. 12r).

IVb-5 was also given during fights. To my ear, it sounded like "pyuweetaweet." The call was usually given by subordinates that were isolated from their flockmates. Other flockmates responded by approaching the calling bird. On one occasion, a titmouse that was foraging at the periphery of the flock discovered another small group of trespassing titmice. It retreated toward its flock, gave IVb-5 calls, and was joined immediately by its flockmates and together they attacked the intruders.

#### Titmouse Rasp

##### Structure, Usage, and Contexts

This section contains only one call that strongly resembles the rasp of the chickadee (Fig. 6v). It was one of the first calls given by developing fledglings and was given in association with overt aggression. The rate of occurrence of this call increased as the fledglings got older and reached its highest occurrence rate during the period of fledgling dispersal. They occasionally gave it during the fall and it became rare during winter. No adult was observed giving this call. It was occasionally associated with IVb-1 and 6 as were the calls of III.

## DISCUSSION

### Functional Interpretations

#### Chickadee Subsystem I

In general, it appeared that the information made available by the calls of subsystem I dealt with the close range maintenance of contact during steady-state flock movements. In addition to indicating position, the type A calls indicated a high activity rate, type B calls indicated a low activity rate, those of type C indicated a disposition to leave, and those of type D indicated leaving. These and all subsequent functional interpretations are summarized in Table 1.

#### Chickadee Subsystem IIa

In general, the calls of subsystem IIa carried information dealing with movement changes and establishment and maintenance of mid-range contact under rapidly changing circumstances. IIa0 carried the message of alarm or of a strong disposition to stop and escape danger. This indication of escape tendency was probably the relevant message when the call was used during fights. A1 appeared to be a milder form of alarm indicating surprise or suspicion of danger, and it appeared to be used as a general alert. The other type A forms, when uncombined with other forms, appeared to indicate the presence of danger. The higher frequency, slower forms indicated greater escape tendency, and the lower frequency, faster forms indicated greater aggressiveness

Table 1. Summary of functional relationships of *Parus carolinensis* and *P. bicolor* vocal communication subsystems.

<i>P. carolinensis</i> Subsystem	Verbal Transcription	Function or Message	Verbal Transcription	<i>P. bicolor</i> Subsystem
I	"tseet"	[close-range contact synchronization of slow and steady flock movements]	]"tseet"	I
Ila0	"high whistle"	[alarm, escape]	]"high whistle"	Ila0
Ila	"chickadee"	[surprise, alert mid-range contact and approach synchronization of changes in flock movement patterns]	]"seejert"	Ila
IlaC	"dee"	[mobbing]	]"jert"	IlaC
Ilb	—	[begging]	]"—"	Ilb
Ilc	stereotyped "chickadee"	[synchronization of retreat]	]"—"	?
Illa	fast, liquid, sputtery, calls	[aggressive threat assertion of dominance readiness to defend position aggressive approach]	]"kwee"	III
IIlb	—	[retreat supplication (?) (?)]	]"peter" variants	IVb
IV	"feebee-feebee"	[long-range contact and approach territorial advertisement aggressive approach]	]"peter"	IVa

and perhaps "indignation" toward the cause of alert. Type A subunits in combination indicated that the caller was arriving in an area or a group.

Type B subunits, used alone and in combination, appeared to indicate that the caller was leaving an area or group.

Type C subunits alone, as used in scolding and mobbing responses, appeared to be requests or perhaps demands for increased distance between the caller and the target animal. (This message can be paraphrased as "go away."). To a predator stalking the birds, the call could indicate that the predator's presence was known and that it would be useless for it to remain in the area. To other flockmates, the call could specify the location of the predator and call for their help in mobbing it. To young and inexperienced birds, mobbing could have educational value, and, in this context, the mobbing calls could carry the message "this is your enemy."

#### Chickadee Subsystem 11b

This call was very distinctive structurally, highly stereotyped, and unambiguous in its meaning. It was clearly a demand for food. Only one variation in this pattern was observed: its use for copulation solicitation.

#### Chickadee Subsystem 11c

Both types of 11c calls appeared to function in synchronizing retreat from some sort of hostile confrontation. This interpretation is well supported in the case of type 1 but tentative for type 2. Type 2 appeared to indicate more of a tendency to retreat than an urgent need.

### Chickadee Subsystem IIIa

The calls of IIIa in general appeared to indicate an aggressive disposition. They appeared to indicate not only a tendency to attack as in T and TR, but also readiness to defend as in those containing X. In TX combinations, the T could indicate readiness to fight and the X could indicate that it is priority of access to a specific location that is to be fought for. This location could be a territory boundary, a roost hole, a pine cone, or perhaps even status position.

### Chickadee Subsystem IIIb

The two calls of this subsystem had very little in common apart from their probable common derivation from calls of IIa. In keeping with their structural distinctiveness, their messages appeared to be well defined: IIIb-1 proposed flock retreat; IIIb-2 indicated a lack of hostile intentions. In the context of an impending interflock or interpair fight, IIIb-2 may say in effect "don't attack me, I'm on your side." (The message of IIIb-1 is not completely distinguished from IIc-2. It appeared, however, that IIc-2 had the function of synchronizing rapid flock retreat.)

### Chickadee Subsystem IV

Calls of this subsystem appeared to express a claim to territory ownership when given by resident males. When given by wandering or invading birds, the calls probably conveyed as much of an inquiry into tenancy as a claim to ownership. I was unable to distinguish specific messages for the different call forms.

### Titmouse Subsystem I

In general, it appeared that the calls of this subsystem dealt with close range maintenance of contact and steady-state flock movement. Calls of types A and B indicated position and activity rate: type A indicated high activity, type B indicated lower activity. Type C also indicated high activity rate but also probably indicated a disposition to leave in long flight. Type D indicated that a long flight was in progress.

### Titmouse Subsystem IIa

The calls of subsystem IIa appeared to deal with the establishment and maintenance of mid-range contact during activities in which the problems of behavioral synchronization were much more complex than in those activities controlled by calls of subsystem I, namely during changes in flock movement patterns, during fights, or over greater distances.

The very high frequency forms indicated alarm and escape tendencies, and the incorporation of the higher frequency forms of type 1 into combination calls probably indicated the extent to which the caller perceived that a dangerous situation was at hand. When type 2 calls were used alone in mobbing and aggressive scolding during fights, they probably expressed a demand for increased inter-bird distance along with a threat of aggressive consequences for noncompliance. Incidental messages in mobbing, as with chickadees, could also be a request for participation in the mobbing to other flockmates, indication of identity of enemies to juveniles, and indication to the predator that its presence

is well known to the flock. When type 2 calls were mixed with type 1 calls, the type 2 calls could have somehow specified the desired inter-bird distance for use in regulation of flock cohesion. These specifications of inter-bird distance could have been the primary messages when used in border exchanges as well as in exchanges by temporarily separated flockmates.

#### Titmouse Subsystem IIb

As with the chickadee, this call was structurally distinct, highly stereotyped, and unambiguous in its meaning. It was clearly a demand for food. No copulations were observed, so the possible use of IIb in sexual solicitation is unknown.

#### Titmouse Subsystem III

When used without the calls from IVb, the calls of III clearly carry a threat of impending attack. The combination of III with IVb (calls derived from distance decreaseers) at greater distances could indicate the desire to come closer to the prospective opponent. Perhaps this was a dare to the other bird to come close and risk attack. The high frequency nature of the calls could indicate a high degree of escape tendency in the caller (cf. Morton, 1977). This could also be interpreted as indicating that a very dangerous situation was at hand.

#### Titmouse Subsystem IVa

In general, the calls of IVa functioned in establishing contact over long distances. The ultimate objective of this association varied with context and call form. In boundary calling and exchanging, claim

to territory ownership was clearly indicated, and association with neighbors was sought for the purpose of confirming those claims and establishing borders. Threat of aggressive retaliation for noncompliance with those claims was also explicit, especially in IVaF. In an intra-flock context IVaM-6 was used for re-establishing contact with separated birds for the purpose of reuniting the flock. IVaM-7 clearly called for decreasing inter-bird distance when used by parents in leading their fledglings. Dispersing young could use these calls for inquiring into tenancy of unfamiliar areas.

#### Titmouse Subsystem IVb

In general, the calls of this subsystem appeared to be specialized applications of the general function of coordinating approach (except IVb-4). IVb-1 appeared to call for closer approach during escalated fights for the purpose of combat. This was especially apparent when combined with III. IVb-3 called for reestablishing contact after the disappearance of an opponent or other interruption. Data on IVb-4 was inconclusive but its use by subordinates and onlookers while others were escalating exchanges or actually fighting suggests that it may have been used to reaffirm support in battle. IVb-5 clearly called for flockmates to come and help fight. IVb-6 appeared to be similar in meaning to IVb-1.

#### Titmouse Rasp

The titmouse rasp was apparently a juvenile version of the calls of III, although the juveniles did use calls of III in addition to the rasp. Its association with IVb-1 indicates an interchangeability with calls of III. Its message was clearly a threat of aggression.

The structural similarity of this call to the rasp of the chickadee, along with its usage in similar contexts, suggests a possible homology. I suspect that the titmouse rasp may be a nearly vestigial remnant of a homologue to the chickadee rasp. This situation is analogous to that found by Dilger (1960) working with lovebirds of the genus *Agapornis*, by Moynihan (1962) with gulls and terns, and by Smith (1977) with tyrannid flycatchers, in which common displays of some species were rarely expressed in other closely related species.

#### Intraspecific Subsystem Comparison

##### Chickadee

Subsystem I was distinct from other chickadee subsystems in call structure and usage patterns. The calls were given during virtually all kinds of behavior and were thus heard in association with calls from other subsystems. In certain cases, the association appeared to be more than coincidental. In these cases, calls of subsystem IIc and IIIa (IIc-1, T8R, T2aXR, T3aR) were prefixed with short call notes that could have been calls of subsystem I. These combinations were repeated without variation in the same bout of calling or, as with IIc-1 from one bout to the next. In all of these combinations, the call from subsystem I that was involved was type A, the type that most clearly correlated with the excited activity that characterized the contexts of these calls. The closeness and regularity of the calls in these combinations could represent compound messages, but the specific nature of these messages was unclear.

Subsystems II and III were made up of relatively distinctive subunits, but the patterns of subunit arrangement bore strong resemblance to each other. Calls of both subsystems were made up of series of several subunits that began with high frequency, harmonically simpler subunits. Except for calls in which X precedes T, successive subunits were at the same or lower emphasized frequency and increased in frequency range and/or harmonic complexity. The calls ended in subunits with very broad frequency range. T1 and T8 of subsystem III were particularly reminiscent of subsystem II. T1bR was prefixed by a subunit that strongly resembled subunit A3 from subsystem IIa.

The calls of subsystem IIa and IIc differed primarily in the extent of their variability. Whereas the calls of IIa were extremely variable, those of IIc, especially IIc-1 showed little variability. The calls of IIc were further distinguished by their repetitive nature, a characteristic that was not observed in IIa but was in IIIa. The calls of IIc thus appeared to represent a transitional stage between IIa and III in that their subunits were structurally similar to IIa but were repeated in stereotyped phrases as in subsystem III. It is conceivable that calls of subsystem III were derived from IIa by the development of stereotypy in certain combinations and their further modification as they became associated with a more specialized message and function. The general function of establishing and/or maintaining contact during rapidly changing conditions that characterized calls of subsystem IIa was extended in the calls of subsystem IIIa to facilitating approach during aggressive encounters or for expressing the intent or willingness to approach aggressively.

Calls of subsystem IV were distinct from the other subsystems both in structure and syntax. When calls of subsystem IV were given near the nest, they were occasionally introduced by type A subunits from subsystem IIa. In their function as long distance contact calls, IV calls shared with calls of subsystem II the general function of contact, but at a greater distance. A combination of the two subsystems in this context was not repeated and may represent a momentary confusion of purposes--the bird was highly motivated to assert territory ownership but at the same time needed to establish contact with his mate and indicate his arrival at the nest.

#### Titmouse

Calls of subsystem I are distinct from the calls of all other subsystems. A call of type A occasionally occurred in introduction to an otherwise un-introduced series of type 2 subunits of subsystem II.

Calls of subsystem III were distinguished from the type A calls of subsystem IIa by their possession of frequency inflection patterns. However, they shared with type A calls of subsystem IIa a common frequency range and harmonic simplicity. They were occasionally introduced by type A subunits of subsystem IIa, and, in other cases, they were followed by Subsystem IIa type C subunits in close association. The relatedness of the two subsystems was further indicated by the occurrence of intergradations between them. Calls of subsystem III thus appeared to be derived from type A calls of subsystem IIa. In terms of information, the two subsystems had in common the message of establishing and/or maintaining contact under rapidly changing conditions. Calls of subsystem III represented application of this message to the

specific function of indicating intent or willingness to approach aggressively.

Calls of subsystem IV were distinct from those of other subsystems. Certain calls of IVb regularly occurred in combination with those of III and probably represented compound messages rather than relatedness.

#### Interspecific Comparison of Subsystems

The calls of subsystem I of the chickadee were very similar to those of the titmouse subsystem I in acoustic structure and usage patterns. Type A calls were nearly identical in duration ( $\Delta\bar{x} = .4$  msec;  $t = .16$ ;  $df = 42$ ;  $p > .5$ ). In terms of the caller's activity rate in two categories (1, active foraging; 2, relaxed foraging, manipulation food, and perching quietly), the two species showed no difference in the contexts of usage of type A calls ( $\chi^2 = .698$ ;  $df = 1$ ;  $.5 > p > .3$ ). Type B calls had similar mean duration (34.7: 37.1 msec) but were very different in range and variation. Nevertheless, in terms of activity rate, analysed as before with type A, no significant difference was shown in the usage pattern of type B ( $\chi^2 = .085$ ;  $df = 1$ ;  $.8 > p > .7$ ). Type C calls showed the greatest disparity in acoustic structure with a mean duration in the chickadee version nearly twice that of the titmouse version. However, the two species' versions were essentially similar in overall inflection pattern and showed no difference in usage in terms of activity rate. Small sample size for this call prohibited statistical testing. The calls of both species also had high likelihoods of being followed by long flight. Type D was also very similar in the two species, both structurally and functionally.

There was thus a high degree of correspondence between the two species both structurally and functionally in subsystem I. This correspondence can probably be accounted for by the high degree of interspecific relevance of the information made available by these calls.

The calls of subsystem II of both species were similar in many features of acoustic structure, rules of syntax, and functions. Type A subunits of both species were characterized by their high frequency and harmonic simplicity. Subunits of titmouse IIa-C were very similar to chickadee IIa-C in that both were harmonic series covering a broad range of frequency. The titmouse apparently had no counterpart to the intermediate subunits of chickadee IIa-B. The rules of subunit combination were the same for both species. The acoustic structure of the very high frequency subunits ( $> 9$  kHz) were indistinguishable in the two species. Otherwise, the structure of the chickadee subunits was distinct from those of the titmouse in duration and in patterns of frequency inflection within the subunits. The chickadees appeared to modulate the high frequency and intermediate subunits to a much greater extent than the broad frequency range forms. The opposite appeared to be the case with the titmouse. On a few occasions, however, the calls of the two species converged to an intermediate form during exchanges between the two species (Fig. 2 k and l).

In terms of the functions of the calls of subsystem II, there is also a high degree of correspondence in that both are involved in the regulation of flock movements under changing conditions and in facilitating mid-range contact and approach. These functions are not always of equal interspecific relevance. Regulating flock movements

certainly was of interest to both species, but the calls were only rarely exchanged by the two species, and the messages carried by the calls appeared to be primarily intraspecific. The two species maintained flock cohesion intraspecifically since they rarely appeared to be evenly mixed throughout the flock, but overall flock velocity and direction must have been synchronized if the two species were to remain together. The calls must therefore have had some components that were sufficiently species-distinctive and others that were held in common to accomplish this duality of purpose.

The very high frequency subunits of both species carried the message that extreme danger was at hand and, in the context of fights, strong escape tendency. The essential ingredient was the same in both cases, *i.e.* avoiding danger. This message was of such immediacy that selection has apparently allowed little ambiguity and the call was strikingly different from all other calls.

Subsystems IIb were clearly derived from calls of IIa. However, they were both structurally and syntactically distinct. Although fledglings of both species were observed making obvious attempts to beg from adults of other species, none of these attempts were rewarded. It appeared that the adult birds have effectively selected for distinctive begging calls.

Subsystem III of the two species appeared to share a common origin in subsystem II. Chickadee III calls appeared to use all subunit types of subsystem II, whereas titmouse II calls used only the type A subunits. Chickadee III calls were much more complex in structure and occurred in more distinctively different forms than titmouse III calls. Although specific messages or even consistent contextual features could

be reliably associated with only a few of the chickadee III calls, it was clear that the range of contexts in which the calls occurred was greater than for the calls of titmouse III. These calls were very rarely directed to the other species and thus had little, if any, interspecific relevance. It is not surprising therefore that the calls of subsystem III should bear no structural similarity between the two species.

Subsystems IV had very little in common outside of their basically repetitive nature. The calls of chickadee IV showed little variety compared to those of titmouse IV and were used in a correspondingly smaller variety of contexts. The messages carried by calls of chickadee IV appeared to be carried by the calls of titmouse IV, which also appeared to cover those messages carried by chickadee III but not by titmouse III. The lack of correspondence between subsystems IV in acoustic structure was consistent with their lack of messages with interspecific relevance.

The relatedness of the major subsystems of the two species is summarized in Table 1.

To summarize this section, I have argued that each of the four call subsystems of the tufted titmouse and Carolina chickadee bore an extent of similarity in acoustic structure and/or syntax that corresponded to the extent of interspecific relevance of their messages and functions. This correspondence is summarized in Table 2.

#### Review of Communication Systems of the Genus *Parus*

Relatively complete surveys of the vocal communication systems of six species in the genus *Parus* have been prepared by various authors. Only three of these, however, were done with the aid of the sound

Table 2. Summary of correspondence between structural similarity and interspecific relevance in the vocal communication subsystems of *Parus carolinensis* and *P. bicolor*.

Subsystems	Structural Similarity	Interspecific Relevance
I	high	high
IIa0	high	high
IIa	intermediate	intermediate
IIb	low	low
III	low	low
IV	low	low

spectrograph (*P. carolinensis*: Smith, 1972; *P. atricapillus*: Ficken *et al.*, 1977; and *P. hudsonicus*: McLaren, 1976). Surveys based on phonetic renderings were made of the vocal repertoires of *P. carolinensis* by Brewer (1961), *P. atricapillus* by Odum (1942), *P. palustris* by Morley (1953), *P. inornatus* by Dixon (1949) and *P. major* by Gompertz (1961). Discussions of several selected vocalizations have also been made by various authors (*e.g.*, Dixon *et al.*, 1970) and two authors have attempted broad surveys of a few vocalizations primarily among European members of the genus *Parus* (Latimer, 1977; Thielcke, 1968).

None of these authors organized the vocalizations as I did, but using their sonograms and descriptions, I have reclassified the vocalizations according to the subsystems that I used in the analysis of *P. carolinensis* and *P. bicolor*. This reclassification is summarized in Table 3.

S. T. Smith (1972) prepared a survey of the vocalizations of *P. carolinensis* in a residential area near Philadelphia, Pennsylvania. Although all subsystems appear to be represented in the vocalizations of the population she studied and most calls appear to be used in basically the same way as the birds I studied in Florida, there are some notable differences. I suspect that these differences are due to three factors. First, her recordings were apparently made primarily at feeders and nest boxes in a residential neighborhood. Although she is confident that no "major categories of behavior were overlooked," the tendency for aggressive reactions to be intensified at feeders, and the limited opportunities for flock movements in gardens and hedgerows may have biased the interpretation of the patterns of usage of the vocalizations. Second, her study population was nearly a thousand miles from

Table 3. Comparison of the vocal communication subsystem of seven species of the genus *Parus*.

	<i>palustris</i>	<i>carolinensis</i>	<i>hudsonicus</i>	<i>atricapillus</i>	<i>bicolor</i>	<i>inornatus</i>	<i>major</i>
Close-Range Contact	I*	I	I	I	I	I*	I*
Flight	?	I-D	IIaC	I*	I-D	I-D*	?
Mid-Range Contact	IIa*	IIa	IIa	IIa	IIa	IIa*	IIa*
Surprise, Alert	IIaA*	IIaA	(?) IIaA	IIaA*	IIa	?	IIaA*
Alarm, Escape	IIa0* IIaA*	IIa0	(?) IIaA	IIa0	IIa0	IIa0*	IIa0
Mobbing	IIaC	IIaC	?	IIaC	IIaC	IIaC*	IIaC
Begging	?	IIb	IIb	IIb	IIb	IIb*	IIb*
Aggressive Conflict	IIaA* III	IIaA III	IIaA III	IIaB III	III	?	?
Supplication	?	HSC III	(?) HSC	HSC III	(?) IVb	HSC*	HSC*
Long-Range Contact, Territorial Advertisement	III* IV*	III IV	III	IV	IVa	III IV	IIa IV

\* Designation based on verbal transcription, no sonograms available.

mine and very close to the border of the range of *P. atricapillus* (Ward and Ward, 1974). Hybrids are known to occur in some areas along this border (Rising, 1968; Johnston, 1971), and they are suspected in others (Brewer, 1963). Third, a very different approach to the problem of organizing the vocal repertoire was taken by Smith. Classification was based on assumed message structure of the calls rather than on an analysis of their physical structure. Sonograms of all call classifications were presented, but these apparently played little part in analyzing the relationships among the calls.

Calls of subsystem I (Smith: "Tseet") were present but they were given a very different interpretation from my own. Smith considered them to indicate a conflict between escape and "general set" (Smith, W. J., 1969), *i.e.* just about anything, possibly encoding "social interaction hesitance," and to "function to alert other chickadees of aversive conditions." As discussed earlier, calls of subsystem I occur during all activities and are associated with nearly all other vocalizations. It must also be true that all activities of the chickadees are accompanied by escape tendencies and "social interaction hesitance" in such a treacherous world as they live in. But to assert that these calls are adaptations for making available information concerning "aversive conditions" is unwarranted by the evidence. Smith's emphasis on aggressive contexts may have resulted from her over-abundance of observations at feeders, where aggression is concentrated, and from an apparent under-representation of observations of more typical flock foraging movements in her sample. Her conclusions regarding this call differ not only from my own but from all other descriptions of this

call's homologues in other congeners (*e.g.*, Odum, 1942; Ficken *et al.*, 1977; etc.).

Calls of subsystem IIaA of *P. carolinensis* are broken down by Smith into several functional categories without providing sufficient physical description to distinguish between them (*e.g.*, lispng tee, loud tee, chip, soft dee). Their relatedness in the continuum of subsystem IIa is obscured by Smith's classification. Nevertheless, the contextual information provided with these calls indicates that their usage patterns are comparable if not identical to those of the Florida population. This is also true of the begging calls (subsystem IIb) and High See alarm calls (IIa0).

Subsystem III was clearly represented in the Pennsylvania population but the calls were very different from those of the Florida population in details of structure. Again Smith's classification system proved unworkable and homologies to the calls of my population are unclear. On first mention of these calls, Smith described them as variable. She later discussed "variants" of these calls apparently treating them as stereotyped. She counted 23 "variants" in the nine most thoroughly studied individuals (I counted 17 in six to ten individuals) with each individual having at least some variants unique to itself within its flock. Her recordings at various distances from the study population revealed distinctly different variants. Smith reported three different calls of subsystem III in a brief period of observation 16 km from her main study population. I recorded only one minor variation, an X-R with no T unit, in many hours of observation of the Gainesville (home) population 20 km from the San Felasco population.

Nearly all of the other III calls of the San Felasco population were represented in the Gainesville (home) population.

One "variant" in Smith's population (not illustrated) was frequently associated with "variable see" (HSC) in situations that, in at least some instances, appeared comparable to situations in which I observed HSC-IIIb-2 in my Florida population. These calls may be homologous.

Smith reported a greater likelihood of attack following calls with rasps than following calls without rasps. This pattern fits well to Morton's M-S rules (1977), but is contradicted by my results. As discussed earlier (see Results), some T forms occasionally were given without the rasp and were associated with a much higher likelihood of being followed by an attack than were the complete T-R forms.

Calls of IV were similar in structure and usage between the two populations. The only song form for which a sonogram was published by Smith was very similar to one in the Florida population. Others, designated "song variants" were not necessarily represented in the Florida population but comparable vocalizations with rearranged subunits did occur there.

Calls of *P. atricapillus* appear remarkably similar to those of *P. carolinensis* (Odum, 1942; Brewer, 1961; Ficken *et al.*, 1977). All subunits were represented in *P. atricapillus* and usage patterns appear to be very similar. The most notable differences occur in the details of structure of subsystem III and IV, but not enough information was made available on III to generalize about the nature of the differences. A "special type" of III (Dixon *et al.*, 1970; not illustrated) was given in sexual contexts. This call may be homologous with IIIb-2 of

*P. carolinensis*. Subsystem IV of *P. atricapillus* differed from IV of *P. carolinensis* in being restricted to two notes instead of four.

*Parus hudsonicus* differed from *P. carolinensis* and *P. atricapillus* in its lack of subsystem IV. McLaren (1976) makes no mention of how the function of territory advertisement was accomplished in her study population in Ontario, but Townsend and Allen (1907) in Labrador and Allen (1910) in New Hampshire reported a "song" that may have been homologous to calls of subsystem III (Townsend and Allen: "low, bubbly, warbling"). Calls of III were regularly associated with border patrolling in *P. carolinensis* and apparently *P. atricapillus* (Odum, 1942), and it is easy to imagine their promotion to the role of song in *P. hudsonicus*. *Parus rufescens*, thought to be a sibling species of *P. hudsonicus* (Grinnell, 1904), also lacked subsystem IV, but compensated with a "repetitive trill" (Dawson, 1923).

McLaren (1976) noted the tendency of *P. hudsonicus* to fuse subunits of Ila type A to type C subunits. This tendency was expressed by *P. carolinensis* and *P. bicolor*.

*Parus palustris*, a Eurasian member of the subgenus *Poecile*, appears to have communication signals similar to those of its North American relatives, the chickadees. Sonograms for only subsystems IV and Ila type C are available in Thielcke (1968) and Latimer (1977). Other calls have been described by Morley (1953). From these descriptions it appears that *P. palustris* uses calls homologous to subsystem I, Ila-0, Ila-A, a combination call of Ila-A and C, and III. These calls appear to have uses similar to those of the North American chickadees.

Sonograms of subsystems IV and IIa in part of *P. inornatus* are available in Dixon (1969). Other calls can be inferred from transcriptions in Dixon (1949). No mention is made in either of these papers of any calls resembling subsystem III of *P. bicolor*, and it is unclear what calls are associated with hostile interactions in *P. inornatus*. A call that appears to be homologous with HSC was used by females early in the breeding season in place of the more normal begging calls of subsystem IIb. Begging calls of IIb were used later in the season. This usage of HSC is consistent with their function of supplication in other congeners. The calls of IIa were considered by Dixon (1949) to be more similar to those of *P. atricapillus* than to those of the more closely related *P. bicolor*.

Sonograms are available for subsystem IV of *P. major* in Gompertz (1961), Thielcke (1968), Krebs (1976), and Latimer (1977) and for IIa in part in Thielcke (1968) and Latimer (1977). Other calls can be inferred from transcriptions in Gompertz (1961) and Hinde (1952). Begging calls that appear to be homologous with IIb, close-range contact calls of subsystem I, and HSC all were represented, but nothing comparable to III of the species discussed above appears to be present in the repertoire of *P. major*. They appear to compensate for this deficiency with calls of IIa and several other calls of uncertain affinities (Gompertz: "tsee, pee, tink;" possibly isolated IV notes).

Thielcke (1968) and Latimer (1977) both made surveys of subsystems IV and IIa (termed alarm calls, but this assumed function appears to be too broadly applied) of many species, primarily European, of the genus *Parus*. The majority of the species surveyed in these works had "songs" similar to subsystem IV of *P. carolinensis* or *P. bicolor* in that they

were repetitive series of a simple phrase. Others appear more similar to *P. carolinensis* subsystem III, for example *P. rubidiventris* in Thielcke (1968). Still others appear more similar to subsystem IIa, for example, *P. caeruleus* in Thielcke (1968), or *P. cinetus* in Latimer (1977). Subsystem IIaC, or at least notes comparable to IIaC of *P. carolinensis*, appear to be a constant feature of the communication systems in the genus *Parus*.

#### Interspecific Effects on Vocal Communication Signals

Vocal communication signals of any species can be expected to be influenced by those of other sympatric species in several ways. In a community of many species, competition for the acoustic medium can be intense. Species may avoid each other by finely partitioning the frequency spectrum (Rand and Drury, ms), by distinctively patterning their calls (Bremond, 1978), by adjusting their schedules to call at different times of the day (Smith, W. J., 1977, pg. 372) or by alternating calls with competitors (Cody and Brown, 1969; Ficken, et al., 1974; Marler and Tenaza, 1977). Distinctive patterning in long distance calls is especially critical for closely related species that are in danger of hybridizing (Brown and Wilson, 1956; Marler, 1957; Sibley, 1961) and sibling species can be expected to diverge in these calls.

The opposite trend, character convergence, has been suggested to account for many cases of similarity in appearance of song between birds that could possibly be interspecifically territorial (Cody, 1969; 1973).

Although none of the cases used by Cody to argue for the idea were adequately supported by evidence, and many have been discredited (Murray, 1976; Brown, 1977; Hardy and Murray, ms), the idea may yet have some validity under certain circumstances. The hypothesis suggested by Cody (1969, 1973) is that birds with considerable resource overlap should be interspecifically territorial and should develop common signals for mutual recognition that will facilitate avoidance. As pointed out by Murray (1971, 1976), such interspecific territoriality is unlikely to be in the mutual interest of both species since one species will tend to dominate the other and exclude it from optimal habitat in keeping with the competitive exclusion principle. Thus, it would hardly be in the interest of the subordinate species to retain the signals that provoke the dominant species to react aggressively to it. Sibling species, however, may be very closely matched in aggressive prowess as well as ecological requirements. In areas of secondary contact, it may serve these species to exclude each other from their territories and to develop the communicative adaptations to facilitate avoidance. Emlen *et al.* (1975) reported that indigo and lazuli buntings (*Passerina cyanea* and *P. amoena*) maintained interspecific territories in their zone of sympatry. "Figures" (syllables) of the songs of the other species were incorporated into each species' songs in sympatry but not in allopatry, and playback response was elicited to the other species song in sympatry but not in allopatry. Similarly, Ward and Ward (1974) found that *Parus atricapillus* and *P. carolinensis* sang both their own songs and songs of the other species in a zone of sympatry in SE Pennsylvania but not outside that zone. Response to

playback was elicited to the other species' song in sympatry but not in allopatry. Interspecific territoriality was not investigated. Abnormal songs have been reported in several areas of overlap (Rising, 1968; Brewer, 1963; Johnston, 1971; Ward and Ward, 1974). "Bivalent" and abnormal song in these areas may be the result of hybridization but they may also be adaptations for facilitating interspecific territoriality.

Convergence, or lack of divergence, has been demonstrated in alarm and mobbing calls among sympatric bird species (Marler, 1957) and monkeys (Marler, 1973). That the calls for alarm should need to be very high frequency, whistle-like tones has been suggested by Marler (1955) since this type of tone is presumably minimally locatable. Shalter (1978) has suggested that a better explanation for the high frequency of alarm calls may be in accordance with Darwin's (1872) principle of antithesis in that the higher the sound, the more unlike it is to aggressive growls and scolds and thus indicative of escape tendency. Both arguments suggest that there is an ideal acoustic form for an alarm call, and, by their arguments, it is reasonable to expect that the alarm calls of titmice and chickadees should converge on this common form.

In the case of mobbing calls, the advantages of recruiting intraspecific participation are clear. Marler (1955) suggests that here too the physical structure of the calls suits them to their function in that their broad frequency-spectrum makes them locatable. Their harsh quality, along with their low frequency components, gives them a universally recognizable aggressive and aggravated connotation. The convergence of mobbing calls to this common form among many species is

to be expected. In my study, chickadees and titmice participated in mobbings with unintroduced series of IlaC subunits. The calls of the two species were distinguishable but similar. Carolina wrens, ruby-crowned kinglets, and solitary vireos also participated in mobbings with the characteristically broad spectrum, harmonically rich calls. The warblers also participated, but with emphatic chips that also covered a broad frequency range but were harmonically simple.

The extent of divergence in the vocal communication systems of the Carolina chickadee and tufted titmouse is in agreement with the conclusions and predictions of Marler (1957) and also with his conclusions on the extent of divergence in the calls of two sympatric and interspecifically social *Cercopithecus* monkeys (Marler, 1973). In his studies, as with mine, the long distance signals (subsystems IV of the parids) were the most distinctive. Unlike the monkeys of Marler's study, however, the subjects of my study were probably in very little danger of hybridizing, and the divergence in their long distance calls was probably due as much to the different strategies of territory defense and aggression by the two species as to the need for species-distinctiveness. Once contact was established with calls of subsystem IV, the chickadees approached each other and exchanged calls of subsystems II and III. The titmice, however, continued to exchange with calls of subsystem IV. The greater communication burden on subsystem IV of the titmouse results in a more elaborate and thus distinctively different complex of calls from subsystem IV of the chickadee. Specific distinctiveness may, however, be important to these two species, not in reference to each other, but to the more closely related and geographically adjacent species of their respective subgenera.

In addition to the high frequency alarm calls and mobbing calls of subsystem II, the calls made up of combinations of other subunits also showed similarities not only in the two parids of my study but in all parid species for which data are available. The extent of divergence in the two species of my study probably represented a compromise in that a certain degree of specificity was necessary for the two species to maintain group cohesiveness independently of each other and at the same time regulate overall mixed flock movements. The problem has apparently been resolved by allowing call subunits to diverge in details of acoustic structure while retaining at least the basic features of a common syntax. This case is similar to that found by Marler (1973) in the *Cercopithecus* monkeys. The calls known as "phrased grunts," were given by both species in similar contexts and appeared to function in coordinating group movements. The calls were very similar in basic acoustic structure between the two species and were considered to be clearly homologous. However, the calls of the two species differed in "phrase" duration, "phrases" per call, variability of these two parameters, and in the extent of high frequency emphasis. Marler interpreted these differences as having arisen in response to the need for maintaining intraspecific cohesiveness within the interspecific group.

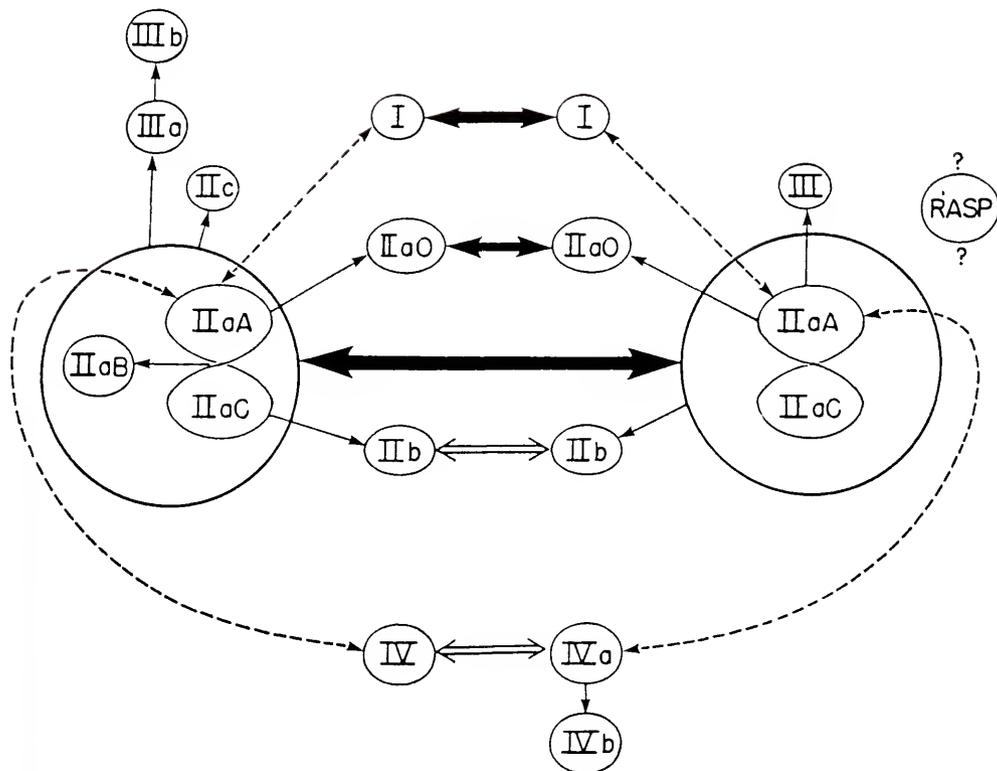
That birds should be responsive to patterns of syntax is not without precedent. The songs of many birds are made up of repetitions of various song types, the precise arrangement of which are species specific. Falls (1963) demonstrated that the exact timing of the subunits in the song of the ovenbird, *Seiurus aurocapillus*, is necessary for species recognition. Boughey and Thompson (1976) found that brown

thrashers (*Toxostoma rufum*) responded to songs of catbirds (*Dumetella carolinensis*) and mockingbirds (*Mimus polyglottos*) when altered to match the phrase repetition pattern of normal brown thrasher song.

Although data are incomplete, the syntax rules of subsystem IIa of *P. carolinensis* appear also to be used by *P. atricapillus* (Ficken, et. al., 1978) and *P. hudsonicus* (McLaren, 1976).

The intra and interspecific relationships of the various subsystems are summarized in figure 14. Subsystems IIa are considered to be central in each species vocal communication systems. Subsystems I and IV are shown as possibly having been derived from IIaA, but these derivations are highly tentative and based only on their acoustic simplicity and common basic functions, i.e. contact at various distances. Subsystems I showed strong correspondence in structure and function, and it is very likely that this was the result of convergence due to an interspecific influence. IIa0, the high whistle alarm calls, also appear to be convergent. This convergence could be due as much to selection for physical properties of the calls as to interspecific influence. Subsystems IIa were convergent primarily in syntax. The precise structural configuration of the subunits showed less correspondence. Subsystems IIb appear to be divergent due to selection for specific distinctiveness. The divergence of subsystems IV could be due as much to differences in strategies of territory defense as to the need for specific distinctiveness.

Figure 14. Summary of intra- and interspecific relationships of vocal communication subsystem of *Parus carolinensis* and *P. bicolor*.

CHICKADEETITMOUSE

- |        |                                             |
|--------|---------------------------------------------|
| -----> | possible derivation                         |
| ————>  | probable derivation                         |
| —————> | intersp. influence resulting in convergence |
| =====> | intersp. influence resulting in divergence  |

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## BIOGRAPHICAL SKETCH

Philip Gaddis was born in Berkeley, California, on 22 November, 1945. He attended public schools in Eugene, Oregon, until 1955, and in Oakland, California, until 1964 when he graduated from high school. He graduated from Lewis and Clark College with a B. A. in biology in 1968. He graduated from Portland State University with a M. S. in zoology in 1975.

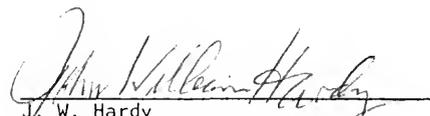
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
John H. Kaufmann, Chairman  
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Peter Feinsinger  
Assistant Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
J. W. Hardy  
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Philip S. Callahan  
Professor of Entomology and  
Nematology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December, 1979

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Dean, Graduate School

UNIVERSITY OF FLORIDA



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