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THE ORGANIZATION OF MAJOR VOCALIZATIONS IN THE PARIDAE[1]

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ABSTRACT.—Vocal organization in Parus species is similar within subgenera, but differs among them. The Crested Tit, *P. cristatus,* has a weakly differentiated repertoire based on a unit-pattern consisting of a string of high-frequency (HF), tonal notes followed by a string of low-frequency (LF), noisy notes. The American titmice (*P. wollweberi, inornatus,* and *bicolor*) are similar, but have well differentiated songs and chick-a-dee-like calls. The Blue Tit, *P. caeruleus,* and probably one close relative, have differentiated song, alarm calls, and conflict calls, each based on vocal patterns similar to the one of the Crested Tit. The Coal Tit, *P. ater,* and its Eurasian relatives have well differentiated song-repertoires, have all but lost the LF-notes from their repertoires including alarm calls, and use calls consisting of a high diversity of single notes. The Great Tit, *P. major,* and its Asian relatives have similar song-repertoires, but use diversified LF-notes for alarm "churring," and combine other notes freely to make unit-calls. American chickadees and their European counterparts have secondarily simplified song, plus well-developed combinatorial chick-a-dee calls and semi-combinatorial, complex gargles. Other subgenera are too little studied for characterization, but the first spectrographic evidence is provided for a number of species. Communicative functions served by "monolithic song" in migratory, north-temperate oscines appear to be divided among two or more major complex vocalizations in almost all species of the non-migratory, permanently mated Paridae. Parid "song," chick-a-dee calls, and gargles have functional equivalents among many parid species, but these are not necessarily phonological homologies. Parids have evolved information-laden vocal diversity both through phonological diversification and through combinatorial principles paralleling those of human language. These two kinds of diversity can be found in "song," chick-a-dee calls, and gargles (and their functional equivalents) in various species, making parid vocalization one of the most interesting and theoretically important communication systems known in the animal kingdom.

The last century of ornithology has witnessed an explosion in knowledge about vocalizations, so periodic summaries are useful for consolidating an ever-growing literature and directing attention to unsolved problems. The Paridae (taken here as coextensive with the genus *Parus,* although recent evidence suggests that genera such as *Sylviparus* should be included), is a particularly interesting family as most of its well-known members have not just one major vocalization ("monolithic" song) but two or more types of complex utterances. This is a preliminary survey aimed at understanding the organization of vocal communication and its evolution in the approximately 45 species of chickadees, tits, and titmice.

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[1] This paper is dedicated to the memory of my colleague and friend, Klaus Immelmann (1935–1987).

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The present paper is in many ways a descendent of Thielcke's (1968) pioneering review, although my emphases and goals are somewhat different from his primarily taxonomically oriented survey. More recently, Latimer (1977) provided a comparison of a number of parid vocalizations, with emphasis on phonological details and hypotheses concerning sound production. The principal motivation for the present ongoing survey is to trace the evolution of "chick-a-dee" calls and related combinatorial vocalizations. Due largely to their combinatorial properties, these calls of the Black-capped Chickadee (*P. atricapillus*) may constitute the most language-like system of animal communication thus far discovered (Hailman et al. 1985, 1987; Hailman and Ficken 1986). In addition the survey helps to elucidate how signal-system repertoires are organized, and how informational capacities of such systems were enlarged by evolution.

By "major" parid vocalizations I refer to sounds other than short, special-purpose calls (such as aerial-predator alarms, copulatory-solicitation calls and the like). Most of the major vocalizations are units composed of two or more different note-types put together in either a fixed sequence or a variable order governed by statistical "rules." For example, in the Black-capped Chickadee the major vocalizations are the whistled "fee-bee" (usually referred to as "song"), the semi-combinatorial "gargle" complex, and the manifestly combinatorial "chick-a-dee" call-complex. These three "major" vocalizations are among about a dozen vocal types used by this species (Ficken, Ficken and Witkin 1978).

METHODS

Recording instruments.—My field tapes were made with a Stellavox Sp7 reel-to-reel recorder or a Marantz PMD 430 Professional cassette recorder, with some tapes in mono but most in stereo with one channel being used for running commentary. All vocalizations were recorded with Sennheiser condenser, highly directional ("shotgun") microphones. Reel-to-reel recordings were made on Scotch 208 "mastering" tape, and cassette recordings used Maxell UR90 normal-bias tape. Once the frequency ranges of a species' vocalizations were determined spectrographically to be above low-frequency noise, subsequent recordings were sometimes made using the low-frequency roll-off filter of the Sennheiser ME88 microphone.

Recordings made by persons who have provided me with tapes were made with a wide range of recorders, microphones, and types of tape. In most cases I have copied their original tapes directly into the Marantz PMD 430, and probably in the majority of instances the original tapes were played back from the same recorder or recorder-type on which they were recorded. I have also surveyed recordings from the files of the Cornell Laboratory of Ornithology (hereafter "CLO") purchased by my coworker Millicent S. Ficken.

Recording sites and contexts.—My recordings of North American species were made at many sites, in eastern U.S. at all times of year, but in the west primarily in late summer. Timing is important because: (a) recordings may often include vocalizations of birds only 1–3 months old, and these vocalizations may not be typical of adult birds; and (b) vocalizations associated with advertising and territoriality may be rare in late summer. Species were flocking by late summer, which was ideal for my principal aim of recording chick-a-dee calls in those species that have them, but other major vocal types are undoubtedly under-represented in my own recordings, made beginning in 1983.

My recordings of European tits are from the period January to June 1987. During March–April 1987 I made field recordings on the continent near Groningen (Netherlands), Antwerp (Belgium), and Radolfzell and Tübingen (Germany). Most of my recordings were made in Norway, in Væretrøa (Ranheim) east of Trondheim, and at Målsjøen (Klæbu), south of Trondheim, but some recordings were made at other sites. At the two sites named I recorded from winter flocks, during mobbing experiments with stuffed owls (Pygmy Owl [*Glaucidium passerinum*] and Tawny Owl [*Strix aluco*]), and from birds at nest boxes (natural cavity in the case of the Crested Tit [*P. cristatus*]). Recordings from other persons were made at various times and sites, spanning a large period and a large geographic area. In some cases recordings were made of captive birds.

Spectrographing.—All spectral analysis was done with a Uniscan (Unigon Corp.) or Uniscan II (Multigon Corp.), the former used in Trondheim, the latter in Wisconsin. All of the figures herein were made with the latter instrument and printed out on an Epson FX80 printer. For illustration purposes the hard-copies were scanned by ThunderScanning (Thunderware, Inc.) to create digitized images in an Apple Macintosh-plus computer, where they were then labeled and printed on an Apple LaserWriter II.

RESULTS

Vocal organizations were found to group approximately according to Thielcke's (1968:162–163) listing of subgenera, by which I present the data (using a different sequence of subgenera). There is a persistent structural theme in the phonology of complex vocalizations of *Parus* species: a series of higher-frequency (HF) notes followed by a series of lower-frequency (LF) notes. The acoustical frequencies differ among species, kinds of vocalizations within a species, probably individuals of the same species giving the same vocalization, and perhaps even repetitions of the "same" vocalization by the same individual. Nevertheless, vocalizations often follow this [HF]-[LF] plan, where the brackets indicate that there may be a number of HF- or LF-notes in a row. (For simplicity, such brackets are omitted from the remainder of the text except where necessary for clarity of a discussion.)

Furthermore, note-types tend to have certain consistent phonological characteristics. The HF-notes confine sound energy mainly in one frequency band, often with frequency modulation (FM). The FM pattern is commonly a chevron on a spectrographic display; when either the ascending or descending arm is emphasized (or the peak of the chevron is missing) I refer to the notes as "slurred." By contrast LF-notes tend to have a wide frequency spectrum. When they are of fairly short duration, they tend to have a number of parallel frequency-bands ("banded" structure) consisting of "stacked" chevrons. Longer-duration LF-notes tend toward frequency-invariance, so that the frequency-bands look like pure-tone harmonics (which they are not: see Nowicki and Capranica 1986a, b; Nowicki 1987).

There may also be note-types intermediate between the HF- and LF-notes: the "IF-notes." These intermediates may have intermediate characteristics, or they may be essentially compound notes, beginning as HF and ending as LF, depending upon the species. The IF-notes almost always occur between the other two types, so the typical parid pattern is [HF]-[IF]-[LF]. Finally, within these note-categories there may be several differentiated types, and in some cases graded series.

Lophophanes and *Baeolophus*: American Titmice and Relatives

Thielcke (1968:163) listed the Bridled Titmouse (*P. wollweberi*) in *Lophophanes* with the Crested Tit (*P. cristatus*) and Grey-crested Tit (*P. dichrous*) while placing the other North American crested forms in *Baeolophus*. I consider them together, and begin with this group because the Crested Tit appears to have the least differentiated vocal organization in the family. I found no information on the Grey-crested Tit's vocalizations; all other species are covered here, with the form *atricristatus* treated with *bicolor*.

Crested Tit *(P. cristatus)*.—The handbook of Bergmann and Helb (1982: 333) characterizes the vocal repertoire of this European species as markedly sparse and weakly differentiated. "Singing" repeats a characteristic "unit-pattern" (Thielcke 1968:151, fig. 2f; Latimer 1977:421; Bergmann and Helb 1982:333, figs. a and b), consisting of a series of HF-notes followed by a series of LF-notes. I found in Norway that these two series could be alternated, with either beginning and either ending. Furthermore, the male of a pair I studied sometimes gave a repeated phrase of purely HF-notes (Fig. 1A, left part), which resembles "song" of many other parids. Sometimes these HF-notes were no different than those of the unit-pattern, at other times slightly more diverse, as figured.

Vocalizations used in winter flocks, disturbance at the nest-site and in response to a stuffed owl are similar to "singing" except that the LF-notes predominate (Thielcke 1968:154; Bergmann and Helb 1982:333, figs. c and d). Fig. 1A (right part) shows one unit of such a repeated vocalization given in response to nest-disturbance; both members of the pair I studied uttered this vocalization.

Latimer (1977:426) shows four repeated notes that look much like the last two notes shown in Fig. 1A (left). He lists these under "alarm and aggression calls." These notes, beginning with a brief transient and continuing with a rising slur, might represent a slight phonological differentiation of special notes used in close aggressive contexts, as reported for other tits. Such a call, although rare, is known to occur in the Crested Tit (Perrins 1979, Dhondt pers. comm., Haftorn pers. comm.).

Bridled Titmouse *(Parus wollweberi)*.—Gaddis (1983) reported that this

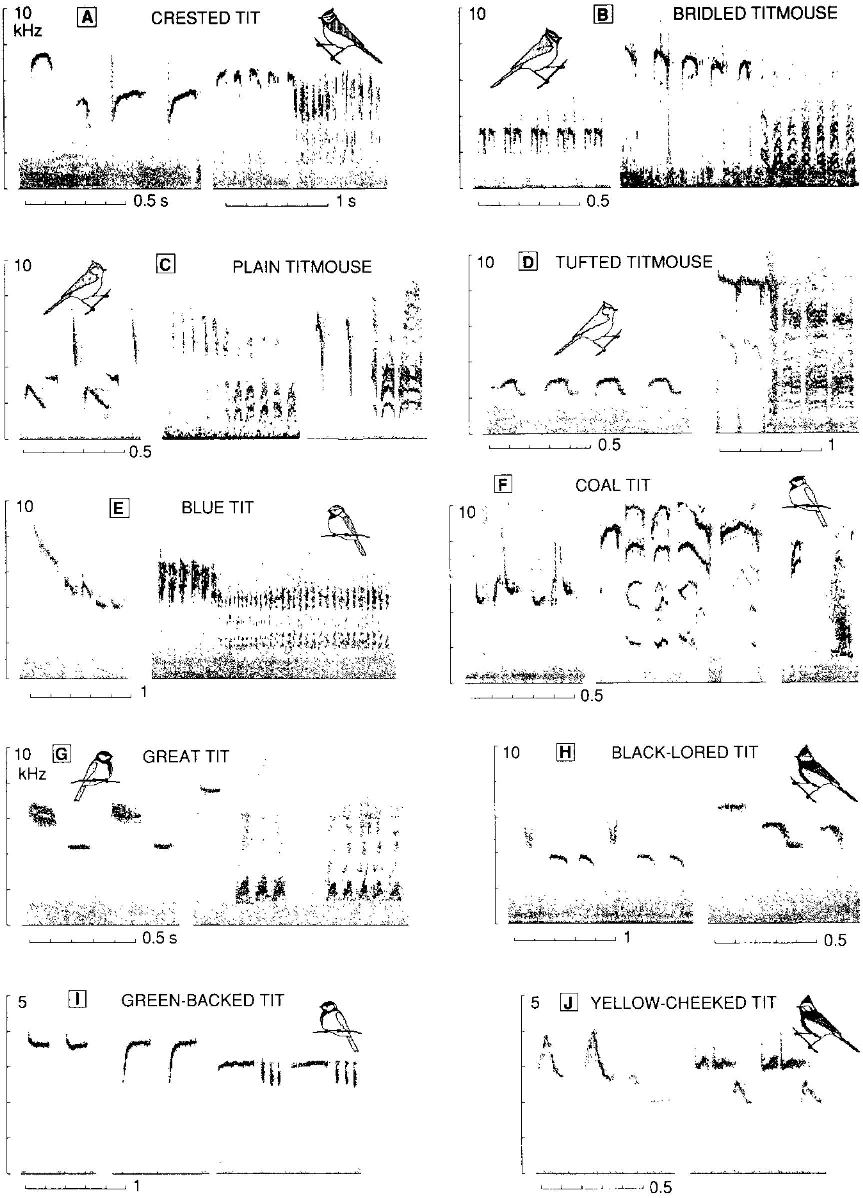

FIG. 1. Sound spectrograms of a sample of vocalizations from primarily European and North American parids other than chickadees and their close relatives (Fig. 2). Sounds were recorded by the author except as noted in the text; for categorization of sounds, see text.

species of Mexico and southwestern United States had three song-types of repeated single notes, which were given by all four of his marked males. One type is an upward slur and the other two are chevrons, one occurring as repeated couplets and the other as repeated notes (op. cit., p. 18). Figure 1B (left) shows an extract from the repeated-couplet type of song from CLO tapes. Gaddis found the three song-types tended to be used in different contexts: the slurred type in spontaneous advertising, the couplet-type in distant exchange (counter-singing by males), and the chevron-type in close exchanges and when approaching the nest.

The other published spectrogram of this species' voice resembles the unit-pattern of the foregoing species (Robbins et al. 1966:216, repeated in the revised edition, 1983:230). Figure 1B (right) shows a typical call, with an opening slurred HF-notes, four chevron-shaped HF-notes and a string of LF-notes. Me recordings appear to show an intermediate between the chevrons and LF-notes. This call-type sounds very much like "chick-a-dee" calls of the Poecile (below), but I cannot say yet whether it has combinatorial properties.

Plain Titmouse *(P. inornatus).*—Dixon's (1949) early behavioral study of this western United States species concluded that the Plain Titmouse had "two basic types" of songs that were used somewhat differently, plus "highly variable call notes." Later, Dixon's (1969) spectrographic study showed that songs consist of strongly slurred HF-notes of one type repeated or short, alternating phrases. Fig. 1C (left) from CLO tapes shows a repeated three-note phrase. Dixon identified no fewer than 17 "song themes" from a study of 12 males, and "the three males whose vocabularies appeared most thoroughly documented, uttered 11, 10, and 9 motifs, respectively" (pp. 96–97). He felt that there was some separation of usage, particularly between agonistic interaction and counter-singing. Gaddis (1983:19) showed similar song spectrograms, and found repertoires of individual males ranging from 5 to 11 of the 12 types he recorded from five individuals. His data indicate a statistical association between song-types and three contexts of use: advertising, exchanging (counter-singing) and approaching nest. Johnson (1987) found that of 14 song-types, five were statistically associated with one or two contexts while others were used interchangeably.

The only non-song spectrograms are four by Dixon (1969:97), only two of which are cited in the text. Three of the four appear to be like chick-a-dee calls, although only the call in his fig. 3C is so designated explicitly: one HF-note followed by four banded LF-notes. He mentions (p. 95) that both sexes give this call. His fig. 3B consists of two HF-notes, a pair of LF-notes, another HF-note, and then two more LF-notes. Finally, his fig. 3D consists of a series of HF-notes, which Dixon terms a "trill." These notes appear to be shorter than the HF-notes of the other calls, and the first note of this series is higher-pitched. My Fig. 1C (middle) shows the beginning of a call in which the banded LF-notes continued for about three times the duration of the string shown. There is a striking aural similarity of this kind of call with that of the Crested Tit (Fig. 1B, right). A recording from CLO tapes (Fig. 1C, right) shows longer LF-notes, which may also be of higher frequency. It is not possible to say if such variation represents different types of LF-notes, or is attributable to individual differences, geographic differences or other factors; nor is it clear whether these chick-a-dee-like calls are combinatorial.

Dixon's (1969:97, fig 3A) other non-song vocalization is "a characteristic utterance" consisting "of several similar, high-pitched notes, followed by two closely spaced, emphatic sounds" (p. 94). The figure-legend terms this "the 'call derivative' song of the Plain Titmouse." It seems possible that this vocalization represents the functional homolog of the Black-capped Chickadee's gargle (discussed below). This might be the same vocalization that Johnson (1987:27–28, figs. 2 and 4) termed song #14 "associated with attack on rival males."

Tufted Titmouse *(P. bicolor).*—The commonly phoneticized "peter" vocalization of this eastern North American species is so frequently uttered that other vocalizations are difficult to record (spectrograms in Robbins et al. 1966:216, 1983:230; Latimer 1977:421; Gaddis 1983:20; Schroeder and Wiley 1983a, b). These "songs" almost always consist of a repeated slurred note or an alternation of two fairly tonal and simple HF-notes. Fig. 1D (left) shows four slurred notes from a longer bout of song. The marked males of Gaddis (1983:19) had repertoires of 7, 12, 14 and 15 song-types; Schroeder and Wiley (1983a, b) report repertoires of 8–12 "song themes." Lemon (1968: plate I) shows spectrograms from the black-crested race of the Tufted Titmouse (*P. bicolor atricristatus*) in Texas, formerly considered a separate species. These songs are similar to those of the nominate race, and Lemon's birds had repertoires of 7–12 different types. Insofar as I can determine there are no published spectrograms of any vocalization besides song for the Tufted Titmouse. Fig. 1D (right) shows an example of its infrequently used chick-a-dee-like calls. At least three note-types make up these calls: a few HF-notes followed by one IF-note and ending with several LF-notes in the longest calls. I cannot say yet if these calls have combinatorial properties.

Cyanistes: Blue and Azure Tits

There are only two species in this subgenus. The Blue Tit (*P. caeruleus*) has a clearly differentiated repertoire, but major vocalizations are built on basic HF-(IF)-LF patterns like the single pattern of the Crested Tit (above). The similar Azure TIt (*P. cyanus*) of Asia ranges westward to eastern Europe; Bergmann and Helb (1982:336) show spectrograms of song (fig. a) and calls (fig. b), indicating that the second might be a type of song.

Blue Tit *(P. caeruleus).*—I believe that this common European (and North African) species is especially important to the understanding of vocal evolution in the Paridae. Compared with the Crested Tit (above), the Blue Tit shows a markedly clearer differentiation of vocalizations into three major types, a pattern that characterizes even more strongly the remainder of the family.

In a novel analytical approach, Bijnens and Dhondt (1984) began by classifying "syllables" (what I term notes: continuous traces on the spectrogram, which may have disjunct frequency components, but are not continuous in time with other such traces). They identified two major types ("A" and "B" syllables), which correspond roughly with my HF- and LF-notes, and within each main type further identified subtypes. Finally, they characterized complex vocalizations according to the composition of note-types, thereby identifying eight alarm and antipredator calls with a broad-spectrum (LF) element (table 1 on p. 250), about 16 distinct combinations in which A- and B-notes (HF- and LF-notes) both occur (table 2 on p. 251), and at least 10 "song-types" (table 3, p. 251) made primarily of A-(HF-)notes.

Vocalizations of the Blue Tit that have been called "song" vary widely (Thielcke 1968:150; Latimer 1977:418; Becker et al. 1980; Becker 1982: 228; Miller 1982:262–263; Bergmann and Helb 1982:337; Bijnens and Dhondt 1984). These songs are typically composed of two or three different note-types, commonly in the sequence of several HF-notes followed by several IF-notes, or less commonly LF-notes (but in some cases alternating between two types). The HF-notes are typically chevron-shaped or tonal, and the IF- and LF-notes range from those of broad-frequency, noisy or banded structure on the one hand, to short, nearly tonal notes on the other. Intermediate types range from downslurs to short-duration, stacked chevrons. Within this vast diversity one can find at least one note-type resembling almost any kind of note given by any parid species. Fig. 1E (left) shows a typical song-like vocalization. It is clear that a given individual sings several types of these complex vocalizations (Becker et al. 1980; Bijnens and Dhondt 1984), and that marked geographic variation in song-structure occurs (Thielcke 1969b, Becker et al. 1980). Both sexes sing (Bijnens and Dhondt 1984), and some song-types tend to be used in different contexts, whereas others appear to be interchangeable.

In the contexts of predator-mobbing or disturbance at the nest, similar but more structured vocalizations are given (Thielcke 1968:154; Latimer

1977:423; Bergmann and Helb 1982:337, figs. d and e; Klump and Curio 1983:80, "scolding"; Bijnens and Dhondt 1984:248–249). All these calls are similar to "songs" in being composed of series of HF-, IF- and LF-notes, but with considerable variability and commonly emphasizing LF-notes. Fig. 1E (right) shows an alarm-type vocalization.

An interesting result from Bijnens and Dhondt (1984) is the isolation of a "conflict call" (fig. 13, p. 256), which they recorded "when tits had physical contact, or when one tit was approached by another one to within 0.5 m during foraging" (p. 257). This conflict call consists of five different note-types, with further variation evident within types. The B4-syllable appears trill-like. The curious notes shown in spectrograms 4 and 5 by Latimer (1977:425) under the title "alarm and aggression calls" resemble somewhat the B4 and B7 notes used in the conflict call of Bijnens and Dhondt (1984).

Periparus: Coal Tit and its Relatives

This subgenus now contains four species, the Rufous-vented Tit (*P. rufonuchalis*) having been separated from the Rufous-bellied Tit (*P. rubidiventris*) subsequent to Thielcke's (1968) listing. The better known vocalizations of the Coal Tit (*P. ater*) are presented first and the other three summarized in a second account.

Coal Tit (P. ater).—This Eurasian species (which ranges southward to the north coast of Africa and eastward to Siberia and Japan) has greatly elaborated the HF-notes and virtually eliminated the LF-notes from its vocalizations. Its vocal organization is like no other western European or North American species.

The Coal Tit has a well-differentiated song consisting most typically of an alternation of two or three types of slurred HF-notes (Thielcke 1968: 150, 151; 1969a; 1973; see also Gompertz 1968:78, figs. 3a and d; Jellis 1977:121, 122, 170; Bergmann and Helb 1982:334; and Martens 1975: 413—all based mainly on recordings by Thielcke and Martens—and Goller 1987). Figure 1F (left) shows two three-note phrases from a bout of singing in which the phrase was repeated over and over. Males may have a repertoire of at least six song-types but the existence of local dialects is problematical, as a given song-type may show up in a distant population. Haftorn (pers. comm.) has recently found in Norway that an individual male sings up to 14 distinct song-types, and there is further variation manifest in frequency-shifts (cf. Black-capped Chickadee account, below) and other small phonological changes in note-types. Goller (1987) found similar results in the Tyrolian Alps, where individual males had repertoires of 12–16 song-types and the acoustic frequency of notes varied through the season. Goller also found evidence for differences in the contextual use of different song-types. The song of the Asian form, *P. ater aemodius* (Jellis 1977:170, figs. 65b and c; Martens 1975:412, 413) is quite similar to that of the nominate race in Europe (*P. a. ater*).

A remarkable characteristic of the Coal Tit is the constant production of extremely varied single HF-notes during social contexts in which most *Parus* use chick-a-dee calls or some other combination of notes (Bergmann and Helb 1982:334, figs. c–d and g–h). Fig. 1F (middle) shows these notes from my Norway tapes on which about two dozen more-or-less distinct note-types occur. The intervals between notes are variable, but do not group into short and long classes that would suggest intra- and inter-call intervals.

Equally remarkable is the near lack of LF-notes in scolding or mobbing contexts, where virtually all other parids commonly employ them. Instead, The Coal Tit utters primarily two types of loud HF-notes: one an inverted chevron on spectrographic display and the other a higher note with a long arm that descends in frequency (Thielcke 1968:153; Löhrl and Thielcke 1973:250; Jellis 1977:171; Bergmann and Helb 1982:334, fig. f). The latter note has two parallel energy bands beginning about 7 and 5.5 kHz. Löhrl and Thielcke (1973) report the use of rare LF-notes once in a "very excited" European Coal Tit. The second note in Fig. 1F (right) appears to be one of these rare LF-notes, which I recorded during an agonistic encounter. Interestingly, the North African subspecies (*P. ater atlas*) does use typical parid LF-notes in scolding (fig. c in Löhrl and Thielcke 1973:114). When birds from the nominate European race (*P. a. ater*) were caged with three individuals brought from Morocco and presented with a stuffed Tawny Owl, the European birds began using the LF-notes like the African subspecies (Löhrl and Thielcke 1973:114, fig. d; recounted in Jellis 1977:171, fig. 67d).

One further call requires mention. Bergmann and Helb (1982:334, fig. e) show a note termed "psich," which resembles the two-banded note used in scolding but is lower-pitched and noisier. A somewhat similar note (first note in Fig. 1F, right), which I termed the "sharp note" in my field commentaries, often occurs during close agonistic encounters.

Related species.—The Black-crested Tit (*P. melanolophus*), restricted to the mountains ringing the north part of the Indian subcontinent, is exceedingly similar to an Asian race of the Coal Tit (Martens 1975), and its songs (Thielcke 1968:151; Martens 1975:415; Jellis 1977:170, fig. 65d) are virtually identical. The HF-alarm notes of *melanolophus* (Thielcke 1968:153 and 154; Löhrl and Thielcke 1973:250, fig. b; Jellis 1977:171, fig. 67b) are also highly similar to those of *ater*, having two or more parallel energy-bands and completely lacking LF-notes. Löhrl and Thielcke (1973) also caged Black-crested Tits with the African race of the Coal Tit, which possesses LF-notes, and found that (like European Coal Tits) the Asian species at first responded to a stuffed owl in the usual species' way but then began making the LF-notes. Based on hybridization evidence (Diesselhorst and Martens 1972) *melanolophus* should be considered conspecific with *ater.*

The Rufous-bellied Tit (*P. rubidiventris*) was once considered to range from western China westward to Pakistan, but the field research of Martens (1975) indicates that the western form should be considered a distinct species, *rufonuchalis* (below). The songs and calls shown in Thielcke (1968: 151) under the name "rubidiventris" belongs to *rufonuchalis* (fide Martens, in litt.). Martens (1975:384, 389) shows songs of *rubidiventris* as now recognized; these songs are quite similar to those of the two preceding species. The alarm calls (Thielcke 1968:153, 154) have the parallel-banded HF-note structure like that of the two preceding species, with no indication of an LF-type of note. However, these calls may belong to *rufonuchalis.* Martens (1975:391) shows a trilled element from the subspecies *P. rubidiventris beavani,* which he considered a possible homolog with trilled song in *rufonuchalis* (see below). This might represent a third major type of vocalization, but at present may be considered a note-variant of song.

The Simla Black Tit (*P. rufonuchalis*), is a Karakoram-West Himalayan equivalent of the foregoing species. Its "trilled song" (Thielcke 1968:151, fig. 21; Martens 1975:382) contains an obviously trilled element of varying phonology, usually at or near the end of the vocalization. The "whistled song" (Thielcke 1968:151, fig. 2m; Martens 1975:383) is variable and shows similarities with song in the three foregoing species. As with *rubidiventris* immediately above, it is not clear if the "trilled" songs should be considered as fundamentally different from the "whistled" songs as a separate major vocalization type. If the alarm calls labeled "rubidiventris" in Thielcke (1968:153, 154) belong to *rufonuchalis* as I suspect, then this species resembles the Coal Tit and Black-crested Tit in having parallel-banded HF-notes and no indication of LF-notes.

Parus: Great Tit and its Relatives

Thielcke (1968) lists five species in the nominate subgenus, but the form *bokharensis* may be a race of the Great Tit (*P. major*) and is not treated here. The Yellow-cheeked Tit (*P. spilonotus*) does not appear in Thielcke's list as it was formerly confounded with the similar Black-lored Tit (*P. xanthogenys*). The well-studied Great Tit is considered first, then related species are summarized in a second account.

Great Tit *(P. major*).—This is one of the largest, most widespread, and best known parids in the world, ranging from European and North Africa eastward across Asia and southeastward throughout the Middle East to the Indian subcontinent. Its song has been studied more extensively than that of any tit, and its complex vocal repertoire was described verbally by Hinde (1952), and then became one of the first to be compiled for any bird after the sound-spectrograph became available (Gompertz 1961). It may therefore seem ironic that I remain uncertain about vocal organization in this species—but for a simple reason: it mimics other species, including other tits.

The repertoire was studied in detail by Gompertz (1961) early in the spectrographic era, and most of her illustrations are of song (see also spectrograms of Gompertz 1968; Thielcke 1968:150, 1969a:149, 151; Krebs 1976; Jellis 1977:55, 145, 167, 203; Hunter and Krebs 1979; Sasvári 1980:393, Bergmann and Helb 1982:335; McGregor et al. 1983; Baker et al. 1986; Klump et al. 1986:386). Song commonly consists of an alternation of two HF-note-types (Fig. 1G, left), or an alternation of couplets of those types. Males usually have a repertoire of 2–7 song-types and there is much geographic variation. Many of the above-cited papers are devoted to analysis and experimentation on Great Tit song (see also Lehtonen 1954; Sasvári 1971a, b; Krebs 1977a, 1977b; Krebs et al. 1978; Bergman 1980; McGregor et al. 1981; McGregor and Krebs 1982a b, 1984; Falls et al. 1982; Lambrechts and Dhondt 1988). Martens (in litt.) has pointed out that the grey forms of middle Asia, India, and the Himalaya) (*P. major cinereus*-group) sing quite differently from the well-studied European subspecies.

Great Tits also employ LF-notes, called "churring" by Gompertz (1961), especially in alarm contexts (Löhrl 1963:547; Thielcke 1968:154, Jellis 1977:81; Sasvári 1980:394; Bergmann and Helb 1982:335, fig. c; Klump and Shalter 1984:194, fig. 2b; Klump et al. 1986:386, two middle figures). With the possible exception of Bergmann and Helb (1982)—where one cannot tell if fig. c is a unitary call or three kinds of notes assembled for illustration—only Jellis (1977:81) shows HF-notes combined with the LF-churrs. I found in Norway that one or several HF-notes commonly preceded a train of LF-notes (Fig. 1G, right), thus conforming to the typical parid pattern. Literature suggests several kinds of LF-notes. Gompertz's (1961) original descriptions were unsupported with spectrographic documentation, but she listed six types of churring and Jellis (1977:81), using recordings made by Gompertz, illustrated several kinds of churrs in small spectrograms. Associated contexts include territorial skirmishes, scolding, excited foraging, seeking contact with the mate, and "situation tricky but not dangerous." Klump et al. (1986:386) distinguish "scolding" and "mobbing" calls given to a cat, and these are both quite noisy calls; neither type is identical with the calls I recorded (Fig. 1G, right). In summary, LF-notes vary greatly and a complete classification is not yet possible. A great variety of other calls is described by Gompertz (1961), with a few spectrograms (see also Jellis 1977, Bergmann and Helb 1982:335). Many of these calls and notes, unlike notes of the Coal Tit (above), are commonly used in various combinations, and some undoubtedly are allied to combinations used in churring. Although not organized like chick-a-dee calls (below), the Great Tit's many LF-churrs and associated HF-notes clearly present at least a semi-combinatorial system of fascinating complexity.

Gompertz (1961:387–388) also describes a "muttered threat" call. This is a three-note phrase "which begins and ends on the same pitch, with the middle note lower." This call is used in close-distance agonistic interactions. The "war-whoops" shown by Jellis (1977:80) might be this muttered threat, and she points out that each male is likely to have variants of this aggressive call. There thus appears to be a third major vocalization in the Great Tit's repertoire that is functionally, if not phonologically, similar to the gargles of species discussed later.

Related species.—The Black-lored Tit (*P. xanthogenys*) of Asia sings at least a three-note, repeated phrase similar to songs of the Great Tit (Fig. 1H, left, taken from CLO tapes). Thielcke recorded responses of captive birds to a stuffed owl and showed a spectrogram (Thielcke 1968:154) of three note-types in a sequence that shows permutation (1-2-1-3). In 1987 we copied his complete tapes of the experiment, and selected the recordings of one individual for extensive quantitative analysis (Hailman and Thielcke MS). Notes, as in the preceding Great Tit, show considerable variety, but there are four modal types, two of which are shown in Fig. 1H (right). Notes are combined in various sequences, which show permutation of order as well as combination of type, and Markov-chain analysis shows that statistical rules govern this combinatorial system.

The Green-backed Tit (*P. monticolus*) of the Himalayas and China signs an alternation of two whistled notes, one tonal and the other steady in pitch then slurred down to a new pitch (Thielcke 1968:151). It is within the variation of the Great Tit songs. Fig. 1I, from CLO tapes and those provided by Jelle Scharringa, shows two phrases from each of three different songs. In all three cases the phrase is repeated over and over, but in the first two (left and middle) the phrase consists of only one note, whereas in the other case (right) it is a four-note phrase with two note-types. This is the sort of interesting song variety shown by the Great Tit. The alarm call (Löhrl 1963:547 and Thielcke 1968:154) is a repeated IF-note, tending toward banded LF-type but quite noisy. Is is similar to one of the several kinds of churring of the Great Tit.

The White-winged Tit (*P. nuchalis*) of the Indian subcontinent has a vocalization with notes similar to types used by the Great Tit and other species (CLO tapes). However, it is unclear whether this represents song or a combinatorial system of call-notes. The Yellow-cheeked Tit (*P. spilonotus*), of the Himalayas and Indian subcontinent through southwestern China and southeast Asia, was recorded in the field by Jelle Scharringa, who kindly provided tapes. Fig. 1J shows two extracts from songs, both composed of repeated three-note phrases (one phrase shown at left and two phrases shown at right). It is not certain that these two songs were from the same individual, but these and other song-types on the tape suggest the possession of repertoires.

Poecile: American Chickadees and their Old World Relatives

This is the largest subgenus, containing a dozen species as listed by Thielcke (1968), all of which are considered here except Pere David's Tit (*P. davidi*). The well-studied Black-capped Chickadee (*P. atricapillus*) is considered first, followed by species with similar vocal organizations, finally by species with repertoire patterns that are obviously different or incompletely described.

Black-capped Chickadee *(P. atricapillus).*—This widespread North American species is the archetype of its major group, which includes all New World forms known as chickadees and certain Old World tits. Perhaps the first (prespectrograph) vocal repertoire of any bird was of this species (Odum 1942); the modern spectrographic study by Ficken, Ficken and Witkin (1978) still stands as one of the most complete repertoires for any bird. All three of its major vocalizations—fee-bee, chick-a-dee calls and gargles—have been subjected to extensive analyses.

Whistled "song" or "fee-bee" (known as "phoebe" in earlier literature) has obvious homologs in closely related species to follow. That both sexes give this vocalization was noted by Dwight (1897) in a two-sentence paper, the second sentence of which was "I am not aware that record has ever been made of this fact, which I determined some time ago by the judicious use of firearms." Many spectrograms have been published (Thönen 1962: 117; Robbins et al. 1966:214, repeated in 1983:228; Dixon and Stefanski 1970:54; Ward and Ward 1974:350; Latimer 1977:421; Jellis 1977:164, fig. 62f; Ficken, Ficken and Witkin 1978:36; Ficken 1981a:385; Ratcliffe and Weisman 1986:362). The typical fee-bee consists of two tonal notes of about 350 msec, separated by about 130 msec silence, the second note about 0.5 kHz lower (Ficken, Ficken and Witkin 1978:35, table 1); the "faint fee-bee," which is given by both sexes, is treated as a distinct vocalization. The fee-bee *sensu stricto* is apparently given only by males (*contra* Dwight 1897); it is basically invariant, so there are no repertoires or local dialects (but see below). This simple vocalization has been termed the species' "song" because it is heard in spring from the male on territory—certainly not because of phonological complexity. The fee-bee has been the subject of much comment and a number of specific investigations (e.g., Dwight 1897; Lumley 1934; Desfayes 1964; Dixon and Stefanski 1965, 1970; Ward and Ward 1974; Ficken, Ficken and Witkin 1978; Ficken 1981a; Ratcliffe and Weisman 1985, 1986, 1988).

In an overlooked report, Bagg (1958) noted that birds on the island of Martha's Vineyard (Massachusetts) sing both notes on the same pitch. Leonard Peyton provided tapes from Alaska: Fig. 2A (left) shows one of several songs in which the two notes are obviously at the same frequency; there is also a tendency for each note to be followed by a very brief pulse at the same frequency.

Like the fee-bee, the chick-a-dee call was well known to field workers before the advent of tape recorders and has been subjected to several kinds of analytical studies. Published spectrograms are many (Thielcke 1968:154; Witkin 1977:490; Latimer 1977:426; Ficken, Ficken and Witkin 1978a:36; Dixon and Martin 1979:422, fig. 1c; Mammen and Nowicki 1981:180; Nowicki 1983:317, 1987:53; Hailman et al. 1985:194, 1987: 67–71; Nowicki and Caprinica 1986a:1298; 1986b:3597, 3599, 3606). The four note-types composing calls are two HF-notes (labeled "A" and "B"), an IF-note ("C"), and a banded LF-note ("D"). Calls are highly combinatorial, with note-types virtually always occurring in the sequence A-B-C-D, from which any note-type may be missing entirely, given once or repeated a variable number of times. Calls have been studied specifically with respect to sound-radiation patterns (Witkin 1977), flock- and individual-specific structure (Mammen and Nowicki 1981; Nowicki 1983), sequential or syntactic structure (Ficken, Hailman and Ficken 1978; Hailman et al. 1985, 1987; Hailman and Ficken 1986), and mechanisms of phonation (Nowicki and Capranica 1986a b; Nowicki 1987).

The third major vocalization is the exceedingly complex gargle, first spectrographed by Dixon and Stefanski (1970:54), who termed it the "fighting call," and by Dixon et al. (1970:324), who termed it a "supplanting call" (see also Ficken, Ficken and Witkin 1978:36; Ficken 1981a: 385; Ficken and Weise 1984:352–253; Ficken et al. 1985:147, 149). Gargles are jumbles of highly slurred, extremely brief notes decreasing in average frequency through the call, commonly ending with a low-pitched trill or banded note of longer duration than the introductory notes. Fig. 2A (right) shows a lengthy gargle, with a trilled note in the middle instead of near the end. The gargle may be given by females but is much commoner in males, and is clearly associated with agonistic encounters. There are 2–13 notes in a call, drawn from a local dialectical "pool" of 16–23 different note-types that are shared almost entirely by all local individuals.

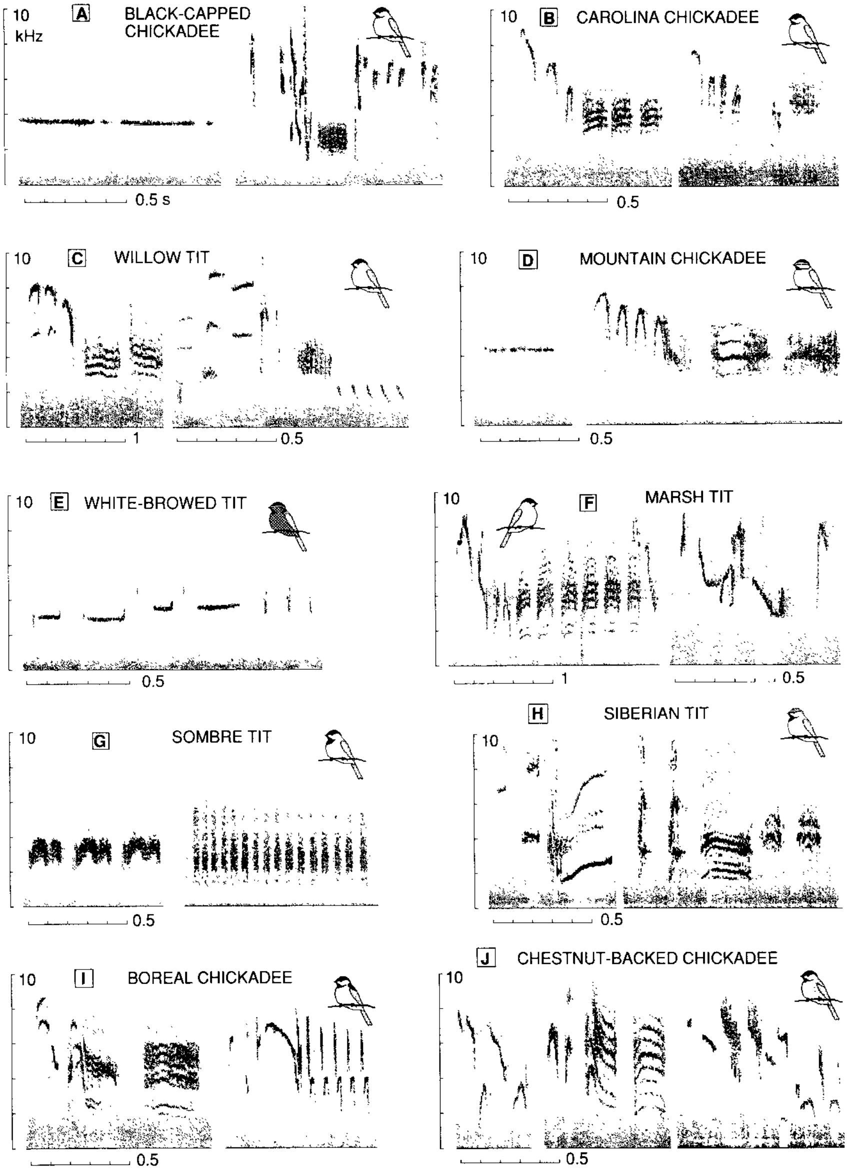

FIG. 2. Sound spectrograms of a sample of vocalizations from North American chickadees and their close Eurasian relatives.

Dialects vary microgeographically, with marked differences in local "pools" of note-types found within 5.7 km. Specific analytical studies of gargles are by Ficken and Weise (1984) and Ficken et al. (1985, 1987).

Carolina Chickadee *(P. carolinensis)*.—The vocal repertoire of this species of southeastern United States is similar to that of the parapatric Black-capped Chickadee, the two hybridizing in certain areas of contact but not in others. The major study of the Carolina Chickadee's vocalizations is Smith (1972).

The tonal "whistled song" was long ago recognized to have about four notes in contrast with the Black-capped Chickadee's two-noted fee-bee (Thönen 1962:117; Robbins et al. 1966:214, 1983:228, Ward 1966:141, 143, 146; Smith 1972:67–70; Ward and Ward 1974:351; Jellis 1977:164, fig. 62g; Latimer 1977:421). In addition abnormal songs from southern Pennsylvania are shown by Ward and Ward (1974:347), who state that these may be the result of hybridization or variants used to defend interspecific territories in an area of overlap. Although the song is typically a doubling of the Black-capped Chickadee's fee-bee, with a drop in pitch for the second couplet, Ward (1966:134, table 2) showed that songs may range from one to 12 notes. Like the fee-bee, these songs are commonly sung on territory by males in spring.

Chick-a-dee calls have been published only as hand-traced spectrograms on a 0-8 kHz scale (Smith 1972:76–78), although emphasized components of some notes commonly lie above 8 kHz. Smith recognized three note-types: an HF-note (termed "High Tee"), an IF-note ("Chick"), and an LF-note ("Dee"). Her fig. 2.15C (p. 76) shows an HF-IF intermediate, and fig. 2.26C (p. 77) shows two longer-duration HF-notes labeled "High See." The text (p. 49) states that these two note-types "intergrade completely." Therefore, in a direct comparison with the Black-capped Chickadee, High See = A, High Tee = B, Chick = C, and Dee = D, except that the first two intergrade in the Carolina Chickadee but do so only rarely in the other species (Hailman et al. 1985). Figure 2B (left) shows a chick-a-dee call, where it can be seen that the first HF-note peaks at about 9 kHz and the three introductory notes appear to present a graded series.

Smith (1972:62–67) showed many spectrograms of obvious gargle homologs to which she gave a variety of names: T-slink, Click-rasp, Tee-rasp, Rasp-slink, and Slink-rasp-slink. The calls are composed of typically slurred notes that tend to decrease in frequency and end with some sort of trill. The note-types shown in 19 spectrographed gargles are more diverse than the verbal labels imply, and the gargle system of the Carolina Chickadee appears virtually identical with that of the Black-capped Chickadee. Figure 2B (right) shows a gargle following a chick-a-dee call; the apparent pause within the vocalization is due to rapid transients that do not show on the spectrogram. This species sometimes runs together chick-a-dee calls and gargles thus, or may have intermediate vocalizations. The next species below sometimes inserts gargles into song, further demonstrating some interesting vocal complexity in this subgenus.

Willow Tit *(P. montanus)*.—Formerly classified as conspecific with the Black-capped Chickadee, this widespread species is common in Europe and ranges east across Asia. The vocal repertoire is very similar to those of the Black-capped and Carolina chickadees. There are two major geographic variants of a simple song. One is a repeated, whistled downslur ending in a pure tone (Thönen 1962:117; Thielcke 1968:151, 1969b:323, figs. 6a and b; Ludescher 1973:13, figs. 4g–m; Jellis 1977:164, figs. 62b and c; Latimer 1977:418 bottom; Romanowski 1978:248, 1979:60; Bergmann and Helb 1982:339, fig. a). The other is a succession of tonal notes, much like the whistled fee-bee of the Black-capped Chickadee, but remaining on virtually the same pitch throughout (Thönen 1962:117; Thielcke 1969b;323, figs. 6c and d; Jellis 1977:164, figs. 62d and e; Romanowski 1979:56, 61; Bergmann and Helb 1982:339, fig. b). Thönen (1962) found in Switzerland that the slurred song is characteristic of the plains and the tonal song of the Alps. However, I have recordings from Norway of nearly tonal notes (with a slight initial downslur). The literature suggests that a male sings only one basic song, with minor variations, and there are no local dialects, but as Haftorn (in litt.) points out, whether the variants are minor variations or major song-types is a matter of definition. Romanowski (1979) found by playback experiments that the downslurred part of the first song-type was relatively unimportant in eliciting responses, the important part being the pure-tone frequency at the end (which is common to both songs).

The chick-a-dee calls are similar to those of the Black-capped Chickadee (Thielcke 1968:154; Ludescher 1973:12, figs. 3m–o; Jellis 1977:171, fig. 68b; Latimer 1977:426; Romanowski 1978:249, figs. 14a and b; Bergmann and Helb 1982:339, fig. d). At least two note-types are revealed in these spectrograms: an HF-chevron (the "zi" of Bergmann and Helb) and an LF-note virtually identical with the D-note of the Black-capped Chickadee except for longer duration (about 400 msec). The LF-note in fig. 14b of Romanowski (1978:249) is somewhat transitional from an HF-note. My Fig. 2C (left) shows three HF-notes followed by the first two of three LF-notes in a typical call. Ludescher (1973:12, fig. 3n) shows three short notes before an LF-note, these consisting of stacked chevrons and probably representing a third type of (IF) note.

The gargle-equivalent of the Willow Tit has at least two interesting properties (Ludescher 1973:12, figs. 3p–5; Romanowski 1978:249, figs. 14c and d; Bergmann and Helb 1982:339, fig. c). In the last reference, a trill begins the call, and after a slurred note, a higher-pitched trill ensues, followed by a regular repetition of an HF-note that is so rapid as almost to be trilled as well. Ludescher's fig. 3q and Romanowski's fig. 14d also show imbedded trills. The Willow Tit's gargles thus depart slightly from the generality of a jumble of diverse FM-notes of descending frequency followed by a terminal or subterminal trill. Fig. 2C (right) shows the trill near the end, after five introductory notes, but followed by a string of five notes of one type. The other unusual characteristic is that the Willow Tit commonly inserts gargles within its song (pers. obs.); indeed, Bergmann and Helb (1982) treat this vocalization as "song."

Mountain Chickadee *(P. gambeli).*—The vocal organization of this western North American species is similar to that of the Black-capped Chickadee. The only published spectrogram of its whistled "song" appears to be in Gaddis (1985:32, fig. 2, lower right): three tonal notes at about 4.4 kHz. My tapes show that the number of notes in a song varies within one individual, thus suggesting some sort of song-repertoire. Figure 2D (left) shows one note from a vocalization of three identical notes, which are typically "broken" in spectrographic displays, suggesting amplitude modulation.

Chick-a-dee calls appear to have at least four different note types (Robbins et al. 1966:214, 1983:228; Thielcke 1968:154; and Gaddis 1985:32, left side of fig. 2). The two most evident types are a chevron-shaped HF-note (Thielcke 1968: Gaddis 1985:32, figs. 2A–F, H–J) and a banded-to-noisy LF-note (Robbins et al. 1966; Thielcke 1968; Gaddis 1985, fig. 2H and I). There is in addition a shorter-duration IF-note that often appears as a down-slur (Robbins et al. 1966, Thielcke 1968) or a noisy chevron (Gaddis 1985:32, figs. 2G and J). A type of note very common in this species is an "attached" HF/LF-note in which the last chevron of a series is continuous in time with the first LF-note. This HF/LF-note is shown in Gaddis (1985, fig. 2I and J, and in a lesser form in 2H). These three note-types (not counting the attached HF/LF) seem to occur always in the order HF-IF-LF. If there are no IF-notes in a call, there is almost always an attached HF/LF-note between the HF-series and the LF-series. Fig. 2D (right) shows a call with three introductory HF-notes, and "attached" IF-note, and two LF-notes. The first LF-note is banded and the second one noisy; in extreme cases, the banded variant becomes a single tone at about 3.7 kHz, thus reminding one of the song-notes (Fig. 2D, left) in this species.

A third category of major vocalization is somewhat problematical. Dixon (1972) first described the "attack call," then Dixon et al. (1970:324, fig. 2A) showed the evidently identical "aggressive call" consisting of slurred notes that decrease in average frequency. Their fig. 2D of a "supplanting call" ends in partially trilled components, much like the Black-capped Chickadee's gargle. Whether the calls shown by Gaddis (1985:32, figs. 2L–N, also fig. 5 on p. 39) belong to this same complex is difficult to decide. He divides them into three subtypes and attempts to correlate them with different behavioral contexts (p. 38, table 4) but the sample sizes do not allow firm conclusions. Gaddis identifies (p. 38) one component note-type with "close aggressive contact."

White-browed Tit *(P. superciliosus).*—There are no published spectrograms for this species of western China, but I found one type of vocalization in the CLO tapes (Fig. 2E). The first note also occurs as a long repeated series, and I preliminarily interpret these vocalizations as song. The whistled notes at about 3 kHz are very similar to songs of the foregoing species in this subgenus, although the vertical "clicks" may be unique.

Marsh Tit *(P. palustris).*—The song of the Marsh Tit, a common European species that also occurs disjunctly in eastern Asia, is clearly elaborate with respect to foregoing chickadees and the Willow Tit (Thönen 1962:117; Thielcke 1968:151; Ludescher 1973:13, figs. 4a–f; Jellis 1977: 164, fig. 62a; Latimer 1977:418, spectrogram 4 of this species; Becker 1978a, 1978b, 1982:224, Romanowski 1978, 1979:50; Bergmann and Helb 1982:338; Rost 1987). Perhaps the most typical song consists of repeating a downslurred note somewhat like the plains' form of the Willow Tit's song. Many songs, however, are alternations between a downslurred note and a tonal whistle, or in some cases even more complexly arranged with two slurs, or trills, or trills and slurs (see esp. Ludescher 1973, Romanowski 1978, Becker 1978b, Rost 1987). The trilled elements in song are unusual for a parid, and suggest affinities with gargles; recall that the Willow Tit inserts gargles within its singing bouts. Marsh Tit males have repertoires of up to 19 different learned songs. Although females sing less than males, the size of their repertoires and tonal quality of their songs are comparable. There are local dialects, and some indication that different songs tend to be used in territorial defense and courtship. Romanowski (1979) found by playback experiments that the most critical variables in song-recognition were the frequency modulation and the intervals between successive notes.

The Marsh Tit also gives typical chick-a-dee calls (Thielcke 1968:154; Ludescher 1973:12, figs. 3a–k; Jellis 1977:171, fig. 68a; Latimer 1977: 425; Romanowski 1978:241, figs. 6c and 7a; and Bergmann and Helb 1982:338, fig. d). At least three, probably four, note-types can be separated. There is a broad HF-chevron and probably a separate HF-type with small-amplitude, rapidly-modulated FM-excursions superimposed on the shallow downslope following the chevron's peak (the "pistjä" note in Bergmann and Helb). An IF-note is a simple, emphatic downslur. The LF-note is of short duration (50–100 msec), called "dä" by Bergmann and Helb, and its frequency banding consists of stacked chevrons. Fig. 2F (left) shows a chick-a-dee call, with introductory chevron followed by a downslur then two further small notes before the string of six LF-notes; another downslurred note concludes the call, showing permutation of note-types in this species. The close relationship between the chick-a-dee call and song in the Marsh Tit is illustrated by fig. 7 in Romanowski (1978:241), showing rare intermediate vocalizations as the bird switches between song and call.

The third major vocalization is included as "territorial song" by Latimer (1977) and as a call by Bergmann and Helb (1982); it appears to be the Marsh Tit's functional equivalent of the gargle, and Ludescher (1973:12) says it is always associated with fighting (see Ludescher 1973:12, fig. 31; Latimer 1977, spectrograms 1–3 of this species; Romanowski 1978:241, figs. 6a, b and d; Bergmann and Helb 1982, fig. c). Ludescher phoneticizes it "si-tlluoi," Latimer "pitchew," and Bergmann and Helb "pistjü." Typical calls consist of a jumble of highly slurred notes that tend to decrease in average frequency. Terminal notes sometimes show rapid frequency modulations superimposed over a downslur (see esp. spectrograms 2 and 3 of Latimer), which are roughly the equivalent of terminal trills in gargles of other species. Fig. 2F (right) shows a typical example of the gargle, but with no indication of the trilling.

Sombre Tit *(P. lugubris)*. —This Eurasian species ranges westward through Turkey to Greece. The phonology of notes in song is unlike that of any other tit voice I have seen (Latimer 1977:421; Bergmann and Helb 1982: 340, figs. a and b): densely trilled HF-notes. Fig. 2G (left) from a tape provided by M. Duijm shows a double-chevron making a phrase that is repeated. The song seems always composed of such two- or three-note phrases repeated up to at least five times.

Alarm-type calls involve about four note-types (Thielcke 1968:154; Latimer 1977:426; Bergmann and Helb 1982:340, figs. c and d), including two HF-notes ("zi" and "tsi" of Bergmann and Helb, those in Thielcke being "tsi" and those in Latimer possibly being "zi"). Both are rapid trill-bursts. The simple, slightly noisy chevrons that Bergmann and Helb term "trerr" (fig. d) are those in Latimer's call, and seem to be a low-pitched IF-note. The LF-note is called "trrr" by Bergmann and Helb, and is the long string illustrated in Thielcke. Figure 2G (right) shows such a string taken from tapes provided by Thielcke. As the number of notes of a given type and the note-type composition of calls clearly varies combinatorially, there seems little question that this is chick-a-dee system.

Mexican Chickadee *(P. sclateri)*. —The spectrograms in Dixon and Martin (1979:422) document at least two major vocal types in this Mexican species, which ranges northward barely into southern Arizona. A forthcoming study by M. S. Ficken (unpubl. data) on the entire species' vocal repertoire will document separate song, chick-a-dee calls and gargles.

Dixon and Martin (1979:423, fig. 2) presented a variety of vocalizations "used in territorial defense" and attempted to show differential use (table I, p. 422), although samples are too small for drawing firm conclusions. They identified the "peeta-peeta" vocalization (fig. 2b) as song, noting that it was uttered at dawn and "functions both in attracting a rival to a boundary and in reiterating boundaries from a distance" (p. 422). Their fig. 2b, however, appears to be of two individuals calling simultaneously. Fig. 2d, which they term the "speetit-speetit" call, shows phrases of similar phonology. Ficken (unpubl. data) found autumnal songs to be relatively simple structures of one type of HF-note followed by several repetitions of a lower note. This song is similar to the vocalizations shown by Dixon and Martin. In spring, however, Ficken found that song was more elaborate, and had combinatorial properties. Her birds used three phrases: a chevron-couplet of higher then lower notes (S), a densely trilled tone (T), and a short, rapid phrase of a chevron with slurred notes (U). Songs consisted primarily of repeated S-phrases or alternating T/U combinations, with one song being SSSTUT. Insofar as I can determine, this combinatorial construction of song has been reported for no other species in the Paridae.

Chick-a-dee calls are composed of four note-types (Dixon and Martin 1979:422, fig. 1): two types of HF-notes, one IF-note and an LF-note. One HF-note is a rapid FM, low-amplitude trill with a steady carrier frequency of about 7 kHz, and the other is a chevron-shaped note. The IF-note is a downward slur, and the LF-note is typically banded. Ficken's (MS) characterization of chick-a-dee calls is similar. A trilled HF-note I found on chick-a-dee calls of CLO tapes is reminiscent of more densely trilled HF-notes of the Sombre Tit.

There are also typical gargle vocalizations consisting of a jumble of different note-types, typically descending in average frequency and commonly ending in a trill-like utterance (Dixon and Martin 1979:422, figs. 2a and c: the "swehbegeet swehbegeet cheeyay" and "swehbegeet cheeyay"). In addition, the "sitchowee" (fig. 2e) seems to be a gargle with only a short concluding trill. Ficken's (unpubl. data) spectrograms are similar.

Siberian Tit *(P. cinctus).*—Unless the Black-capped Chickadee and Willow Tit are considered conspecific, the Siberian Tit is the only *Parus* common to the Old and New Worlds, due to its quasi-circumpolar distribution that extends from Norway east to Alaska and western Canada. Its vocal repertoire was sketched by Haftorn (1973), revealing three major vocal types, perhaps organized somewhat differently from all foregoing species.

The first major vocalization is what Haftorn (1973:94, fig. 1f) shows as the "p'tri poi"—an unusual vocalization that begins with a faint HF-note, followed by one or two broad-frequency notes of very short duration, and ending with a rising, tonal glissando. His spectrograph shows a tonal note at about 4 kHz overlying the first part of the call. A variant is phoneticized in the text (p. 95) as "ptri-pyy." Haftorn refers to this vocalization guardedly as "song" with analytical notes worth reading. Fig. 2H (left) shows this vocalization, taken from one of Haftorn's recordings; two faint HF-notes begin this particular example. The "territorial song" pictured by Latimer (1977:421) does not show the faint introductory note, and the final note of his song falls rather than rising in frequency. The repeated "tschi" shown by Bergmann and Helb (1982:341, fig. a) is similar. Haftorn (p. 96) notes that this is usually a male vocalization but the "female can sing on rare occasion." Bergmann and Helb (1982:341) also include as song combinations containing the LF "dschee" notes, which clearly belong to the chick-a-dee complex (below). Finally, Holm (1982), without citing Haftorn (1973), argued that the term "song" should be applied to the last of the three major vocalizations (discussed near the end of this account).

Combinatorial chick-a-dee calls involve several note-types (Haftorn 1973:94, Bergmann and Helb 1982:341). Calls tend to conclude with an LF-type of note termed "tææ" by Haftorn and "dschee" by Bergmann and Helb. These are typical LF-notes whose structure ranges from banded to noisy (compare spectrograms in fig. 1a, b and c of Haftorn, loc. cit.). The middle note in Fig. 2H (right) is one of this LF-type. Notes associated with (and usually preceding) the LF-notes appear to be unusually diverse. The commonest, and one often given in isolation uncombined with other note-types, is a variable HF-note consisting of an emphasized chevron peaking at variable frequencies, with possible parallel components at higher and lower frequencies. This note-type is termed "piv" by Haftorn (1973: 94, fig. 1e). Haftorn (fig. 1d) shows a noisier variant called "pev" and refers in the text to a yet hoarser variant ("pæv" not spectrographed); the last two notes in Fig. 2H (right) are of the "pev" type. A second kind of introductory note is termed "tsi" but not figured in Haftorn (1973). I believe this to be the shorter-duration, chevron-shaped HF-notes "zi, dü" and "ti" shown by Bergmann and Helb (1982:341, fig. d). The note "pst" preceding LF-notes in Haftorn (fig. 1b) appears to be identifiable with the "zi" of Bergmann and Helb. A third kind of chick-a-dee note is the "ti" of Haftorn (1973:94, fig. 1a), which is a noisy chevron of the IF-type somewhat similar to the Black-capped Chickadee's C-note. This "ti" is probably the "zit" of Bergmann and Helb (1982:341, fig. c). Haftorn (p. 96) refers to a double "titi" form of this note. The first two notes in Fig. 2H (right) may be this repeated "titi." In addition to the four or more foregoing chick-a-dee notes, Haftorn detected combinations with other kinds of notes. He thus refers (p. 98) to a "sisisitææ" call combining the "hawk alarm" sisi with the tææ notes of the chick-a-dee call. Another variant mentioned is "pist pist tææ tææ tææ," where the "pist" may be a variant of the pst-note mentioned above.

The third major vocalization is the "trryy" trill shown in Haftorn (1973: 94, fig. 1g), which he notes (p. 97) is a "warning or aggression call." This call was given in response to playbacks near the nest site, and consists of a simple 300-msec trill centered at 3–3.5 kHz. There is no indication of this vocalization being used combinatorially, but it appears similar to trills concluding gargles of the Black-capped Chickadee; however, it may also be allied phonologically with the trills used in other vocalizations by the Sombre Tit and Mexican Chickadee. Holm (1982) argued that the trill (which he phoneticized "yrr") is the true "song" of the Siberian Tit, as he could hear it over relatively long distances in spring. What I have listed at the outset as "song" (and Holm phoneticizes "titsiloi"), he says is used in direct aggressive interactions. Clearly, further study of this species is warranted.

Boreal Chickadee (P. hudsonicus).—McLaren (1976) remains the sole modern study devoted to vocalizations of this basically Canadian species. It has been recorded recently and extensively by M. S. Ficken (pers. comm.). Early field workers reported that the Boreal Chickadee lacked simple whistled songs of more familiar chickadees, and used more-or-less in its place a varied "warbling song" (e.g., Allen 1910). McLaren (1976: 455, fig. 2A) stated that this was the vocalization she spectrographed and termed the "musical call." The call or song consists of a repeated sequence of about four highly slurred HF-notes that descend in frequency through the phrase. It thus has phonological affinities with the gargle of the Black-capped Chickadee and similar species. The musical call is given only by males in territorial situations.

A chick-a-dee call of HF-LF notes was first published as a tiny spectrogram in Robbins et al. (1966:214, 1983:228); see also Thielcke (1968: 154) and Latimer (1977:426). McLaren (1976:452, figs. 1A and B) provided two other spectrograms ending in LF-notes, but pointed out that two further note-types are commonly incorporated into chick-a-dee calls. The introductory HF-notes appear as chevrons of decreasing peak frequency, the last emphasizing the descending arm so as to appear almost as a downward slur (esp. her fig. 1B) or being virtually continuous with the first LF-note (esp. fig. 1A). The LF-notes have a broad frequency range and are distinctly banded. A longer-duration HF-note, which McLaren calls the "seep" (fig. 4C, p. 459), may be incorporated into chick-a-dee calls or given as common, separate notes. Also, the "chit" (fig. 4E, p. 459) may be a component of chick-a-dee calls; it is a short-duration IF-note with noticeable banding in the lower frequencies and upward frequency modulation. McLaren mentioned several ways in which chick-a-dee calls vary. Fig. 2I (left) shows a typical chick-a-dee call, provided by Leonard Peyton from Alaska. The near attachment of the last HF-note to the first LF-note is typical for this species, and reminiscent of the Mountain Chickadee's calls.

Similar in usage to the musical call, but distinct phonologically, is the "trilled call" (McLaren 1976:455, figs. 2C and D). This trilled call consists of a jumble of highly slurred notes ending in a trill of distinct notes. The jumble is highly variable, and this call seems equivalent with the gargle of the Black-capped Chickadee. Furthermore, I think it likely that what McLaren termed the "rapid musical call" (fig. 2B) is in fact a gargle lacking the terminal trill, as it is a jumble of notes unlike the repeated phrases of the musical call. Fig. 2I (right), taken from CLO tapes, shows a trilled call that is nearly identical with McLaren's fig. 2C (p.455). In fact, it is not certain that the musical and trilled calls represent separate vocal systems; if they are all allied to gargles of typical chickadee species, then the Boreal Chickadee could be said to lack separate song.

Chestnut-backed Chickadee *(P. rufescens).*—I cannot find spectrograms from this species of the Pacific coastal region of Canada and northwestern United States. Bowles (1909:56) likened the "very pleasing and quite lengthened song" to that of the Chipping Sparrow (*Spizella passerina*). Bent (1946:390), quoting a description by Dawson, added a repeated double-noted song "chlulip, chulip," etc. Figure 2J (left) shows a five-noted phrase from repeated song on CLO tapes.

Early workers also realized that the Chestnut-backed Chickadee possessed a chick-a-dee-like call (Bent 1946:389). Figure 2J (middle) shows a short chick-a-dee call from my tapes that suggests at least three note-types are used. Figure 2J (right) shows part of an apparent gargle taken from CLO tapes, consisting of a typical jumble of notes decreasing in average frequency. However, this type of call is so similar to the apparent song of this species that they may simply be variants of one vocalization type.

Melaniparus: African Tits

All the *Parus* of Africa south of the Sahara, about a dozen species, are in this subgenus. For no species could I find a published spectrographic study. No distinction is made below between *afer* and the South African African endemic *cinerasens,* as the two were not distinguished at the time recordings available to me were made. The survey lacks several African forms: *griseiventris* (a South African endemic), *leucomalas, leuconotus,* the *niger-carpi* complex, and *rufiventris.* The species treated are presented in alphabetic order of their Latin names, and spectrograms are from CLO tapes except where noted.

Tapes of the African Grey Tit (*P. afer*) made by H.-W. Helb were supplied by G. Thielcke. Fig. 3A (left) shows a repeated note, which apparently represents song. Figure 3A (right) shows the last part of a chick-a-dee-like call; it was preceded by two HF-notes similar to the first shown. There are thus at least an HF- and LF-note, with some tendency toward intermediates between the two strings.

The White-bellied Tit (*P. albiventris*) of east Africa possesses a chick-a-dee-like vocalization (Fig. 3B). All but the first slurred note show signs of frequency-banding, and there seems to be a variety of LF-type notes. The fourth note from the left (complexly banded and at higher frequencies) appears to belong to another bird (probably another species) calling at the same time. Fig. 3C shows two chick-a-dee-like calls taken from CLO tapes of the Striped-breasted Tit (*P. fasciiventer*). The calls suggest a combinatorial system with at least two types of HF-notes and an LF-type. Figure 3D shows a chick-a-dee-like call from the Red-throated Tit (*P. fringillinus*) with at least one HF- and one LF-note and a possible intermediate type.

The Dusky Tit (*P. funereus*) is the only species besides the African Grey Tit for which I have evidence of possible song (Fig. 3E, left). Whether or not this four-note phrase actually is used like song remains to be determined; similar phrases repeat on the tape in the manner of a perched male singing. The Dusky Tit also has a chick-a-dee-like call (Fig. 3E, right). Here the double couplet of unstructured introductory notes is shown with the first two of a long string of virtually identical LF-notes, which show typical frequency-banding.

Paradaliparus: Three Far-eastern Endemics

Little is known of the voice of the Palawan Tit (*P. amabilis*), a Philippine endemic from the island of Palawan. Tapes provided by Jelle Scharringa contain at least two types of song-phrases (Fig. 3F). One consists of two notes repeated over and over (left) whereas the other is a repeated note (right); these songs were adjacent on the tape so probably came from the same individual, suggesting the possession of song-repertoires.

The Elegant Tit (*P. elegans*) of the Philippines was also recorded in the field by Scharringa. Fig. 3G (left) shows an extract from one of several song-types, consisting of a two- or three-note phrase repeated over and over. Fig. 3G (right) shows a call composed of two LF-notes that strongly

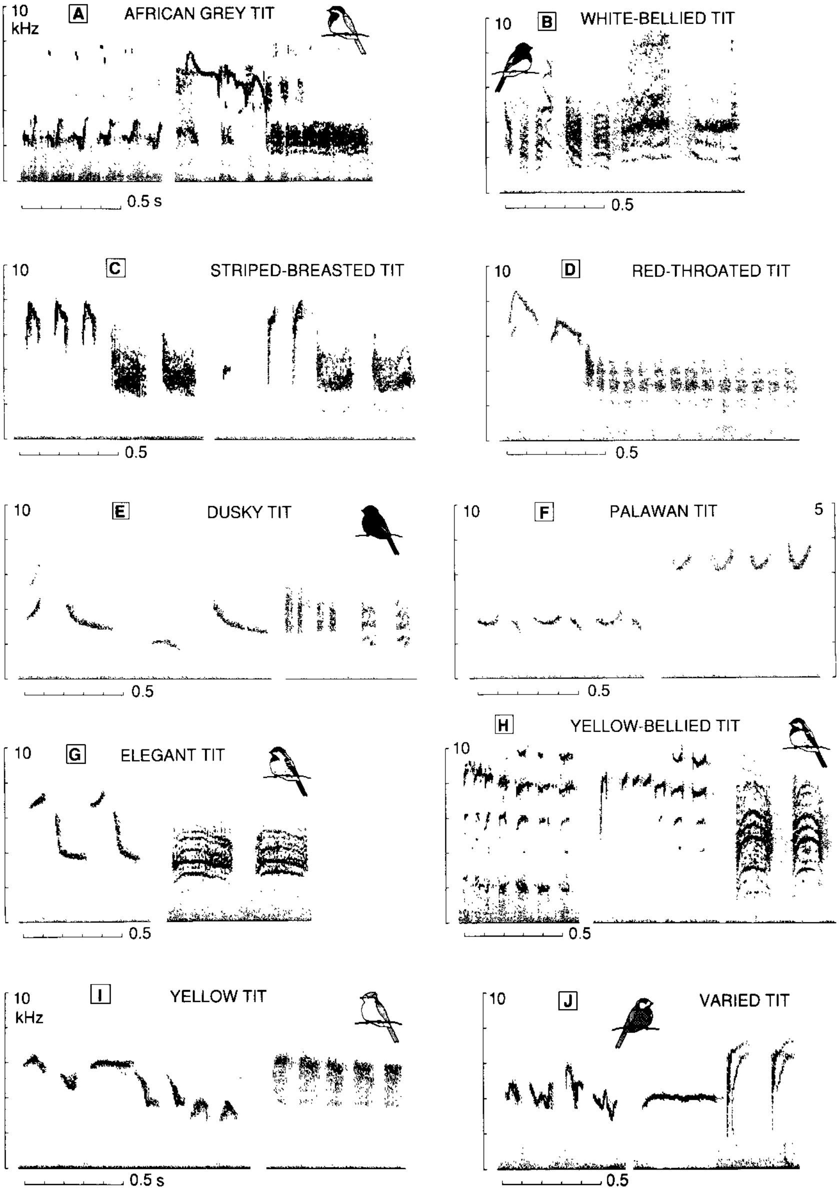

FIG. 3. Sound spectrograms of a sample of vocalizations from parid species that do not occur in North America or Europe.

resemble the terminal notes of typical chick-a-dee calls in other species. There is no evidence, however, of this type of note being combined with HF-notes.

The Yellow-bellied Tit (*P. venustulus*) is a species of China which Hans Löhrl had in captivity at Vogelwarte Radolfzell. Through the aid of Gerhard Thielcke and Roland Rost I recorded in a room where many adults and juveniles were caged together. The birds gave spontaneous notes not assembled into calls (Fig. 3H, left), and hence reminiscent of the Coal Tit (cf. Fig. 1F, middle). Thielcke and I copied his tapes of these birds. Figure 3H (middle) shows a commonly occurring series of HF-notes; another form simply repeats the same note in very long strings. These might represent forms of song. That the species also has banded LF-notes is shown by Fig. 3H (right). However, I could not find in any of the tapes indications of combinatorial or semi-combinatorial call structures resembling chick-a-dee calls or gargles.

Machlolophus and *Sittiparus:* Two Monotypic Subgenera

Scharringa provided the tapes of the Yellow Tit (*P. holsti*), a Formosan species which clearly has some kind of song-repertoire, as continuous recordings reveal switches in song-types. Tapes show at least two kinds of phrases, one of three HF-notes and another of four. It is typical that the last two notes of a phrase are of the same type. A given phrase is repeated over and over again without pause. The Yellow Tit also possesses combinatorial calls. Fig. 3I (left) shows five note-types in a seven-note call, of which the first three notes are HF-types, the next repeated doublet is more like an IF-type, and the final doublet is one kind of LF-note. There seems to be another LF-like note, shown in Fig. 3I (right), which occurs in long strings (only the first five notes of the call are shown). In a preliminary search I was unable to find this second kind of LF-note combined with any other notes. This situation is reminiscent of the Great Tit, where several kinds of churring occur, not all of which are known to be combined with HF- or IF-notes.

The Varied Tit (*P. varius*) of Japan and Formosa has vocalizations that remind me of no other tit. Fig. 3J (left) shows a repeated two-note phrase that may be song; the doublet of a chevron-like note followed by a W-shaped note occurs commonly in isolation on the CLO recordings. The three-note phrase shown in Fig. 3J (right) is also repeated, and may thus also be song.

DISCUSSION

Perhaps the most striking characteristic of vocal organization in the Paridae is that no tit is known to have just one major complicated vocalization as songbirds are "supposed" to have. All well-studied parids have at least two distinct, complicated vocalizations or vocal complexes.

What is song?—There are many discussions in the parid literature concerning how "song" is used (Dixon and Stefanski 1965, 1970), which vocalizations should be considered "song" (Haftorn 1973:95–96, Holm 1982), whether "song" is being evolutionarily reduced (Ficken, Ficken and Witkin 1978, Ficken 1981a), and whether certain species even have "song" (McLaren 1976). A phonological approach views oscine song as the longest and most complicated vocalization in the species' repertoire. Such a view is patently inapplicable to tits; e.g., the Black-capped Chickadee's fee-bee "song" fits neither stipulation: it lasts less than 1 sec, compared with some chick-a-dee calls that have durations of 4–5 sec (longer in bouts of mobbing; K. Apel pers. comm.), and chick-a-dee calls are much more complicated (and even they are simple compared with gargles). There exists no single vocalization that is both the longest and most complicated in the repertoire. If one takes a more functional view that "song" is an exclusively male-uttered, long-distance advertising vocalization used simultaneously to repel neighboring territorial males and attract unmated females, the definition again utterly fails with parids. In most parids that have been studied carefully both sexes are known at least occasionally to give all the species' major vocalizations. Furthermore, in some species (especially *cinctus, hudsonicus* and *rufescens*), no vocalization seems to carry far enough for long-distance advertising.

The problem with a monolithic view of "song" is that it stems largely from sexually dimorphic, north-temperate, migratory passerines—in which males tend to arrive on the nesting grounds and set up territories before females arrive. Virtually all the world's tits, by contrast, are sexually monomorphic, non-migratory and permanently paired. When the winter flocks break up into pairs, the pairs nest in the same general area. The birds usually already know their neighbors individually so have less need for typical long-distance territorial advertising to newly arriving, unfamiliar males from distant wintering grounds. And males have less need to attract unfamiliar females to their territories.

Haftorn (1973:95–96), following Thielcke (1970), articulated the problem of parid "song" clearly by listing some known functions of song: (1) territorial defense, (2) mate-attraction, (3) strengthening of the pair bond, (4) stimulation of conspecifics in colonial nesters, and (5) synchronization of reproductive development in the mate. The list could be augmented, but its point is clear enough: the usefulness of a signal needs to be judged by the behavioral needs of the species. The present survey shows that almost all parid species possess two or more major vocalizations, suggesting that parid life history is such as to promote evolution of several major signals in place of monolithic song in many other oscines. I envision a contextual or functional hyperspace into which the communicative domains of major vocalizations map differently in different parids, but all within the domain of monolithic vocalization of most oscine birds. That is, if we could identify the variables defining contexts in which vocalizations were given, these variables would probably be more than three in number, so define a hyperspace. Monolithic song of most passerines would plot over a large portion of this hyperspace; in tits, that portion would be broken into three or more parts for the major vocalizations, but in each species the partitioning of the hyperspace would be somewhat different.

Communicative functions of the major vocalizations.—Based on obviously fragmentary evidence I will speculate about the communicative functions of the three classes of major parid vocalizations: (1) What has been termed "song" is given more commonly by males than females and more commonly on spring territory than at other times of year or elsewhere. Such song is elaborated differently in different species: some have only a single kind (e.g., the Black-capped Chickadee's fee-bee), others have several song-types that tend to be used in different contexts (e.g., Blue Tit), and still others have repertoires that are apparently not contextually differentiated (e.g., Great Tit). At heart, what unites "songs" is their species-specificity: closely related sympatric species can be separated readily by song. Whatever else they do in a given species, songs may insure that mistakes in mate-choice are rarely made. My colleague Charles T. Snowdon (pers. comm.) trapped reputed Carolina Chickadees near Philadelphia at the study site of Smith (1972), and his caged birds formed pairs. When spring came one male unexpectedly began singing the fee-bee song of the Black-capped Chickadee and his mate suddenly and permanently deserted him. (2) The chick-a-dee call-complex *sensu stricto* occurs only in certain species but roughly equivalent vocalizations of various degrees of "alarm" exist in most parids. These are the vocalizations given in mobbing of predators by almost all tits, but clearly used in a variety of other contexts depending upon the species. This is the functionally most complicated major vocalization in many tits, and may be related primarily to movements of the birds in space. (3) Gargles have been studied intensively only in the Black-capped Chickadee, but many other species possess an equivalent vocalization and still others a probable equivalent (e.g., "conflict call" of Blue Tit, "muttered threat" of Great Tit, "call derivative" of Plain Titmouse). These usually complex calls are uttered in very-short-distance communication: commonly accompanying physical combat or in propinquitious agonistic encounters, but also reported in some species as given by mates at the time of copulation.

What is vocal homology?—Various kinds of vocal "equivalencies" do not covary in tits. For example, "song" may be roughly equivalent functionally but is phonologically so diverse that no individual note-homologies can be drawn among any but closely related species. Another kind of equivalency is the basic HF-(IF)-LF plan, which underlies nearly all parid vocalizations: "song" of the Blue Tit, churring of the Great Tit, all chick-a-dee calls and gargles of species that have them, as well as functional equivalents in other forms (e.g., "conflict" call of the Blue Tit). The very fact that the same organizational plan underlies all major vocal types shows that there is no contextual homology. Furthermore, phonological similarity in specific notes occurs among different major types of vocalizations; e.g., diverse notes in Blue Tit songs may be likened to notes found in chick-a-dee calls of other species. Ficken (unpubl. data) found that one "simple" call of the Black-capped Chickadee's repertoire is missing from that of the Mexican Chickadee, yet in the latter species another call's domain of contextual use is expanded to cover the context of the "missing" vocalization. Indeed, some calls are phonologically different in the two species while having the same use-pattern, whereas other calls that are phonologically very similar have different uses in the two species. In sum, to draw a parallel (Hailman 1976): a bird's wing and a bat's wing are not homologous structures *as wings* but they *are* homologous as vertebrate *forelimbs*. When one asserts that two vocalizations appear to be "homologous" it is necessary to make clear in what way they are homologous.

Types of vocal diversification.—Vocalizations are virtually always communicative; communication is the transfer of information; information is variety; therefore, vocalizations must vary in some way in order to communicate information. The differentiation of two or more kinds of major vocalizations in parids is itself a form of information-laden variety, but within kinds can be seen two principles of vocal diversification.

First is variety of phonological structure. This is the common pattern in song of oscines, where repertoires are almost always strictly non-combinatorial. Each song-type may be composed of two or more kinds of note-types, but usually those note-types are unique to that song-type and not used in some different pattern of another song-type. Note-diversity is also evident in the large repertoire of isolated call-notes of the Coal Tit.

The other principle is analogous with human language: a relatively few acoustical elements are used combinatorially to produce a far larger diversity of unit-utternaces. Thus in the Black-capped Chickadee's chick-a-dee call-system four distinct note-types are used in combination to produce hundreds of different call-types. In fact, mathematical analysis shows that there is no limit to the number of different chick-a-dee calls—the repertoire is "open" or theoretically "infinite" (Hailman et al. 1985). Note-types virtually always occur in a fixed sequence within the call, but in the Black-lored Tit's mobbing calls note-sequences are not so constrained: permutation can also diversify vocal systems beyond the variety created by combination alone. The principle of combination-permutation can also occur in parid song, as evidenced by the Mexican Chickadee—highly unusual for an oscine.

These two principles of vocal diversification can also operate together as in gargles of the Black-capped Chickadee. Here there exists a local "pool" of phonologically distinct note-types. A given gargle utterance draws notes from this pool and strings them together according to a pattern of decreasing average frequency, commonly ending with one of the trill-types from the "pool." This vocal procedure produces a huge variety of gargles, with nearly every utterance sharing at least one note-type with most other such utterances.

It is possible that acoustical variety represents information at a different level: instead of each variant representing a different message, it is the ensemble's diversity per se that is informative. For example, several hypotheses have been proposed to account for diversity of song in tits (see, for example, the following references on the Great Tit: Baker et al. 1986: Krebs 1976, 1977a, 1977b; Krebs et al. 1978; Lambrechts and Dhondt 1988; McGregor and Krebs 1982a; and others cited in the species-account above). These hypotheses include: (1) avoiding habituation in the receiver by frequent switching of song-types; (2) deceiving neighboring males into believing that many different males are present; (3) stimulating females, which reputedly prefer males with large repertoires, perhaps because these correlate somehow with good genes for passing to the offspring; and (4) avoiding motor-exhaustion of the muscles of the syrinx, necessitating switching to a new vocalization in order to keep singing. Whether or not other parid vocalizations similarly show variety "for the sake of variety" is unknown but it seems possible. For example, gargles of the Black-capped Chickadee show immense variety based on combinatorial principles and it seems unlikely (to me) that every combination could "mean" something different.

Vocal evolution in the Paridae.—Finally, I attempt a tentative overview of the evolution of vocal organization in the Paridae, restricted to the six subgenera in which vocalizations have been studied extensively. (1) The Crested Tit must be something like the ancestral parid, with a weakly differentiated vocal repertoire consisting of the basic HF-LF unit-pattern shown in Fig. 1A (above). Advertising seems to consist of repeating this unit; alarm-calling consists of giving fewer introductory HF-notes and extending the train of LF-notes. Shorter calls consist of weakly modified "extracts": several HF-notes, or several LF-notes or a few of each in the sequence HF-LF. The transition between the two note-types often produces phonologically distinct notes, and these proto-IF-notes may sometimes be used in short calls. However, Martens (in litt.) points out that the vocalizations of *cristatus* might be secondarily simplified, as its poorly studied relative *P. dichrous* apparently has rich song.

From this poorly differentiated vocal organization, evolution appears to have taken at least two initial routes. (2) The American titmice possess more clearly differentiated vocalizations of songs and complex calls. The songs, emphasizing repeated HF-notes, form large repertoires in some species, and song-types tend to be used differentially in different contexts. The calls seem to be intermediate between the unit-pattern of the Crested Tit and the chick-a-dee calls of chickadees and their close relatives. (3) The Blue Tit has differentiated and more-or-less stabilized several versions of the unit-pattern. A number of these versions are used as "song," where LF-notes tend to be dropped and HF- and IF-notes differentiated. As in the titmice, these versions are not song-repertoires in the usual sense of equivalent vocabularies, but rather tend to be used in different behavioral contexts. Other variants concentrate on the LF-end of the continuum, yielding "alarm" vocalizations that are not as chick-a-dee-like as those of the titmice. Still a third vocal type may be differentiated into the "conflict" call used for social interactions at close quarters. The result of these evolutionary changes is differentiation of the forerunners of three major types of vocalizations that characterize many of the remaining parids.

The remaining three paths lead to more complex vocal organization. (4) In the Coal Tit and its relatives the presumed ancestral diversity of contextually different songs is solidified into a repertoire of more-or-less equivalent song-types. Probably quite independent is the near loss of LF-notes from mobbing and alarm vocalizations, with the elaboration of isolated HF-notes in this context and in general social interactions covered contextually by chick-a-dee calls in other species. (5) The Great Tit and its relatives represent a similar route of development, having solidified a song-repertoire parallel with that of the Coal Tit. Alarm and mobbing, however, have gone exactly in the opposite direction, emphasizing the "churring" LF-notes with apparent reduction of the HF-introductions. And unlike the isolated-note calls of the Coal Tit, the Great Tit has evolved fewer note-types but uses them together to make calls of various combinations. Finally, (6) typical chickadees and their European counterparts are characterized by usually simple song, well-differentiated chick-a-dee calls, and well-developed gargles. Typically there is only one song-

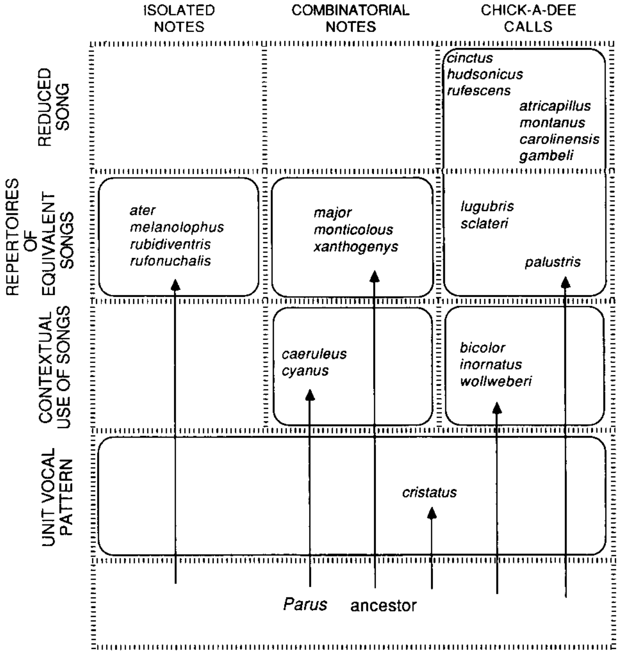

FIG. 4. A tentative model for the evolution of vocal organization in the six best-studied groups within the Paridae. For details, see text.

type—thus rendering the distinction between differential usage and repertoire-equivalents a moot question. The Marsh Tit's more repertoire-like organization suggests primitiveness within the subgenus. These species are also characterized by the evolution of a manifestly combinatorial chick-a-dee call-system employing four (or more) stable note-types. Finally, the chickadees have well-developed gargles based on structural rules for selecting a diversity of note-types from a shared "pool" which shows microgeographic dialectical variation.

Figure 4, a tentative model of parid vocal evolution, takes a novel approach by creating a matrix of song-organization vertically and call-organization horizontally, with gargle-like vocalizations omitted due to the uncertain comparative evidence available. Species are placed together in the most appropriate cell(s); in some cases there is sufficient diversity within a group that not all species fall unambiguously into one cell, even though placed there together; in the case of chickadees and related species the song-diversity is sufficiently great that I have scattered the species into subgroupings in the rightmost column of the figure to suggest this diversity.

All groupings are shown by the vertical arrows as independently evolved from a common ancestor, with the horizontal juxtaposition of arrows suggesting affinites of groups (thus the *caeruleus-cyanus* group may be close to the *major-monticolous-xanthogenys* group, and *cristatus* may be close to the North American titmice). When an arrow passes through a cell, this suggests that an intermediate ancestor may have possessed the cell's vocal organization (e.g., the immediate ancestor of the *ater* group may have had contextual songs, and its ancestor may in turn have had a "unit-vocalization" of the *cristatus* type). Fig. 4 is a crooked wheel, but as it is the only wheel in town it may be sufficient to get us to the next way-station of understanding parid vocal evolution.

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