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STRUCTURE AND VARIABILITY IN THE VOCAL REPERTOIRE OF THE MOUNTAIN CHICKADEE

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The vocalizations of North American chickadees (*Parus*, subgenus *Poecile*) are diverse and complex. The complete vocal repertoires of a few species have been described and illustrated with sound spectrograms (Smith 1972, McLaren 1976, Ficken et al. 1978) and various other vocalizations from other species have been discussed (e.g., Sibley 1955, Dixon et al. 1970). These works indicate a great deal of variability in the chickadees' vocalizations, but, except for songs, no attempts have been made to analyze their patterns of variability quantitatively. As a first step toward an understanding of the communicative significance of this variability, I attempt in this paper to characterize the patterns of variability of different vocalization categories in the repertoire of the Mountain Chickadee (*Parus gambeli*). Comparisons are then made with existing information on the vocalizations of other chickadee species in an attempt to define general patterns of repertoire organization in these birds.

METHODS

The vocalizations of Mountain Chickadees were tape recorded between February 1980 and February 1981. The majority of the recordings were collected between February and May 1980 and between November 1980 and February 1981. The primary study area was located just north of Flagstaff, Coconino Co., Arizona, in second growth forest of ponderosa pine (*Pinus ponderosa*) and Gambel oak (*Quercus gambeli*) at an elevation of 2200 m. Recordings were also made at five other sites (elevation 2130–2740 m) located 2–10 km from the primary study area.

Recordings were made with a Uher 4400 recorder with a Dan Gibson parabolic reflector microphone and also on a Superscope CD330 cassette recorder with a Bell and Howell directional condensor microphone. Tapes were analyzed on a Kay Elemetrics 6061B Sona-Graph using 80–800 Hz, wide-band, linear display modes. The resulting spectrograms were sorted into categories based on structural similarity.

Two techniques were used for evaluating the thoroughness of sampling of the various call categories and measured characters. Completeness of sampling was determined by plotting the cumulative repertoire size (number of distinctive states for the parameter being considered) as a function of call number. In order to overcome artifacts arising from possible nonrandom selection of call forms during bouts of calling, all of the calls to be considered were pooled and drawn randomly. The cumulative repertoire size was then plotted against the number of calls considered to that point. The resulting plot tends to level off as the limit of all possible states is approached asymptotically.

A similar technique was used to evaluate the extent to which the variability of a continuously varying parameter was characterized by the sample. Instead of repertoire size, the standard deviation (SD) at every 5th or 10th datum (for $N > 200$) was plotted as a function

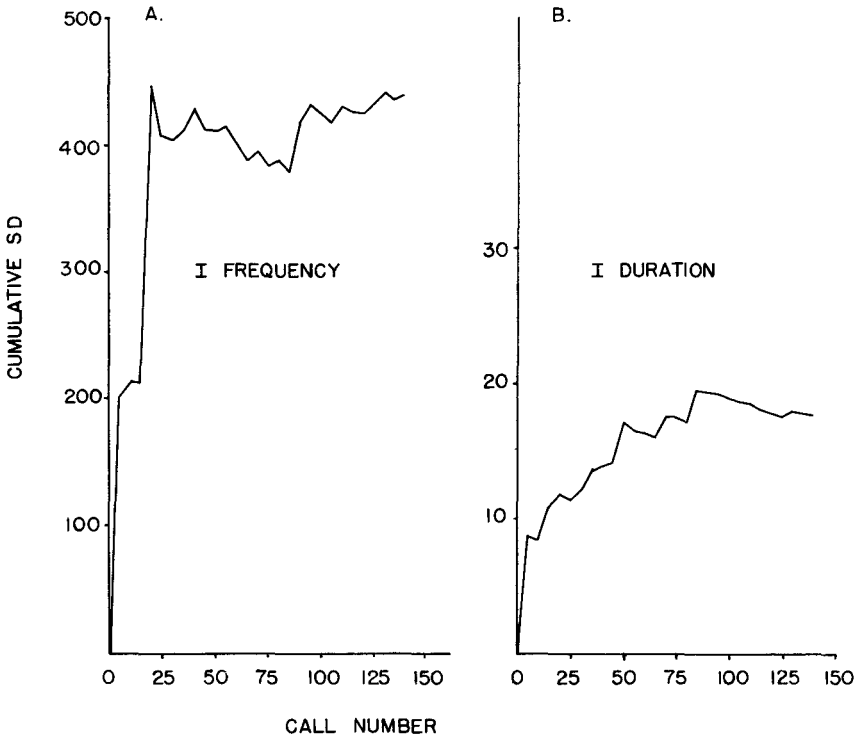

FIG. 1. Cumulative standard deviation of category I element frequency (A) and duration (B).

of randomized datum number. These plots rise steeply at first, then asymptotically approach the true value for the population (two representative examples are shown in Fig. 1). The magnitude of the fluctuations can be taken as an indicator of sampling completeness and expressed in two ways. First, the extent of SD fluctuation (maximum SD − minimum SD) in the final 50%, 25%, and 12.5% of the randomized data sequence was expressed as percentages of the final SD. Second, the 95% confidence interval of the variance was calculated (Sokal and Rohlf 1969, p. 154) and accommodated to the SD plot. The magnitude of fluctuations in the final 25% of the randomized data sequence was expressed as the percentage of the 95% confidence interval.

These calculations were intended to broaden the basis for assessing sampling thoroughness and the variability of various measures. They will also provide a means of comparing the variability of comparable vocalization characteristics of other species when suitable data become available.

Levene's test (Van Valen 1978) was used to compare the variability of characters with different distributions. In this test, deviations from the mean were compared for the two distributions in a one-way analysis of variance.

Behavioral correlates of category II calls were analyzed using a Chi-square contingency

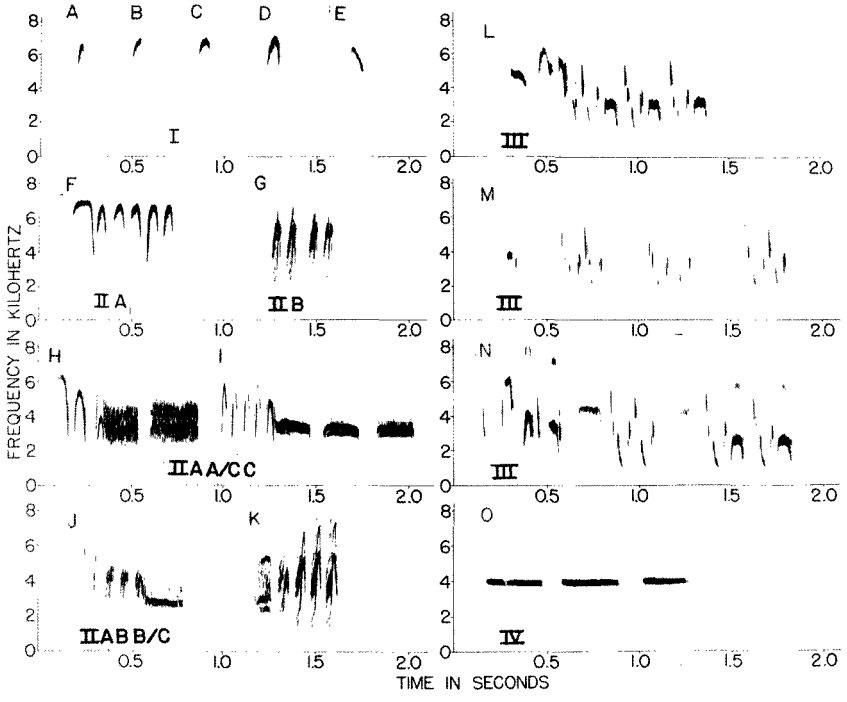

FIG. 2. Overview of the vocal repertoire of the Mountain Chickadee. A–E, representative examples of short-range contact calls, category I; F, series of IIA elements; G, series of IIB elements; H and I, two series containing IIA elements, a fused IIA/C element, and IIC elements; J, series containing two IIA elements, two IIB elements, and a fused IIB/C element; K, series given by a female during courtship begging; L–N, calls of category III—L, A_1–B_1–B_1–B_1; M, A_2–B_2–B_1–B_1, lower harmonics of the high frequency elements appear before and after the B_2 phrase; O, whistled song category IV.

table. Occurrence frequencies were considered large enough for statistical testing if the expected frequency for each cell was larger than one (Snedecor and Cochran 1967).

RESULTS

Three hundred and fifty-nine calls were analyzed spectrographically. Extensive variation was found in the acoustic structure of these calls, but they were separable into four general categories on the basis of a few simple criteria. That these were natural categories was confirmed by the apparent separation into usage categories (see below). The four categories were: I, single, arch-shaped elements; II, multi-element series consisting of elements from any of three types in a characteristic order (the "*chick-ka-dee-dee*" call); III, fast, sputtery calls consisting of rearrangeable phras-

TABLE 1

FREQUENCY (HZ) AND DURATION (MSEC) OF CATEGORY I AND II ELEMENT TYPES

	N	$\bar{x}$	±SD	CV	% ΔSD^{50}	% ΔSD^{75}	% $\Delta SD^{87.5}$	ΔSD as % of 95% confidence interval
I frequency (Hz)	139	6857	±440.8	6.4	14.9	5.9	2.1	23.6
I duration (msec)	139	58.6	±18.0	30.7	13.4	5.8	1.8	24.5
IIA frequency	248	6758	±542.5	8.0	10.1	2.4	1.8	10.1
IIA duration	248	62.7	±20.9	33.4	3.0	3.0	2.2	18.1
IIA^1 frequency[a]	83	7101	±540.5	6.7	8.9	3.3	3.3	10.3
IIA^1 duration	83	81.3	±19.6	24.1	15.5	4.3	1.2	13.5
$IIA^{A/C}$ frequency[b]	80	5237	±324.8	6.2	3.6	3.6	0.7	11.1
$IIA^{A/C}$ duration	80	43.9	±10.2	23.3	11.6	3.9	3.9	11.8
IIA–IIA ied[c]	120	37.3	±5.4	14.3	10.3	5.9	2.9	21.3
IIA–$IIA^{A/C}$ ied	65	56.5	±22.3	39.5	19.9	4.7	4.7	12.9
IIA/C duration	70	191.2	±30.0	15.7	30.7	1.8	1.8	5.4
IIA/C–IIC ied	33	70.1	±15.8	22.5	—	—	—	—
IIB duration	115	40.1	±5.9	14.8	14.3	13.0	6.5	39.9
IIB–IIB ied	90	60.4	±24.0	39.7	11.5	9.8	9.8	34.2
$IIC^{A/C}$ duration	76	134.0	±31.9	23.8	21.6	3.5	3.5	10.7
IIC duration	130	249.8	±35.0	14.0	8.9	2.5	1.8	16.3
IIC–IIC ied	32	76.5	±19.2	25.1	—	—	—	—

[a] IIA^1 = first IIA element of series.
[b] $IIA^{A/C}$ = IIA portion of fused A/C element.
[c] ied = inter-element duration.

es; and IV, series of long whistle-like elements. These were not entirely discrete categories; intermediate calls containing features of two categories were occasionally expressed. These intermediates, however, were rare, and the great majority of calls fell clearly into one of the four categories.

Category I.—Calls of category I consisted of a single arch-shaped element, which varied in frequency, duration, and in the details of shape (Fig. 2A–E). Table 1 and Fig. 1 indicate that the sample is sufficient to represent the true variability of the measured parameters. There was no correlation between frequency and duration of category I elements ($r = 0.04$, $P > 0.05$).

Category I calls were given during virtually all observed activities and could be mixed with all other kinds of calls, but they were the predominant calls for long periods, during slow and even flock movements as the birds foraged. The chickadees tended to forage discontinuously, spending 30–60 sec in a given tree or ground patch and giving three–five calls there before flying to another patch.

Category II.—Calls of category II consisted of series of several elements

TABLE 2
CATEGORY II CALL STRUCTURE IN TERMS OF ELEMENTS/SERIES OVERALL AND ELEMENTS/SERIES OF THE DIFFERENT ELEMENT TYPES

	N	$\bar{x}$	±SD	CV
Elements/series	129	5.3	±2.0	37.8
IIA elements/series	110	2.5	±1.2	47.6
IIB elements/series	29	3.9	±2.0	50.4
IIC elements/series	81	1.7	±0.7	42.9
IIA/C elements/series	87	1.0	±0.0	—

drawn from three basic types (Fig. 2F–I). Although graded intermediates were possible between types, these were unusual and type divisions within call series were usually discrete. Call elements of type B were distinguished from those of type A by the presence of additional, higher frequency components in the ascending portion of the arch. Call elements of type C consisted of relatively long duration, broad-spectrum elements that occasionally showed the evenly banded structure indicative of harmonics. Series usually contained a fused A/C element (Fig. 2H,I), and a few fused B/C elements were also recorded (Fig. 2J). The fluctuations of all SD plots were within the final 95% confidence interval through the second half of the randomized data points (Table 1). Temporal variation was consistently greater than frequency variation.

Within a given series the arrangement of element types, with rare exceptions, followed the pattern A before B before C. Series could contain one to several elements of any of these types, but elements were segregated according to type. Fused A/C elements, when present, occurred between A and C elements and never in the same series with a B element. The series averaged 5.3 elements per series with a strong mode (31% of the sample) of four elements per series (Table 2, Fig. 3).

Although the composition of category II calls was restricted by these patterns of element arrangement, there nevertheless remained considerable freedom for the expression of a great diversity of arrangements (Fig. 4). The majority (70%) of forms occurred only once. Many other arrangements are conceivable, and it appears likely that continued sampling would result in an extended repertoire. Furthermore, the variability in frequency and duration of the elements afforded this species a potentially enormous repertoire of calls in this category.

Type A elements varied considerably within a given series, but not without definable pattern. These elements invariably descended in frequency within a series (Table 3) and, at the same time, became shorter

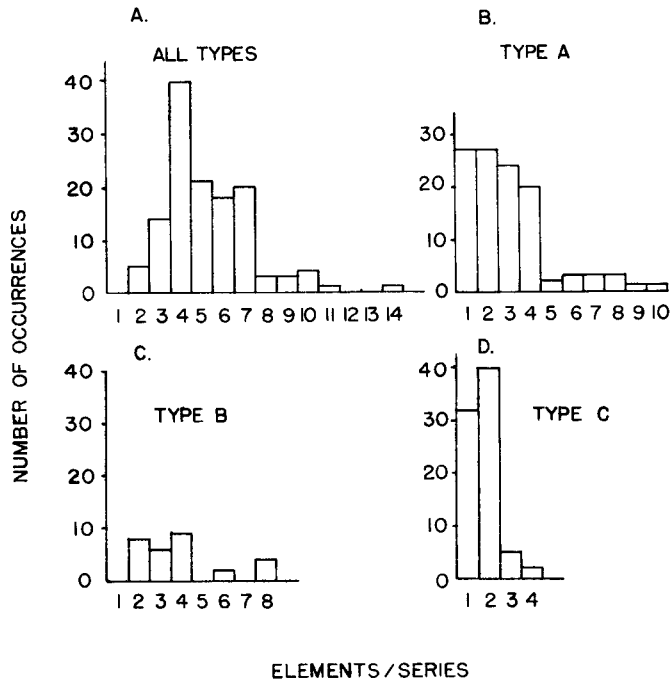

FIG. 3. Occurrence frequency histograms for category II elements/series; A, all element types considered together; B, elements of type IIA; C, elements of type IIB; D, elements of type C.

in duration (linear regression of frequency against duration: $r = 0.66$, $P < 0.01$). No such patterns were found in the variability of type B or C elements.

Linear regression of inter-element duration against the duration of the preceding element showed a significant correlation for only one of five element types, the C–C interval ($r = 0.51$, $P < 0.001$). Intervals between A elements, between A and A/C, A/C and C, and between B elements showed no such relationship (intervals between A and B, and between B and C were too rare for testing). This suggests that cadence (i.e., even rhythmicity) was an important feature only in series of C elements. Furthermore, only in the case of C series is there an indication that onset to onset duration (the beginning of one element to the beginning of the next) is conserved. This is indicated by a lower coefficient of variation for onset to onset duration (7.1) than for element duration (14.0) (Levene's test, $F = 13.12$, df = 1, $P < 0.01$).

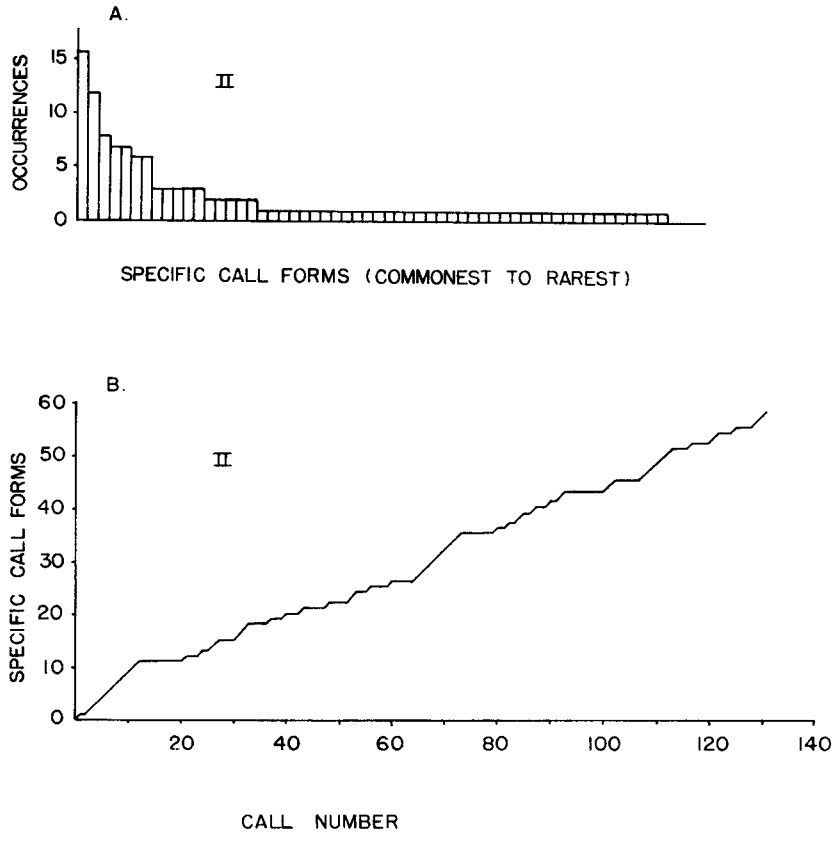

FIG. 4. A, occurrence frequency histograms for specific call forms of category II, arranged in order of abundance in the recorded sample from commonest to rarest; B, cumulative repertoire size for specific call forms of category II.

Chickadees rarely, if ever, repeated a given call form identically in every detail, but forms given in the same bout usually showed common features. This tendency was evaluated for several bouts by an analysis of variance of three parameters, all of which showed significantly greater between bout variation than within. These parameters were: elements/series ($F = 26.2$; df = 3,41; $P < 0.001$), frequency of first A element ($F = 42.3$; df = 5,41; $P < 0.001$), and duration of C elements ($F = 43.7$; df = 4,64; $P < 0.001$).

Calls of category II were typically associated with changes in the movement patterns of the callers or of the entire flocks of up to eight individuals. The calls were usually answered by others and occasionally many ex-

TABLE 3

RELATIVE FREQUENCIES OF IIA ELEMENTS FROM DIFFERENT POSITIONS IN CALL SERIES, EXPRESSED AS PERCENTAGE OF THE HIGHEST FREQUENCY ELEMENT FROM A GIVEN SERIES

IIA element position	N	$\bar{x}$	±SD	CV
1	78	100	±0.0	–
2	64	92.8	±4.2	4.5
3	45	91.5	±2.9	3.2
4	23	88.2	±3.2	3.6
$A^{A/C}$	71	78.6	±7.4	9.5

changes were made and chorused by many members of the flock. Analysis of the behavioral contexts of call types (Table 4) shows a significantly non-random distribution of these call types among the behavioral contexts ($\chi^2 = 73.2$, df = 12, $P < 0.001$). Further, all call categories (columns) showed non-random distributions in the contextual categories ($P < 0.001$ for each column). In only one contextual category (flock fights) were calls used according to their overall abundance ($\chi^2 = 1.08$, df = 3, $P > 0.5$). Otherwise, a non-random sample of calls occurred in each context ($P < 0.01$ for each row except flock fights).

Category III.—Calls of category III were made up of one to four multi-element phrases (Fig. 2L–N). In a sample of 101 calls, six phrase types were recognized, some of which occurred in several variant forms in the population. These types were separated into two divisions on the basis of acoustic structure (division A, four types; division B, two types). The phrase types of division A (Fig. 5) contained three–five basically arch–shaped elements which varied in the details of shape within a given phrase. The elements also varied in frequency but tended to descend within a given series.

Long series of very high frequency (8.5–9.5 kHz), long duration (150–180 msec) elements were frequently interspersed with calls of category III. Series containing type B_2 phrases invariably contained one of these high frequency elements immediately before and after each B_2 phrase. Phrase type A_3 as well as A_1 were often followed by an element of similar shape but much lower in frequency ($\bar{x} = 2.88$ kHz, SD = ±0.75) and longer duration ($\bar{x} = 33.4$ msec, SD = ±4.3).

Phrase types A_1 and B_1 occurred most frequently in the sample (Fig. 6), and call forms containing either or both of these phrases accounted for 55.4% of the recorded forms. Call forms containing more than one

TABLE 4
BEHAVIORAL CONTEXTS OF CATEGORY II CALLS CONTAINING DIFFERENT COMBINATIONS OF ELEMENT TYPES

Context	A only	A–A/C–C[a]	B only	A–B–C[b]	Total
Leaving forage patch	0	5	8	8	21
Arriving in new forage patch	0	15	0	1	16
Vocal exchange after isolation	0	19	0	1	20
Startled, flying up	11	5	4	0	20
Flock fight	5	10	3	2	20
Total	16	54	15	12	97

[a] Combinations A–A/C, A–A/C–C, and A/C–C.
[b] Combinations A–B and A–B–C.

phrase type nearly always (98%) contained a representative from both major divisions. Two call forms, A_1–B_1–B_1 and A_3, constituted 42% of the forms recorded (Fig. 7A). The relatively small number and the discrete nature of the component phrase types in category III calls afforded a virtually complete sampling (Fig. 7B).

Although many variant forms occurred within each of the A type phrases, their pattern of delivery suggested that these variants were stereotyped and individually specific. This was indicated by the observations that, during flock fights, the same phrase type was exchanged in different variants by different individuals. Sample sizes of these calls were too low for statistical evaluation, but, when tracings of calls were overlaid on calls from the same bird later in the same bout, they showed only slight variation in call structure. One variant of A_1 was recorded in the same locality on four different occasions over a period of 2 months. Different variants of A_1 were recorded at three of the five study sites.

Although the sample sizes for the contextual correlates of III calls are too small for statistical testing, certain patterns of usage are apparent (Table 5). Phrase types A_1 and A_3 unassociated with type B phrases had the most distinctive usages. A_1 appears to be associated with an increasing likelihood of an aggressive encounter, A_3 with close aggressive contact. The other phrase types and phrase combinations were given primarily while the callers were more or less isolated from their flocks or while also giving their whistled song (category IV, below).

Category IV.—Calls of this category (whistled song) consisted of two short elements followed by two longer ones (Fig. 2O). All seven observed bouts of singing consisted of this song type interspersed with calls of category III. Recordings of Mountain Chickadee songs from other regions, obtained from the Library of Natural Sounds (Laboratory of Ornithology,

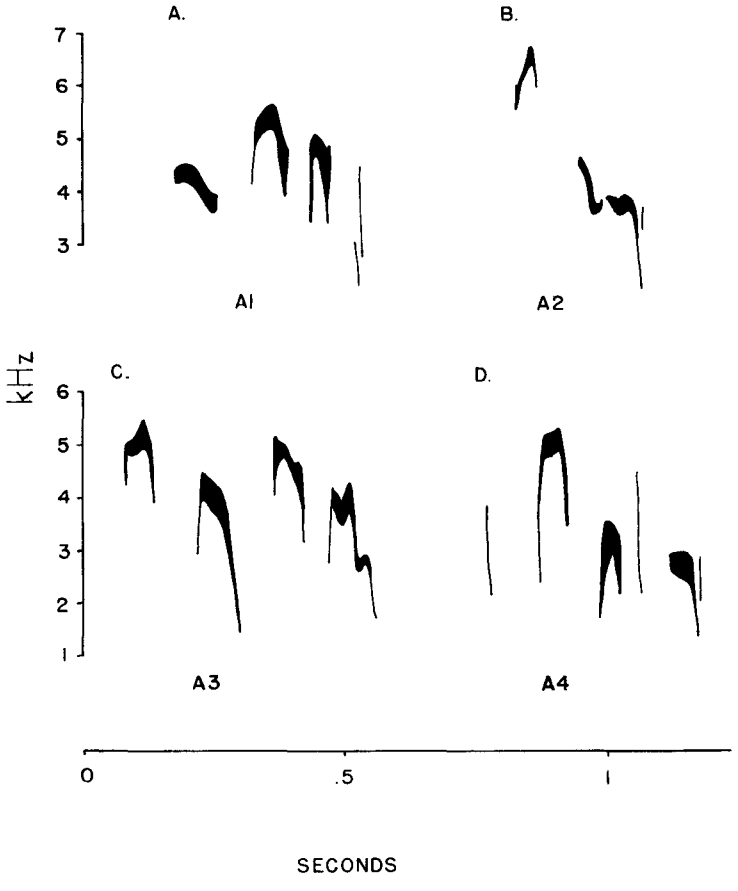

FIG. 5. Representative examples of the four category II division A phrase types.

Cornell University), contained elements at two different frequencies, thus indicating regional dialects.

Courtship, begging, and miscellaneous calls.—The calls given by begging females early in the breeding season and by fledglings during their first few weeks out of the nest contained elements that were structurally similar to those found in the category II calls, but these elements were arranged in reverse order (Fig. 1K).

During two overflights by Cooper's Hawks (*Accipiter cooperii*), chickadees gave very high frequency (9–10 kHz), whistle-like calls. These calls lacked measurable onset or cutoff points, but the duration of single ele-

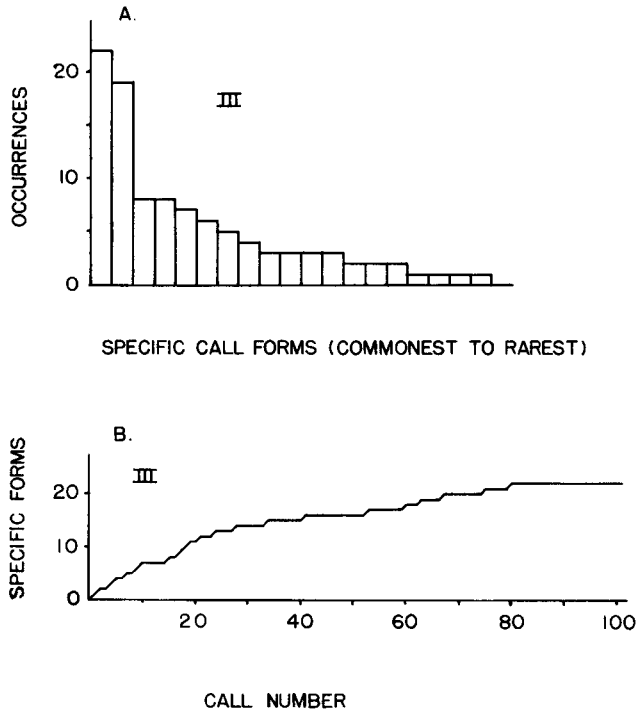

FIG. 6. A, occurrence frequency histogram for specific call forms of category III, arranged in order of abundance in the recorded sample; B, cumulative repertoire size for specific call forms of category III.

ments exceeded 250 msec. Several elements were associated in long series. The Mountain Chickadee is also reported to give a "hissing" call when disturbed in the nest hole (Grinnell et al. 1930).

DISCUSSION

The four major categories of the Mountain Chickadee's vocalizations can be considered to occur in two larger divisions based on patterns of variation. Categories III and IV varied discretely in that they were made up of discrete phrase types (six for category III, one type for category IV), which varied only slightly between occurrences. Intermediates between phrase types did not occur. Categories I and II, however, were made up of element types within which there occurred considerable variation. The various forms in the element types (one type for category I, three types for category II) could be arranged in graded continua. Considerable gradedness occurred within calls of category II as well as between calls of both

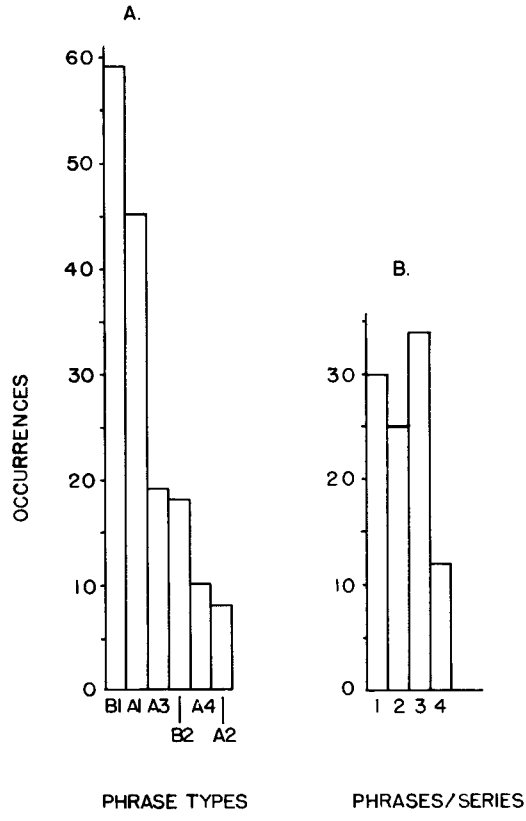

FIG. 7. A, occurrence frequency histogram for specific call forms of category III; B, cumulative repertoire size for specific call forms of category III.

categories I and II. The presence of both continuously and discretely varying categories in the same species' repertoire suggests that the difference is communicatively meaningful. Since distinctive behavioral patterns can be associated with the different vocalization categories, functional correlates of their two patterns of variability may be indicated.

One possible functional correlate of variability patterns could be associated with the greater semantic reliability of discrete signals. The discretely varying calls of categories III and IV were used either for long distance communication, where signal degradation was likely to be a problem, or in aggressive confrontations, where unambiguous signals would be important, either for regulating flock advance or retreat, or for signalling aggressive intentions to opponents. The distances over which the calls of

TABLE 5
BEHAVIORAL CONTEXTS OF CATEGORY III CALLS CONTAINING DIFFERENT PHRASE COMBINATIONS

	A_3	A_1	A_1–B_1–B_1	All other combinations	Total
No apparent provocation, caller isolated	1	2	19	53	75
Approaching flock fight	1	5	0	0	6
Flock fight	14	0	3	0	17
Supplanting attack	3	0	0	0	3
Total	19	7	22	53	101

categories I and II were used, however, were usually not so great that signal degradation was likely to be a problem. Nor were the situations in which the calls were given characterized by an urgent need for a correct response. It thus appears that there is an inverse relationship between the need for reliability and certainty in a signal and its variability; precision of meaning and subtlety of expression are apparently sacrificed to urgency.

The repertoire of the Mountain Chickadee is typical of North American chickadees (Table 6). The vocal repertoires of three species have been described with the aid of the audiospectrograph (Carolina Chickadee [*P. carolinensis*] Smith 1972, Gaddis 1979; Boreal Chickadee [*P. hudsonicus*] McLaren 1976; Black-capped Chickadee [*P. atricapillus*] Ficken et al. 1978). Certain other vocalizations of other chickadee species have also been described (Dixon et al. 1970, Dixon and Martin 1979). With few exceptions, evaluations of quantitative variation are not available, but the comparative material shows that all major call categories except IV, the whistled song, are possessed by the group as a whole. In Mexican (*P. sclateri*), Chestnut-backed (*P. rufescens*), and possibly Boreal chickadees, territorial advertisement is accomplished by vocalizations with the acoustic structure of category III.

Category I calls appear to be most diverse in the Carolina Chickadee. Figures of several variant forms are presented in Smith (1972) and Gaddis (1979). Some of these appear comparable in structure to IIA elements (i.e., high pitched arch), but others appear to be unrelated. For all other species, the category I elements are very similar to the category IIA. The two species with frequency modulated IIA calls, the Mexican and Chestnut-backed chickadees, also have frequency modulated I calls. In all species, these category I calls were used as close-range, contact calls.

In category II, all three element types and fused A/C elements are

TABLE 6
VOCAL REPERTOIRES OF NORTH AMERICAN CHICKADEES

	P. gambeli	*P. carolinensis*	*P. atricapillus*	*P. sclateri*	*P. hudsonicus*	*P. rufescens*
I	+[1]	+[2,3]	+[1,4,7]	+[1]	+[6,7]	+[1,7]
IIA	+[1,7]	+[2,3]	+[1,4,7]	+[1,5]	+[6,7]	+[1,7]
IIB	+[1]	+[2,3]	+[1,7]	+[1]	+[6,7]	+[1,7]
IIC	+[1,7]	+[2,3]	+[1,4,7]	+[1,5]	+[6,7]	+[1,7]
IIA/C	+[1,7]	+[3]	+[7]	+[1]	+[6,7]	+[1,7]
Alarm whistle	+[1]	+[2,3]	+[4]	+[1]	+[6]	+[1]
III	+[1,7]	+[2,3]	+[1,4,7]	+[1,5]	+[6,7]	+[1,7]
IV	+[1,7]	+[2,3]	+[1,4,7]	−[1,5]	−[6]	−[7]
"Hiss"	+[8]	+[8]	+[8]	?	+[6]	+[8]

[1] Pers. obs. and recordings.
[2] Smith 1972.
[3] Gaddis 1979.
[4] Ficken et al. 1978.
[5] Dixon and Martin 1979.
[6] McLaren 1976.
[7] Recordings from Library of Natural Sounds, Laboratory of Ornithology, Cornell University.
[8] Sibley 1955.

present in the repertoires of all six species. In all species, the pattern of element type arrangement is the same, i.e., A before B before C. Furthermore, runs of A elements descend in frequency in all species.

Neither the high whistle alarm calls nor the high pitched elements associated with the category III calls of the Mountain Chickadee appear to fit well into any of the four categories. However, both may be related to IIA calls. Series containing only IIA elements were typically associated with circumstances of at least mild alarm, and here the successive elements occasionally ascended in frequency while also becoming longer in duration. These ascending series did not quite attain the frequencies of alarm calls, but occasionally had frequencies and structures of the elements associated with the category III calls. Carolina Chickadees possess alarm calls, which are very similar to, and probably homologous with those of the Mountain Chickadee. Category IIA calls of Carolina Chickadees, when used in circumstances of comparable apprehensiveness, often contained the full range of graded intermediates between IIA elements and the high whistle alarm calls, thus indicating a relatedness of these alarm calls to category IIA.

Calls with the general acoustic structure of category III occur in the repertoires of all six species. In the Mountain and Mexican chickadees, category III calls appear to be highly stereotyped with individuals possessing repertoires of several forms.

The high frequency elements that are frequently interspersed into bouts of category III calls of the Mountain Chickadee are also given by Carolina, Black-capped, and Mexican chickadees. These high frequency elements are referred to as "Variable See" in the repertoires of the Carolina (Smith 1972) and Black-capped chickadees (Ficken et al. 1978), and appear to be used comparably to those of the Mountain Chickadee.

Dixon et al. (1970) reported that both male and female Mountain Chickadees from northern Utah gave series of high pitched (>8 kHz) elements during precopulatory interactions. The spectrograms of these calls, however, strongly resemble the high frequency elements that were often interspersed in bouts of category III calls in the Flagstaff population. In Dixon et al.'s (1970) account, these elements ended in a category III call. It appears possible that the calls they recorded during courtship and copulation were not restricted to those activities.

In general, the calls of category III are used in aggressive contexts. They are also frequently mixed into bouts of whistled song in those species which have it, and substituted entirely for whistled song in those species which do not.

Six other species occur in the subgenus *Poecile,* but spectrographic analyses of their repertoires have not yet been made. Various vocalizations from their repertoires have, however, been described. Calls with the structure of category II from three of these species, the Sombre Tit (*Parus lugubris*), the Willow Tit (*P. montanus*) and the Marsh Tit (*P. palustris*) are figured in Thielcke (1968) and Latimer (1977). These calls contain elements of types A and C arranged according to the same pattern as in the North American species. The Marsh Tit and the Willow Tit both possess territorial advertisement calls that are very different from those of the North American species. According to Thönen's (1962) verbal transcriptions, the Willow Tit also has calls of categories I; II with element types A, B, and C; a high frequency alarm call; and III. Moreover, except for some territorial advertisement calls, the Willow Tit appears to have a typical chickadee repertoire.

According to the verbal descriptions of the vocalizations of the Marsh Tit (Morley 1953), it appears that this species possesses several other calls besides those shown in Thielcke (1968) and Latimer (1977) that are comparable in structure and usage to the other chickadees. These calls include a single element call used for close-range contact, a high whistle alarm call, a multi-element series that appears comparable to IIA–C, and calls that appear to be comparable to III and used in aggressive situations.

It thus appears that there is a generalized chickadee repertoire, with category II representing a conservative core. Interspecific differences in

this category occur, primarily in element duration, but the same element types are widespread and are arranged according to a common syntax.

SUMMARY

The vocal repertoire of the Mountain Chickadee (*Parus gambeli*) is described with particular emphasis on the quantitative evaluation of variability patterns. The vocalizations were separated into four major categories: single element, close-range, contact calls (category I); multi-element, mid-range, contact calls (category II); threat calls consisting of rearrangeable, stereotyped phrases (category III); and whistled songs (category IV). The arrangement of elements in category II calls was tightly restricted by simple rules, but the number of potentially distinctive call forms was nevertheless large. The threat calls (category III) appeared to consist of a small number of stereotyped phrases, whose arrangement was also restricted by simple rules.

A comparative review of vocal repertoire organization in all North American chickadees, except the Alaskan form of the Siberian Tit (*P. cinctus*), shows that each of the six species possesses categories I, II, and III. Three species lack the whistled song. All three element types of category II are possessed by the six species and are expressed according to a common syntax.

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