A COMPLEX CALL OF THE BLACK-CAPPED CHICKADEE (*PARUS ATRICAPILLUS*). I. MICROGEOGRAPHIC VARIATION

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ABSTRACT.—We studied the syllabic structure of the Gargle, a complex vocalization of the Black-capped Chickadee that is often associated with agression, at three main sites in southeastern Wisconsin, at one site over an 11-yr period. Sites as close as 5.7 km showed major differences in syllables, and birds at some sites differed somewhat in the number of syllables per call. Each individual probably uses all the syllables (16–23 different ones) occurring at a particular site. The syllables occurring at the end of the vocalization were shared among different demes, while the introductory syllables were usually different. Syllables showed relatively little change with time. Dialects apparently correspond to demes in this species.

The syllables are arranged in many combinations and permutations to generate a large variety of Gargle types, most of which are very rare. A few Gargle types are more common ("universals") and are usually confined to a particular site. Such a complex dialect pattern is unusual in a call. *Received 27 April 1983, accepted 5 December 1983.*

SONG dialects have been much studied, and the picture that emerges is one of considerable variability among species (for review, see Mundinger 1982). No general rules apply to all species about the nature of the dialect variation, size of dialect groups, stability of dialects with time, or the correspondence of dialect groups to demes. Certainly, detailed studies are needed of a variety of avian species. Although song dialects occur and have been studied in many species, few researchers have dealt with nonsong vocalizations, i.e. those not involved with the dual role of territorial advertisement and pair formation. The exceptions are Thielke's study of Chaffinch vocalizations (*Fringilla coelebs*), Bertram's (1970) work with mynahs (*Gracula religiosa*), and Adkisson's (1981) work with Pine Grosbeaks (*Pinicola enucleator*).

We investigated the microgeographic distribution of the Gargle, a vocalization of the Black-capped Chickadee (*Parus atricapillus*), at five sites in southeastern Wisconsin, at one site for an 11-yr period. We were concerned with the following questions. (1) What is the syllabic composition of this call in different areas? (2) Does this pattern correspond to dialects? (3) Is there any evidence that dialects correspond to demes? (4) How is information about the identity of the individual, population, and species coded? (5) What is the pattern of transmission from generation to generation? Elsewhere, we examine individual repertoires, the functional significance of Gargles, and the possible selection pressures affecting Gargle dialects (Ficken et al. in prep.).

Black-capped Chickadees are highly social, relying strongly on vocal signals (Ficken et al. 1978). Two vocalizations are especially complex: the commonly uttered Chick-a-dee, which has flock-specific characteristics (Mammen and Nowicki 1981), and the Gargle, a sputtery, explosive-sounding vocalization, which occurs year round, primarily in agonistic situations (Ficken et al. 1978). Gargles have several song-like properties: they have much greater syllabic complexity than the whistled "Fee Bee" (usually considered the "song" in this species) and are given primarily by males (Ficken 1981). Gargles often occur when males from adjacent territories engage in boundary conflicts, but they are not used in territorial advertisement. These calls also often precede copulation (Ficken et al. 1978). In the nonbreeding season, Gargles are usually associated with agonistic encounters, often when one bird directly faces or supplants another. In these contexts Gargles are a potent threat display, affecting access to food at feeders (Wipf 1981). Gargles are most often given singly, but, if the opponent does not leave immediately, a few additional ones may be given.

An understanding of the social behavior and population ecology of the chickadee is necessary for an interpretation of their vocalizations.

The following is a brief summary of certain relevant aspects of the life history of the nonmigratory populations we studied in southern Wisconsin. Chickadees live in small flocks comprised of 4–8 individuals, including adults and juveniles of both sexes, for most of the year (late July to April). A flock is not necessarily permanent in composition, as some birds may leave or join. Certain individuals, however, tend to remain in association (Odum 1942). Pair formation occurs within the winter flock (Ficken et al. 1981).

In spring (March–April), the flock gradually disrupts, pairs spending more and more time each day on their territories near or on the winter flock range (Odum 1942; pers. obs.). The young fledge in mid-June, stay with their parents for several weeks after fledging, and then disperse, mainly in early July, moving 0.24–11 km (median 1.1 km) from their birth places in our study area in Wisconsin (Weise and Meyer 1979). Following dispersal, young chickadees join flocks in their new area and are very likely to remain there permanently (Weise and Meyer 1979). Thus, the flocks formed in late summer consist of the resident adults of the area and juveniles that have dispersed to that area. Many chickadees live to be 2–5 yr old, and some very few survive 7–10 yr.

MATERIALS AND METHODS

We recorded vocalizations at five feeders in Ozaukee County, Wisconsin. Three are at the University of Wisconsin-Milwaukee Field Station, a site described by Weise and Meyer (1979). Two of these feeders (F9 and A8) are at the edge of Cedarburg Bog, where the predominant vegetation is white cedar (*Thuja occidentalis*) and tamarack (*Larix laricina*). The third (D7) is in a small swamp-hardwood forest at the edge of a large beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) forest. The Field Station and adjacent areas of Cedarburg Bog that we studied comprise 440 ha, which support 250–325 chickadees. Each year about 200 chickadees frequent the six feeders in the area, which are stocked with sunflower seeds and suet from mid-November through April. We selected three feeders that were among those most distant from one another and supported a moderate number of birds. The birds using each feeder came daily from distances of up to 1 km or more. Each feeder had two perches 15 cm apart at the entrance. Although two chickadees frequently perched on the feeder at once, only one at a time would enter to feed. Agonistic interactions were frequent. Recordings were made from November to April each year.

TABLE 1. Number of recordings of Gargles by year and site.

Year	Field Station			River-edge	Grafton
	D7	F9	A8		
1970–1974	251	0	0	0	0
1974–1975	140	0	0	0	0
1975–1976	91	0	0	0	55
1976–1977	16	0	176	91	248
1977–1978	296	439	139	22	0
1978–1979	473	580	109	104	18
1979–1980	845	0	0	281	36
1980–1981	183	0	0	4	107
Total for site	2,295	1,019	424	502	464

The Grafton site was a backyard feeder in a suburban area, a narrow wooded strip along the Milwaukee River. The fifth feeder was at the Riveredge Nature Center, a wooded area of about 120 ha. The Field Station feeders usually served several flocks each, and some flocks used two different feeders. Only rarely, however, was there an interchange of individuals among the three feeders we selected. At Riveredge and Grafton birds were not color-banded, and we have no information on flock size or movements, except that there were four or more birds. The chickadees at the Field Station were individually color-banded.

Riveredge is 5.7 km northwest of the Field Station; Grafton is 9.8 km southeast. Grafton and Riveredge are 15 km apart. All Field Station feeders are within 650 m of each other.

The sample sizes of vocalizations obtained from each feeder each year are listed in Table 1. The years 1970 to 1974 were combined, as these recordings were made as part of another study (Ficken et al. 1978). This sample, however, is useful for comparisons with recordings made at later dates at the same feeder. Intensive recordings were made from fall 1975 to January 1981. We recorded at feeders because of the ease of reading color bands and the ability to obtain good-quality recordings by placing the microphone close to the feeder.

We recorded calls at 9.5 c.p.s. with a Nagra III 4.2 L tape recorder and Sennheiser omnidirectional microphone. Occasionally, we used an Uher 4000 tape recorder and Electrovoice 644 Soundspot microphone. The microphone was placed within 1 m of the feeder.

We analyzed the vocalizations with a Kay 6061B Sona-Graph on an intermediate band-width setting (150 Hz). We refer to the discontinuous individual components of a Gargle as syllables and have assigned a letter or letter-number combination to each different syllable. In the preliminary analysis we

measured the frequency and duration of syllables and compared unknown syllables with these. Later, we determined syllable identity by comparing unknowns with tracings of syllables from sonograms, as it became apparent that syllables were quite stereotyped. Identification of syllables was based on their shape on sonograms and their frequency (Hz) and temporal characteristics. Although variation in frequency (pitch) occurs, syllables are usually very discrete. Rarely was syllable identity questionable, and then usually because the recording was poor; such syllables were not used in this analysis. The data were prepared for analysis using the Univac 1100 computer.

Results

We examined Gargles at two levels of organization: component syllables and the syllabic combinations constituting the call (the Gargle type). It might have been possible to devise a scheme for lumping call types with similar syllabic composition and ordering of syllables, but, because of the complex arrangements of syllables in the calls and our lack of knowledge of the functional significance of the various syllables and syllable combinations, we treated every unique syllable combination as a different call type, e.g. EVRFSQ is a different type from EVFSQ.

Syllabic composition of gargles.—Sonograms of the more common syllables at the various sites are presented in Fig. 1. Many are frequency sweeps, often covering wide frequency ranges very rapidly. Only three syllables (I, Z, and the very infrequent M) are short pure tones. Three syllables are buzzes or trills (P1, P2, and Q). Usually, all the syllables in a single call are different. (Fig. 2 presents some representative calls.)

Number of syllables in calls.—As calls vary in the number of syllables, possible a principal difference among populations is the number as well as the kind of syllables.

The number of syllables in a call varied from 2 to 13 (Fig. 3). The following are the means and standard deviations of number of syllables per call at the various feeders: D7: 5.9 ± 3.84; A8: 6.1 ± 1.82; F9: 6.04 ± 3.06; Grafton: 5.69 ± 1.68; Riveredge: 7.25 ± 1.89. The overall distribution of number of syllables per call is not a normal one. For example, calls with 2 and 3 syllables are rare at all feeders (5% of total), whereas 4-syllable calls are much more frequent (about 20% of all calls, except at Riveredge). Riveredge (and to a lesser degree Grafton) birds tend to give more calls of 10–13 syllables than do the Field Station birds. The incidence of 10- and 11- syllable calls at Riveredge is significantly different from the Field Station sample ($\chi^2_1 = 9.56$, $P < 0.01$). The calls of all Field Station birds tend to peak at 4 syllables and at 6–8 syllables, then to decline rapidly at 9–10 syllables. Among Grafton birds there is the same trend toward 2- to 4-syllable calls, but they differ in having a sharp peak at 5 syllables and then a rapid decline; they also have a higher proportion of calls with 9–13 syllables than do the Field Station birds. Riveredge birds have a lower proportion of 4-syllable calls than the others do and a higher proportion of 10- and 11-syllable calls.

Considerable variation in syllable number occurred from year to year at the same feeder, and only at F9 feeder was there no statistical difference between years ($\chi^2_6 = 12.1$, $P > 0.05$).

We combined data from all Field Station feeders and compared syllable number with the other sites. The Field Station was significantly different from Riveredge ($\chi^2_8 = 516$, $P < 0.001$). Grafton and Riveredge were also significantly different ($\chi^2_{12} = 154$, $P < 0.001$) in syllable number. There were also significant differences among the three feeders at the Field Station ($\chi^2_{12} = 154$, $P < 0.001$).

Individual repertoires of syllables.—We tested the hypothesis that all individuals produce the full syllable repertoire of their particular population by surveying the repertoires of four individuals at D7 feeder for which there were sample sizes of over 100 calls (Table 2). The individuals differed significantly in the frequency of usage of syllables ($\chi^2_{48} = 480$, $P < 0.001$). All birds shared the more common syllables, however (excluding the rare I, U, and R4, the latter given by only one individual).

Syllables at different sites.—We tested the hypothesis that the syllabic composition of calls is different at different sites. Because all three Field Station sites are very close together, we expected that syllable sharing would occur among them, that Riveredge would differ somewhat from the Field Station, and that Grafton, because of its distance, would be very different from both the Field Station and Riveredge.

The feeders differed in the syllables present (Table 3). We calculated a coincidence index (Dice 1945): $2h/(a + b)$, where h = total number

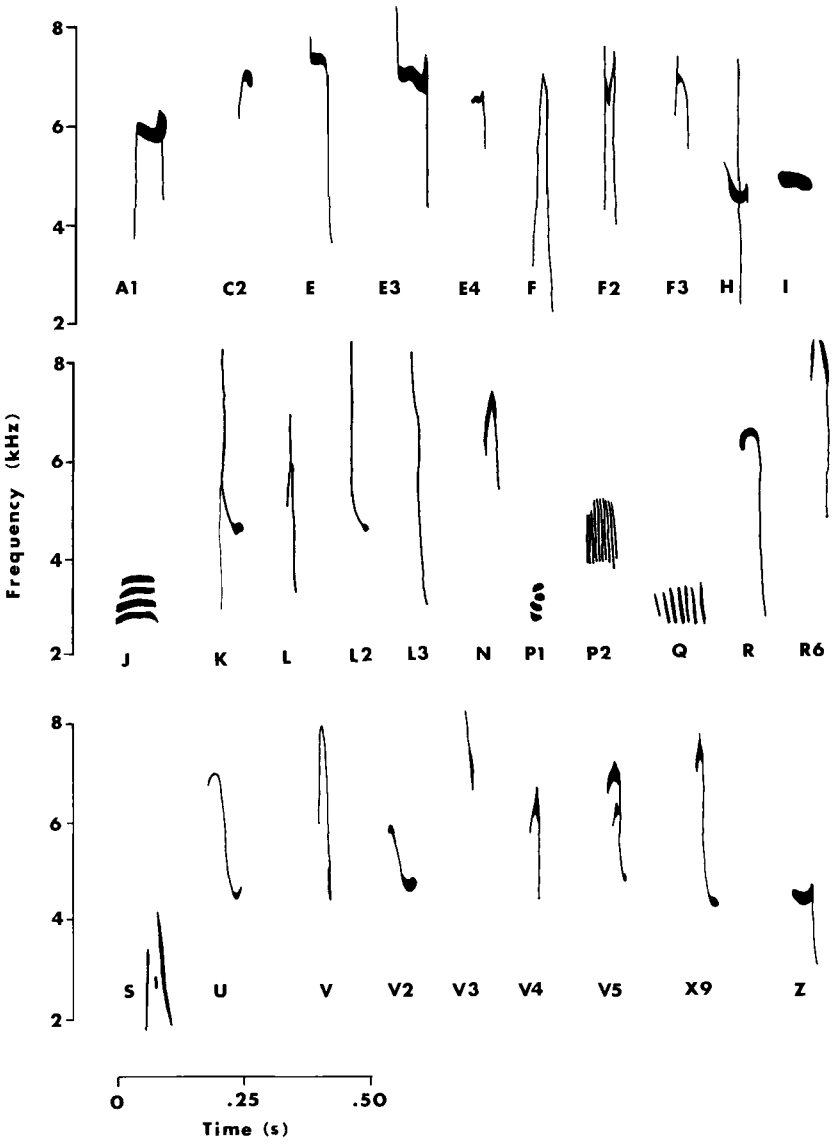

Fig. 1. Syllables of Gargles at the five study sites. (A few very rare syllables were omitted.)

of shared syllables, a = total number of syllables at one feeder, and b = total number of syllables at the other feeder. Syllables at the three Field Station feeders were very similar, but these sites showed a lower degree of similarity with Grafton and Riveredge; and the lowest degree of similarity occurred in the two feeders that are the most distant from each other—Grafton and Riveredge (Table 4).

One syllable (C2) was unique to the three Field Station feeders, while Riveredge had 8 syllables not shared with any other study site, and Grafton had 5. These unique syllables were usually at the beginning of the call. For example, these site-specific syllables were involved in 142 Gargle types; they were the first syllable in 109, the second in 18, and the third or more in only 15.

Birds at the three Field Station sites and at Grafton used 16–17 different syllables. The

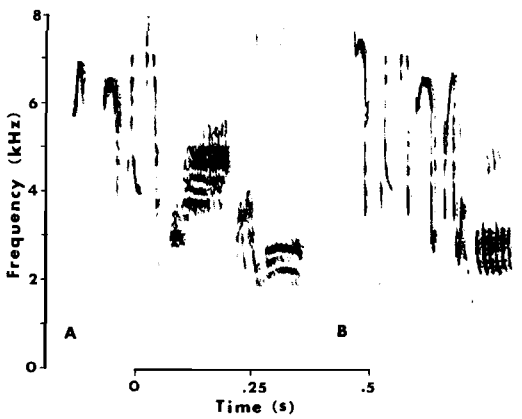

Fig. 2. Two common Gargle types at the Field Station. A. Syllabic combination C2RKVP1P2SJ. B. Syllabic combination EKVRFSQ.

number (23) was unexpectedly higher at Riveredge, however. To understand this phenomenon, it would be important to know the number of birds using each feeder and the immigration rates from other sites.

One interesting finding was that those syllables that are usually near the end of a Gargle, if they occur at all (P1, P2, S, Q, and J), were found in all the populations studied. All populations also shared 5 other syllables (E, F, K, L, and V), but 18 other syllables were not found universally. Clearly, microgeographic variation occurred in the distribution of many syllables, although those syllables typically near the end of the call were found at all sites.

As differences occurred in the frequency of usage of syllables at the same site in different years, it is not surprising that there were also

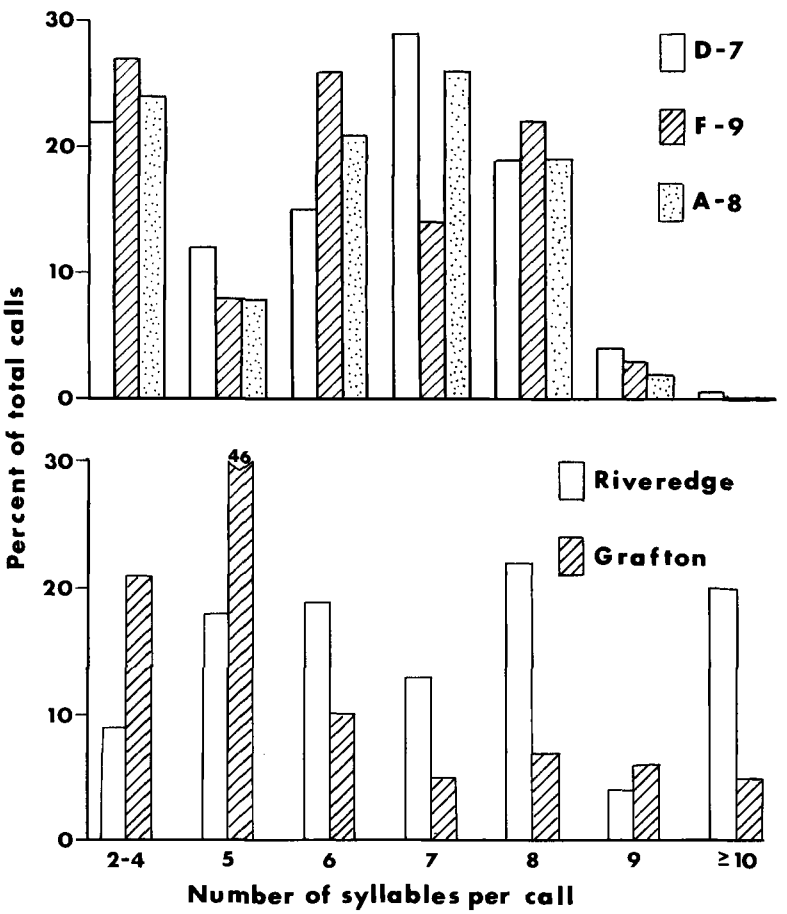

Fig. 3. Distribution of number of syllables in a call at all study sites.

TABLE 2. Frequency of occurrence of syllables for four individuals at D7 feeder.

Syllable type	Individual[a] AOCJ ($n = 133$)	AOYR ($n = 122$)	PCAO ($n = 134$)	AOPB ($n = 146$)
C2	47	1	24	3
E	38	111	68	90
F	77	107	74	108
H	33	6	14	18
I	0	0	1	8
J	73	9	22	13
K	90	112	83	98
L	34	6	15	27
N	30	3	5	4
P1	65	10	22	14
P2	66	10	49	35
Q	35	96	67	97
R	92	119	100	118
R4	0	0	0	4
S	110	110	99	94
U	0	0	2	6
V	93	116	99	114

[a] n = total number of calls for that individual.

significant differences in the frequency of usage of syllables that comprised more than 1% of the total among the three Field Station sites ($\chi^2_{30} = 477$, $P < 0.001$).

Rank order of frequency of occurrence of syllables.—Although considerable variation occurred in the frequency of usage of particular syllables at the same site from year to year, we postulated that the rank order of frequency of occurrence of syllables would be the same at the same feeder in different years, as well as at different feeders. In other words, the most common syllables at one feeder would also be the most common ones at other sites, and the rare ones would be rare at all sites.

First, we compared rank order using Spearman's rho for different years at the same site. All the seven periods at D7 feeder compared individually with one another were significantly correlated ($P < 0.01$), except for 1975–1976 versus 1979–1980 and 1980–1981, and 1970–1974 versus 1974–1975 ($P > 0.05$). Thus, at D7 the rank order of syllables of some of the earlier years was not correlated with some of the later years. At F9 feeder data for 1977–1978 were compared with 1978–1979 ($\rho s = 0.83$, $P < 0.01$); the same trend occurred at A8 in a comparison of 3 yr ($P < 0.01$). Grafton exhibited a similar pattern for the 2 yr tested ($\rho s = 0.57$, $P < 0.05$), as did Riveredge ($\rho s = 0.84$, $P < 0.001$).

TABLE 3. Occurence of syllables at the various sites (syllables that were more than 1% of total syllables for that site).

Syllable	Sites D7	F9	A8	River-edge	Graf-ton
A1	0	0	0	0	+
C2	+	+	+	0	0
E	+	+	+	+	+
E3	0	0	0	0	+
E4	0	0	0	0	+
F	+	+	+	+	+
F2	0	0	0	0	+
F3	0	0	+	0	+
H	+	+	+	+	0
I	+	+	+	+	0
J	+	+	+	+	+
K	+	+	+	+	+
L	+	+	+	+	+
L2	0	0	0	0	+
L3	0	0	0	+	0
N	+	+	+	+	0
P1	+	+	+	+	+
P2	+	+	+	+	+
Q	+	+	+	+	+
R	+	+	+	+	0
R6	0	0	0	+	0
S	+	+	+	+	+
U	+	+	+	+	0
V	+	+	+	+	+
V2	0	0	0	+	0
V3	0	0	0	+	0
V4	0	0	0	+	0
V5	0	0	0	+	0
X9	0	0	0	+	0
Z	0	0	0	+	0
Total number of syllables	16	17	16	23	16

We tested the hypothesis that, despite the differences in syllables among sites, there would be a correlation for shared syllables in rank order of the syllables. All the Field Station sites were significantly correlated in rank order ($P < 0.01$). Grafton and Riveredge were significantly

TABLE 4. Coincidence indices of syllables at all sites.

Site	D7	F9	A8	River-edge	Graf-ton
D7		1.0	0.97	0.67	0.63
F9			0.97	0.72	0.63
A8				0.75	0.67
Riveredge					0.51
Grafton					

TABLE 5. Number of different Gargle types in which a particular syllable was used at D7 feeder. (Total number of Gargle types = 182. In the rare cases when a syllable was used more than once in a Gargle type, it was scored only once. * = syllable also present at Riveredge and Grafton.)

Syllable	Number of Gargle types in which it occurred
F*	118
S*	114
V*	105
K*	97
R	76
E*	72
P2*	71
Q*	64
P1*	59
L*	57
J*	47
H*	32
C2	19
N	11
I	11
U	5
C	2
V3	2
M	2
A	1
Y	1
R3	1
R4	1

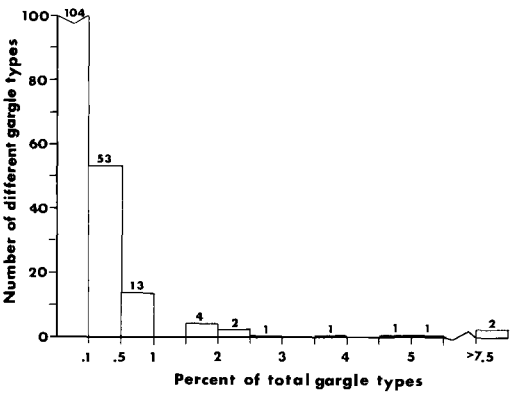

Fig. 4. Frequency distribution of Gargle types at D7 feeder.

correlated ($\rho s = 0.83$, $P < 0.01$), but Grafton was not significantly correlated with D7 at the Field Station in either of the 2 yr ($P > 0.05$). Riveredge and the Field Station were significantly correlated ($\rho s = 0.7$, $P < 0.01$).

A general pattern of rather stable rank ordering of the frequency of occurrence of syllables among the various sites occurs. As the earlier and later samples at the Field Station were often not significantly correlated, however, there may be some shifts in rank order with time, and rank order may be different at more distant sites (i.e. Grafton and Field Station).

Distribution of syllables over time.—The syllables at D7 feeder were assessed over an 11-yr period, and most syllables were present in all years. Exceptions were some of the rarer syllables (C2, N, and U), present in some years but not others. These three syllables were unusual, however, in that each was associated with only a few Gargle types (Table 5). The syllable M was rare in 1970–1974 and was never recorded after that time. Syllables L and H were absent in the earliest period (1970–1974) but were common thereafter.

There were similar trends at the other feeders: some rare syllables were not present in all years, but the common ones persisted. The most common syllables at D7 were also found at Riveredge and Grafton; this was not true of the rarer syllables. As might be expected, the more common syllables, involved in a large number of call types, persisted over 11 yr at D7.

Relatively little change occurred over a span of 11 yr except for the introduction of two syllables. There was no trend for very rare syllables to become well established over the years, nor did any of the more common syllables become extinct, although there was substantial variation in the frequency of occurrence of many syllables from year to year at the same site.

Distribution of gargle types.—A system based on 2–13 syllables that can be combined in many different ways generates an incredible variety of call types. While our sample probably includes all syllables uttered at the feeders during the years studied, except perhaps for the very rare ones, the situation with Gargle types is much more complex. Most Gargle types are very rare (Fig. 4). Of a sample of 182 Gargle types at D7 feeder, 104 of these comprised less than 0.1% each of the total Gargles given. Many Gargle types occurred only once in our sample. Because Riveredge and Grafton have a number of syllables differing from those at the Field Station, the Gargle types there would be expected to be largely different.

TABLE 6. Coincidence indices for Gargle types at the various sites (* = total number of Gargles).

Site	D7	F9	A8	River-edge	Grafton
D7 (1,635*)		0.76	0.62	0.38	0.01
F9 (813)			0.68	0.36	0
A8 (349)				0.33	0
Riveredge (414)					0
Grafton (453)					

Each male probably has at least 15 Gargle types (Ficken et al. in prep.). Coincidence indices of Gargle types were calculated to examine sharing of Gargles at all feeders (Table 6). The amount of sharing of Gargle types among the three Field Station feeders was relatively high (0.62–0.76); the similarity with Riveredge was lower, and Grafton shared almost no Gargles with the Field Station. Thus, although birds at different sites may share some of the same syllables, different sites may have few or no Gargles in common due to the large number of syllable combinations possible.

The distribution of the 12 most common Gargle types at D7 was examined over 11 yr. The frequency of occurrence of the various Gargle types in different periods at D7 was significantly different ($\chi^2_{55} = 881$, $P < 0.001$) (Table 7). Thus, there are year-to-year differences, even in the most common Gargles, in the frequency with which they occur at the same site.

Although most Gargle types are very rare, a few at each feeder are much more common. Table 8 indicates that two Gargle types occurred at a high incidence at all three Field Station feeders, the two comprising about a third of all Gargles given. These we term the Field Station "universals." Although all the syllables of the universals are present at Riveredge, Field Station universals made up less than 0.1% of the total Gargles at Riveredge. One of the two most common Gargle types at Riveredge did not occur at all at the Field Station. The frequency of usage of the two universals at D7 feeder over the 11-yr period differed significantly ($\chi^2_6 = 64$, $P < 0.001$).

TABLE 8. Frequency of occurrence of the two most common Gargle types at Field Station sites.

Site	Gargle type[a]	
	EKVRFSQ	VRP2Q
D7	525 (19.7)	208 (7.8)
A8	48 (12.2)	83 (21.0)
F9	84 (9.2)	196 (21.6)
Riveredge	0 0	2 (4)
Grafton	0	0

[a] Percentage of total Gargles in parentheses.

We hypothesized that endings of Gargles (defined as the last two syllables, regardless of the number of syllables in the vocalization) might be more conservative than the beginning (defined as the first two syllables of the Gargle). These numbers of syllables were chosen, as the average number of syllables in the vocalization is about six. Although there are a variety of endings, most are very rare. SQ and

TABLE 7. Occurrence of the 12 most common Gargle types at D7 feeder in different years.

Gargle type	1970–1974	1974–1977	1977–1978	1978–1979	1979–1980	1980–1981
C2RKVP1P2SJ	18	15	14	42	53	0
RKIFSQ	6	16	13	18	24	1
EKVFP1P2SQ	2	7	7	31	29	0
EKVFSQ	0	4	4	22	43	0
EKVR	0	3	11	10	31	4
LEKVFSQ	0	0	0	27	18	5
LHRF	0	2	1	1	16	6
LHRFP1P2SJ	0	43	0	7	65	5
LHRFSJ	0	0	51	7	1	0
KIFSQ	34	16	0	2	0	0
EKVRFSQ	30	30	75	130	184	38
VRP2Q	58	13	14	29	85	6

SJ are the most common ones at all sites, accounting for 56% of the endings at D7, 70% at A8, 55% at F9, 37% at Grafton, and 62% at Riveredge. Grafton differed somewhat from the other sites in having another common ending (FS). Statistically significant differences are evident among sites in the frequencies of occurrence of the two most common endings ($\chi^2_4 = 11.2$, $P < 0.05$). One interesting feature is that these common endings occur at all feeders, although other syllables in the vocalizations may be very different, varying microgeographically. We also tested the hypothesis that the frequency of the syllables ending Gargles would not be significantly different at the three Field Station feeders, and this hypothesis was rejected ($\chi^2_8 = 68$, $P < 0.001$). Thus, although these syllables are universal at the sites studied, the frequency of usage of the syllables differs from site to site.

The most common beginnings were EK and LH at D7 and A8 feeders; at F9 EK and ER were the most common, with LH being the next most common. Gargles beginning with F2K predominated at Grafton, followed by E4K and KF; at Riveredge V3L and LH were the most common beginnings. At these latter two feeders, Gargles most often began with syllables that were rare or absent at the other feeders.

When very rare syllables occurred (comprising less that 10 observations each), they were usually the first syllable (10 cases) or, more rarely, the second (3 cases) ($n = 15$), supporting the idea that it is the ending rather than the beginning syllables that are more widespread. In summary, although most Gargle types were rare, the two most common ones were shared at all Field Station sites and may be considered specific to that population. Even more distant sites shared endings, however.

Discussion

Microgeographic patterns of variation.—Dialects are generally considered to occur if conspecifics in a particular geographic area share vocalizations that are different from vocal patterns in different geographic areas (Thielcke 1969, Krebs and Kroodsma 1980, and Mundinger 1982, review avian dialects). A dialect pattern is evident in Black-capped Chickadees at the level of syllables and at the level of syllabic combinations (Gargle types). Furthermore, the pattern is microgeographic, as marked differences occur in areas as close as 5.7 km. The three Field Station sites, separated by only a few hundred meters (but including birds with breeding sites up to 3 km distant), were very similar, particularly in the call syllables. Similar microgeographic distributions occur in other species. For example, Mundinger (1975) found that dialects in House Finches (*Carpodacus mexicanus*) were confined to a few square kilometers, and Payne (1973) noted that in Village Indigobirds (*Vidua chalybeata*) neighbors shared most song types, but birds 6.5 km away shared no song types.

All chickadees seem to possess the full repertoire of syllables of their population, although a few very rare syllables may be specific to certain individuals. Birds at different sites may differ in their syllables, but most sites have about the same number of syllables, indicating that there may be an optimal repertoire size of syllables. Another feature common to all sites is that the rank order of shared syllables is usually similar, indicating that the same basic "vocal rule" holds for the occurrence of syllables at the various sites. At certain sites calls tend to have more syllables than at others.

Much variation in vocal dialects occurs among different species. Some, such as the White-crowned Sparrow (*Zonotrichia leucophrys*), have only one song type that varies geographically (Marler and Tamura 1962). In the Indigo Bunting (*Passerina cyanea*), unlike the chickadee, most song figures (these correspond to our syllables) occur in only a few individuals (Thompson 1970). The chickadee dialect pattern is similar to that of the Northern Cardinal (*Cardinalis cardinalis*) (Lemon 1966), in that most birds in a locale share the same syllables; although some syllables are widespread, others have a more restricted distribution. Most of the song types of territorial neighbors are similar in Cardinals, and in the chickadee there is some sharing of call types in birds of the same locale.

Our data indicate that it is necessary to examine vocalizations and their variation at two levels: that of syllables and that of the combination of these in various call "types." In chickadee Gargles, the distribution of syllables is independent of that of the call types, in that some syllables have a wider distribution than do the call types. For example, even though Riveredge birds had the component syllables

of the two most common Gargle types at the Field Station, one of these types was very rare at Riveredge and the other apparently absent.

Coding of information in the call.—Rare syllables were more common at the beginning of the call than at the end, and more differences occurred among localities in the beginning syllables than in the ending ones. In fact, the most common endings were found even in our two most distant localities, Grafton and Riveredge. Two recordings of a Black-capped Chickadee from the Great Smoky Mountains (Cornell University collection) had three beginning syllables not found in our Wisconsin sample, but the terminal syllables were also common endings in southeastern Wisconsin. We therefore suggest that the terminal syllables of Gargles may be species-specific features, while the beginning ones may specify the particular population.

Relationship of dialects to demes.—A central question concerning avian dialects is whether or not these vocalizations act as barriers to gene flow (Nottebohm 1969). Several workers have suggested that dialects may reduce gene flow between demes (Baker 1974, Baker and Mewaldt 1978), while others doubt that this is the case (Petrinovich et al. 1981). Clearly, more data on a variety of species are necessary to resolve the question.

Do dialects correspond to demes in Black-capped Chickadees? As the Field Station supports some 200–300 chickadees during the breeding season and, although movements occur within the area, there is not much immigration or emigration apart from juvenile dispersal, the Field Station chickadees might be considered to constitute a deme. A minimum estimate of median dispersal distance is 1.1 km (Weise and Meyer 1979). Howitz's (1981) estimates of 1.34–2.39 km for a Minnesota population are consistent with these data. Riveredge Nature Center (5.6 km from the Field Station) probably constitutes another deme. There are four other bird-trapping stations where chickadees are banded within 6 km of the Field Station. Yet, of over 2,000 birds trapped at the Field Station since 1970, only three have been retraps from the other stations. Two Field Station birds have been retrapped at the other stations. This part of southeastern Wisconsin is a mosaic of woodlands, most very small except for the Field Station area. The Field Station is separated from areas such as Riveredge and Grafton by habitats unsuitable for breeding, especially agricultural fields. Grafton and Riveredge are both well beyond the median dispersal ranges of Field Station birds, and Grafton and Riveredge are even more distant from one another. Thus, we can probably conclude that different demes of chickadees have somewhat different syllables and, of course, different combinations of these in their call types.

Dialects would be expected in the vocalizations of species, such as Black-capped Chickadees, that are largely sedentary, disperse as juveniles over relatively short distances, and have discontinuous habitats. Dialects in Cardinals are maintained because of high site fidelity, low annual mortality, and a relatively short dispersal distance (Lemon 1975).

Dialects over time.—Detailed studies of how song patterns in the same area change over time have been done for only a few species (e.g. Lemon 1975, Cardinal; Baptista 1975, White-crowned Sparrow; Jenkins, 1977, Saddleback, *Creadion carunculatus*; Slater and Ince 1979, Chaffinch; and Payne et al. 1981, Indigo Bunting). Avian patterns of cultural transmission are reviewed by Slater and Ince (1979) and Payne et al. (1981). In Indigo Buntings a few song types persisted over 15 yr, suggesting that local songs may remain similar for several generations, although some year-to-year changes occurred in the frequency of occurrence of syllables (Thompson 1970). Baptista (1975) found a marked change in songs of White-crowned Sparrows in 2 yr. Jenkins (1977) noted that the distribution of song-dialect patterns was stable over a 4-yr period but found some changes in note structure and the combinations of parts of songs. Ince et al. (1980) studied changes in Chaffinch song over a 20-yr period that involved 8–10 generations of Chaffinches. He found that some syllables stayed the same while others changed, and a reassortment of syllables occurred between song types. Lemon (1975) postulated that changes will occur over time because of the processes of cultural transmission involving copying errors, improvisations by individual birds, and immigration of birds with different cultural experiences. As chickadees average only 2–3 yr of survival, we probably sampled at least three generations of chickadees.

The most common syllables persisted over a long term at a Field Station site studied over 11 yr. Rare syllables, usually occurring in the

Gargle types of only a single individual, seemed to disappear rather than to become incorporated into the population's repertoire. Because of insufficient data, we could not follow the transmission of Gargle types as well as that of syllables. The most common Gargle types persisted over our sampling period at the Field Station, however. Ince et al. (1980) noted that the more common song types of Chaffinches persisted for a longer time than did the rarer ones, probably because a bird had more individuals from which it could learn the common than the rarer songs.

Some of the more unusual features of chickadee vocal dialects.—Dialects occur in chickadee vocalizations at the levels of the syllable and of the more common Gargle types. What is noteworthy of the chickadee, as compared with most other avian species, is its use of an array of different syllables that occur in a great variety of combinations. Each individual uses about 15 syllables, which it combines in various ways to generate a large number of call types. Such complexity of dialect pattern is unusual in avian calls, which, if there is a dialect pattern at all, usually have a macrogeographic rather than a microgeographic pattern (Mundinger 1982).

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The **XIX International Ornithological Congress** will take place in Ottawa, Canada, from **22 to 29 June 1986.** Prof. Dr. Klaus Immelmann (West Germany) is President and Dr. Henri Ouellet (Canada) is Secretary General. The program is being planned by an international Scientific Programme Committee chaired by Professor J. Bruce Falls (Canada). The program will include plenary lectures, symposia, contributed papers (spoken and posters), and films. There will be a mid-congress free day. Pre- and post-congress excursions and workshops are planned in various interesting ornithological regions of Canada. Information and requests for application forms should be addressed to: **Dr. Henri Ouellet, Secretary General, XIX Congressus Internationalis Ornithologicus, National Museum of Natural Sciences, Ottawa, Ontario, Canada K1A 0M8.**

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