

# A COMPLEX VOCALIZATION OF THE BLACK-CAPPED CHICKADEE. II. REPERTOIRES, DOMINANCE AND DIALECTS<sup>1</sup>

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*Abstract.* The *gargle*, a complex call of the Black-capped Chickadee (*Parus atricapillus*), was studied during the flocking period at two feeders in southeastern Wisconsin. *Gargles* are usually associated with aggression and are given more frequently by males than females, the gargler almost always winning the encounter. Dominant birds give *gargles* more frequently than subordinates. Particular *gargle* types (unique syllable combinations) are not addressed to specific individuals.

Birds have at least 13 *gargle* types in their repertoires, some having over 30, although the total repertoire size could not be determined. Dominants did not have larger or more diverse repertoires, nor did they show differences as compared with subordinates in the amount of sharing of *gargle* types. Most *gargle* types are shared, but each individual has some very rare ones that may not be shared. The frequency with which particular *gargle* types are uttered varies from year to year at the same feeder and also in different parts of the winter. The frequency of occurrence of particular *gargle* types indicates that selection may favor call-sharing.

At two feeders, 383 m distant, which we studied for 2 years, no flock specific dialects were detected, but in one of the 2 years birds visiting the same feeder tended to share *gargle* types more with each other than with those at the other feeder. Birds that had strong proximity associations with each other, however, did not show stronger sharing compared to those that were more weakly associated.

*Key words:* Repertoires; calls; vocalizations; *Parus atricapillus*; Black-capped Chickadee.

## INTRODUCTION

The Black-capped Chickadee (*Parus atricapillus*), as is the case with many other members of its widespread genus, has a complex life history involving both social and nonsocial periods. Calls of parids, particularly those associated with flocking, are often very complex (*P. major*, Gompertz 1961; *P. carolinensis*, Smith 1972; *P. atricapillus*, Ficken et al. 1978; *P. sclateri*, Dixon and Martin 1979; *P. hudsonicus*, McLaren 1976). The *gargle*, a sputtery-sounding vocalization occurring year-round, is one of the most complex nonsong vocalizations known in birds. Each call is composed of two to 13 syllables (of the approximately 16 syllables used by a single population) that can be recombined in many ways, generating a great variety of call types (each unique combination of syllables is referred to as a "type"; Ficken and Weise 1984). The distribution of these syllables and call types exhibits

a microgeographic pattern in southeastern Wisconsin (Ficken and Weise 1984).

*Gargles* show some song-like properties such as their complexity, more frequent use by males, involvement in territorial defense, and presence of dialects (Ficken 1981). However, they differ from the songs of most birds in being given year-round, not being involved in territorial advertisement, being used as short range rather than long distance signals, and usually being given only singly and rarely in bouts.

Some observations during the breeding season showed that *gargles* occurred during agonistic interactions among neighbors at territorial boundaries. Such interactions were frequent, especially early in the breeding season. As far as we were able to determine, only males *gargled* during these encounters. Each male gave several *gargle* types, and the calls were of the same syllable composition as those given by those individuals during the nonbreeding season.

The present study concerns the role of the *gargle* in the nonbreeding season. At this time the Black-capped Chickadee is very social (Odum

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1942). Chickadees live in flocks of six to eight individuals of all ages and both sexes between July and April in Wisconsin. A linear dominance hierarchy is evident (e.g., Weise 1971, Glase 1973). Some movement occurs among flocks, but most individuals remain associated with the same individuals throughout the nonreproductive season. Territorial neighbors in the spring are usually members of the same winter flock.

The objectives of this study were to determine: (1) whether a relationship exists during the nonreproductive season between individual repertoires of *gargles* and dominance, (2) the role of *gargles* in affecting the outcome of aggressive interactions, and (3) the amount of sharing of *gargles* among birds visiting the same feeder vs. different feeders.

## METHODS

Two feeders (F9 and D7) at the University of Wisconsin-Milwaukee Field Station, Saukville (Ozaukee Co.), Wisconsin were the study sites. Ficken and Weise (1984) described the study sites and the methods of sound recording and analysis.

The birds were individually color banded. Sex was determined for most individuals on the basis of wing length (Weise 1979) and observations of reproductive behavior. In addition to recording vocalizations, we observed agonistic interactions at the feeders and whenever possible, identified the winner and loser of the encounter. In many cases, one bird simply supplanted another without vocalizations. Sometimes one bird *gargled* at another and if the opponent did not immediately leave, the *gargler* often supplanted it. Another common situation occurred when two birds were perched on the feeder (there were two perches), and one turned its back as the other went in and fed. If the first bird to arrive waited while the second fed, the bird that waited was considered the "loser." Dominance matrices (Brown 1975) were constructed for each feeder each year based on the percent wins by an individual. Several flocks often used the same feeder (however the F9 and D7 feeders were used by different flocks) and the dominance hierarchy constructed for each feeder included the combined flocks. In order to assess the amount of visitation of feeders by particular individuals, we noted whether a bird was present during a 15-min period of observation. We calculated a coefficient of association (Ficken et al. 1981) based on these data, so that pair-wise associations of

individuals visiting the same feeder could be determined. In this case the coefficient of association =  $2h/a+b$ , where  $h$  is the number of times two individuals were noted during the same observation period in the vicinity of the feeder, and  $a$  and  $b$  are the total number of times each individual was observed. The same index (based on Dice 1945) was used for assessing sharing of *gargles* by individuals, in which case  $h$  is the number of times shared *gargle* types occurred and  $a$  is the total number of *gargles* of individual A,  $b$  is the total number of *gargles* of individual B. We used the Shannon-Wiener Diversity Index (Cox 1967) in examining individual repertoires:  $D = \sum - p_i \log_2 p_i$ , where  $p_i$  = decimal fraction of the  $i$ th type in the repertoire.

*Gargles* are given infrequently and it was difficult to collect large samples from known individuals. For example, for most of the winter only one or two calls were given per hour at the feeder despite visits by large numbers of individuals. The incidence of calling was often much higher in late November and early December; 20 to 40 calls per hour were sometimes produced. For most of the analysis we used birds from D7 feeder because the sample size from known individuals was larger than for F9 feeder. We recorded at feeders between mid-November and late March to facilitate the collection of data on known individuals.

## RESULTS

### GARGLES DURING AGONISTIC ENCOUNTERS IN THE NONBREEDING SEASON

Males *gargle* much more frequently than females. Of 1,336 *gargles* from birds of known sex, 96.5% were produced by males (49 males, 13 females).

The occurrence of *gargles* is often strongly correlated with the outcome of agonistic encounters. We analyzed 846 interactions which included *gargles* at D7 feeder and found that in 837 cases (98.9%) the *gargler* won the interaction. At F9 feeder *garglers* won every interaction ( $n = 193$ ). Not only do *garglers* almost invariably win, but the bird that *gargles* is almost never attacked by the other. *Gargles* are usually uttered while facing the opponent (92% of cases,  $n = 75$ ). If the recipient does not leave following a *gargle*, the actor then often lunges, usually resulting in the opponent's departure. Because of the rapidity with which these interactions took place, it was not

TABLE 1. Comparison of dominance rank and the use of the three most common *gargle* types at D7 feeder. In parentheses is the number of *gargles*. ( $\rho_s$  = Spearman's rho.)

Year	Dominance rank of individual	% Common <i>gargles</i>	
1977-1978	1	69 (9)	$\rho_s = -0.72,$ $P > 0.05$
	3	70 (38)	
	4	26 (13)	
	5	50 (4)	
	6	26 (13)	
1978-1979	1	18 (40)	$\rho_s = 0.70,$ $P > 0.05$
	2	27 (55)	
	4	87 (52)	
	5	47 (17)	
	7	59 (22)	
1979-1980	1.5	76 (30)	$\rho_s = -0.37,$ $P > 0.05$
	1.5	57 (57)	
	3	42 (24)	
	4.5	72 (32)	
	4.5	28 (88)	
	6	23 (47)	
	7	0 (23)	
9	62 (13)		
1980-1981	1	44 (9)	$\rho_s = -0.50,$ $P > 0.05$
	2	27 (15)	
	3	25 (4)	
	4	41 (22)	
	7	26 (35)	
	11	0 (5)	

possible to record all the events in an encounter. *Gargles* may affect priority of access to food at feeders, and similar situations occur when food is more dispersed as dominants use specific foraging sites (Glase 1973).

As garglers almost always win, we anticipated a correlation between uttering these vocalizations and position in the dominance hierarchy. Dominant birds gave more *gargles* per observation period than did subordinates (Kendall's tau =  $-0.541$ ,  $P < 0.001$ ,  $n = 94$ ). Correlations are negative because the most dominant bird is given a rank of 1). As females tended to be lower in dominance rank than males, the trend might simply reflect the infrequency of female calling. However, dominance rank and frequency of uttering *gargles* were correlated when only males were considered (Kendall's tau =  $-0.464$ ,  $P < 0.001$ ,  $n = 48$ ). Considerable variability occurs in the frequency of *gargling*, particularly among high-ranked birds. Males that *gargle* win that encounter, but of course many encounters are won without *gargling*. A correlation occurs be-

tween the number of *gargles* given per encounter won and dominance (Kendall's tau =  $-0.246$ ,  $P < 0.001$ ,  $n = 119$ ), indicating that encounters won by high-ranked individuals are more likely to include a *gargle* than those won by low-ranked birds.

Since *gargles* are not involved in all agonistic encounters (of 334 encounters at D7 feeder in 1979 to 1980, only 24.2% involved *gargles*), some selectivity might be expected with reference to the dominance rank of the recipient of the *gargle*. As garglers almost always win, the call might be directed primarily at birds close in rank, at those with whom there might be expected to be more dispute and uncertainty about the outcome of the encounter. We computed the difference in rank between the winner and loser of two types of encounters, those in which at least one *gargle* was used and those with no *gargles*, at D7 feeder in the winter of 1980 to 1981. The median rank difference for encounters with *gargles* was 5, for the other encounters 7, but the difference was not significant (Mann-Whitney *U*-test, one-tailed,  $P > 0.05$ ,  $n_2 = 36$ ,  $n_1 = 211$ ). Thus chickadees do not give *gargles* more frequently to those close in rank.

We also examined whether a relationship occurs between the form of the *gargle* and the identity of the recipient. We did not have sufficient data for a statistical analysis of this question. However, the same *gargle* type was given by an individual to many different recipients. For example, one bird gave one particular *gargle* type 47 times to 22 different individuals. Sample size was also too small to test whether particular *gargle* types were more likely to be given to subordinate vs. more dominant individuals; however, the data do suggest that a particular *gargle* type is not "addressed" only to one or a few individuals.

We tested whether the more dominant birds gave *gargles* of different syllabic composition than the more subordinate members of the flock. It might be advantageous to give the most common *gargles* rather than the rare ones which might not be as familiar to the listeners. No correlation existed between dominance rank and relative use of the three most common *gargle* types for four time periods at D7 feeder (Table 1).

The number of syllables in a *gargle* ranges from two to 13 (Ficken and Weise 1984). No correlation was found between dominance and number of syllables in the call (Spearman's rho  $\rho_s =$

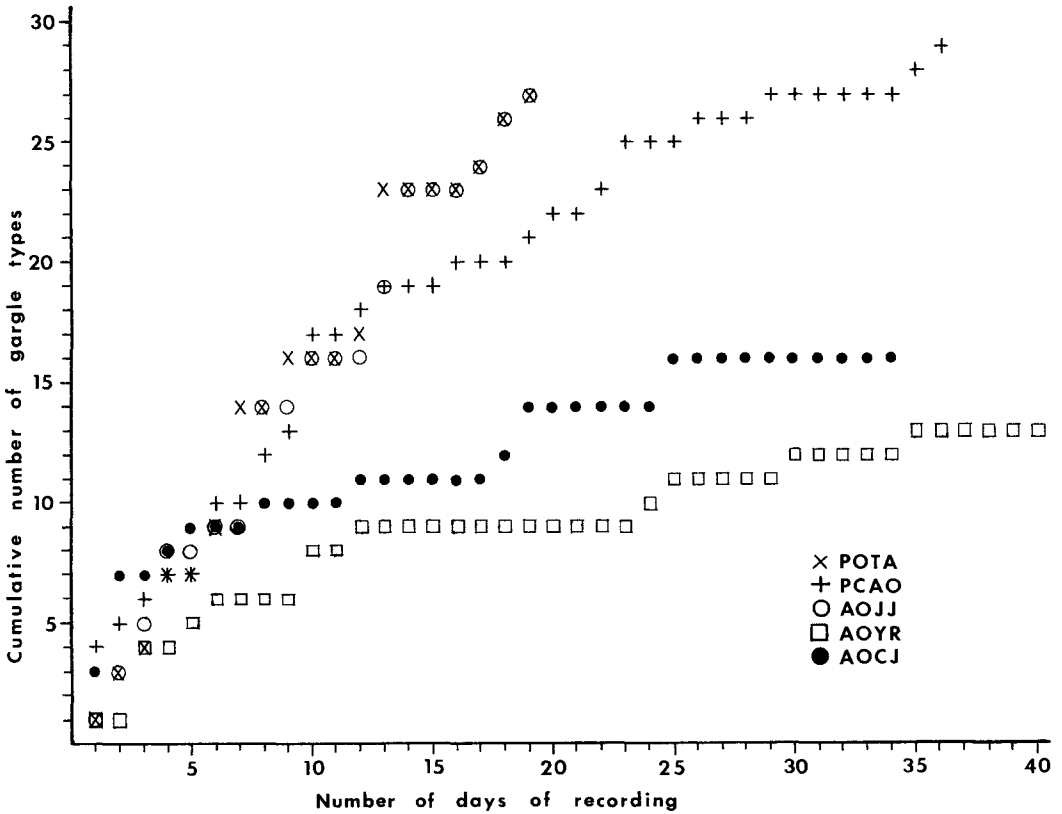


FIGURE 1. Cumulative plot of repertoire size of five individuals. Each recording day involved at least 2 hr of recording.

-0.034,  $P = 0.114$ ,  $n = 1,236$ ), but more dominant birds showed a significantly larger coefficient of variation (SD/mean) of number of syllables in a call than more subordinate birds (Kendall's tau = -0.293,  $P < 0.001$ ,  $n = 64$ ).

REPERTOIRE SIZE

As most *gargle* types are very rare (Ficken and Weise 1984), our sample sizes were not adequate for determining absolute repertoire size of individuals. Figure 1 shows a cumulative plot of repertoire size of five individuals. Over the period of recording, three birds gave almost 30 *gargle* types each. Two others appear to be accumulating calls at a much lower rate, and at the end of the recording period there were 16 *gargle* types in the case of one bird and 13 for another. Thus, considerable individual differences may occur in repertoire size. PCAO, one bird with a large repertoire, was the top bird in the dominance hierarchy for 2 years of the study. However, the four other birds, including two with

large repertoire size, were not among the top dominants in the years studied.

The frequency distribution of *gargle* types in the repertoires of three different birds is indicated in Figure 2. Individuals AOCJ and AOYR each had one or two *gargle* types that were much more common than the others, while BOAG showed much more evenness in the distribution of his *gargle* types. Repertoires of two birds are shown for two different years. AOYR shows a very consistent pattern in the two years; for AOCJ differences occur in the frequency distribution of the most common *gargle* types in the two years. (In AOYR the most frequent *gargle* was not the same in the two years.) There was no change in dominance status of these two birds between years.

The *gargles* of six individuals for which there were the largest samples (often over at least two years) were examined (Table 2). The three most common *gargle* types in the population occurred in the repertoires of all six males but differed

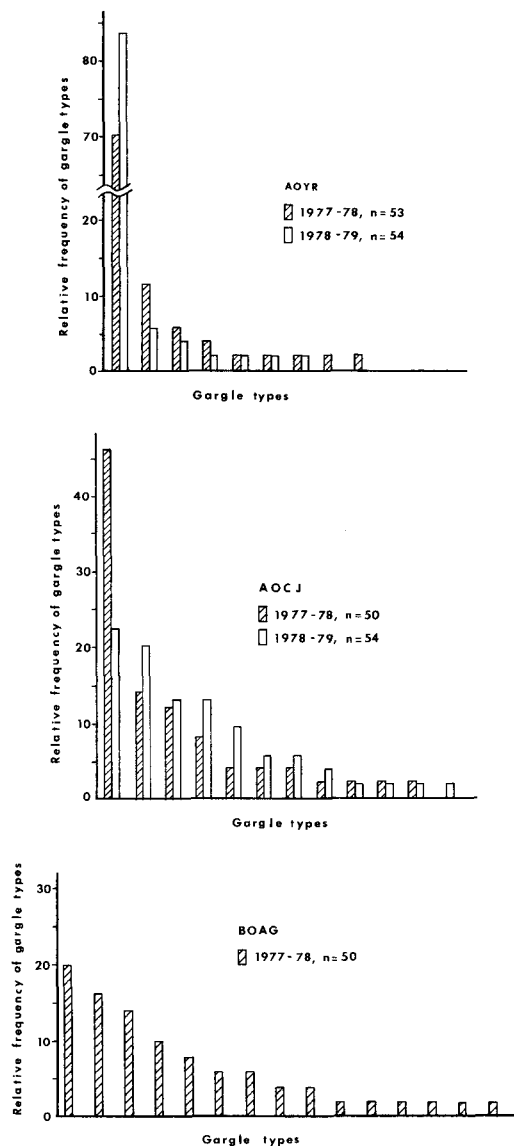


FIGURE 2. Frequency of occurrence of gargle types in the repertoires of three individuals.

markedly in the frequency of use ( $\chi^2 = 187$ ,  $df = 10$ ,  $P < 0.001$ ). Most gargle types are shared with others (59% to 88%, depending on the individual). The percent of total gargles recorded that are of types that are shared with at least one other bird was also high. We conclude that while many gargle types are very rare, most gargle types are shared with at least one other individual in the flock. The most common gargle types are shared with all other flock members.

We tested the hypothesis that dominants have a greater percentage of total gargles that are shared, but no significant correlation occurred ( $\rho_s = -0.60$ ,  $P > 0.05$ ,  $n = 6$ ). Also dominants do not have a larger percentage of gargle types that are shared ( $\rho_s = 0.04$ ,  $P > 0.05$ ,  $n = 6$ ). Although no significant differences occurred, it should be noted that our sample sizes of gargles may have been too small.

Considerable variation occurs in the number of different gargle types given by different individuals. We tested for a relationship between dominance and diversity of repertoire of an individual using the Shannon-Wiener Diversity Index which measures not only the number of different gargle types in the repertoire but also the evenness of their distribution (Table 3). No correlation occurred between dominance and repertoire sizes as measured by the number of different gargle types of an individual or by the diversity index. We conclude that dominant individuals do not have larger or more diverse repertoires than more subordinate individuals. As most gargle types are shared with others, there are no indications that dominants use gargle types that are not also used by more subordinate individuals.

#### TEMPORAL DISTRIBUTION OF GARGLE TYPES

If an advantage of a large repertoire is enhanced sharing of calls, then birds might tend to give similar gargles on the same days, rather than distributing their gargles randomly on a temporal basis. Chickadees do not "match" gargles in the same manner as some birds match songs, whereby one bird gives songs very similar to those given recently by its territorial neighbor (e.g., Payne 1981, Krebs et al. 1981, Schroeder and Wiley 1983).

However, in chickadees sharing of gargle types with rivals occurs and birds might tend to distribute their gargle types so that different individuals give similar ones during short time periods. Due to the large repertoires of individuals, samples sizes were too small to test for possible matching of gargle types on a daily basis. In order to obtain adequate cell frequencies, we lumped gargles that had the same first three syllables (e.g., those starting with the syllables EKV), and they were combined (for all other analyses each unique syllable combination was treated sepa-

TABLE 2. Repertoires of six individuals at D7 feeder.

	Individual					
	AOCJ	AOYR	PCAO	AOJJ	AOPR	POTA
Average dominance rank	4.7	5.3	1	9.5	1	3.5
Frequency of the three most common <i>gargle</i> types						
Type A	18	1	10	3	15	3
Type B	7	91	27	36	21	5
Type C	3	0	14	5	0	18
Frequency of other <i>gargles</i> that are of types shared with at least one other bird	86	26	59	47	8	56
<i>Gargles</i> of nonshared types	13	4	22	18	24	7
% of total <i>gargles</i> that are of types that are shared (total no. of <i>gargles</i> in parentheses)	89.8 (127)	96.7 (122)	83.3 (132)	83.5 (109)	64.7 (68)	92.1 (89)
Total number of <i>gargle</i> types	16	13	29	27	10	27
No. of shared <i>gargle</i> types	14	10	20	16	7	20
% <i>Gargle</i> types that are shared	87.5	76.9	69.0	59.3	70.0	74.1

rately). The distribution of *gargle* types during early, mid- and late winter for one individual for which we had obtained the largest samples was significantly different ( $\chi^2 = 26.2$ ,  $df = 6$ ,  $P < 0.001$ ). Year-to-year differences in the frequency distribution of the beginning three syllables of *gargle* types occurred for one individual ( $\chi^2 = 50$ ,  $df = 6$ ,  $P < 0.001$ ), but not for two others ( $\chi^2 = 7.1$ ,  $df = 4$ ,  $P > 0.05$ ;  $\chi^2 = 4.2$ ,  $df = 2$ ,  $P > 0.05$ ). For all the *gargles* given at a single feeder, significant differences occurred for four periods of the winter (20 November to 1 January, 2 January to 1 February, 2 February to 15 March and 16 March to 30 April) (F9 feeder for 2 years: 1977 to 1978,  $\chi^2 = 13.6$ ,  $df = 6$ ,  $P < 0.001$ ; 1978 to 1979,  $\chi^2 = 47.7$ ,  $df = 9$ ,  $P < 0.001$ ; D7 feeder, for two years: 1979 to 1980,  $\chi^2 = 26$ ,  $df = 9$ ,  $P <$

0.01; 1977 to 1978,  $\chi^2 = 66.3$ ,  $df = 9$ ,  $P < 0.001$ ). Significant differences also occurred in the distribution of major *gargle* types in two different years at the same feeder (for D7 feeder  $\chi^2 = 133$ ,  $df = 16$ ,  $P < 0.001$ ; for F9,  $\chi^2 = 271$ ,  $df = 8$ ,  $P < 0.001$ ).

The results indicate that great variability occurs in the distribution of *gargle* types on a temporal basis. While variability occurs in the pattern of frequency shifts of the first three syllables of *gargle* types, no consistent pattern emerged. Completely different syllable combinations caused statistical significance in one year vs. another. No repeated seasonal shifts occurred, and apparently popular *gargle* types change from time to time and individuals shift their usage to give the most frequent *gargle* types.

TABLE 3. A comparison of dominance rank, individual repertoires, and Shannon-Wiener Diversity Index. (Total no. of *gargles* in parentheses.)

	Dominance rank	No. of different <i>gargle</i> types	S-W index
D7 (1978-1979)	1	14 (40)	3.35
	2	12 (50)	2.37
	3	7 (54)	0.88
	7	8 (22)	2.17
	11	8 (26)	2.47
		$\rho_S = -0.68$ , $P > 0.05$	$\rho_S = -0.30$ , $P > 0.05$
D7 (1979-1980)	1.5	5 (30)	1.64
	1.5	11 (52)	2.88
	3	18 (34)	3.75
	4.5	7 (32)	2.31
	4.5	20 (83)	3.60
	6	22 (42)	4.35
	11	15 (65)	3.28
		$\rho_S = 0.52$ , $P > 0.05$	$\rho_S = 0.46$ , $P > 0.05$

TABLE 4. Coefficients of association for comparison of sharing of *gargles* by individuals at the same feeder (D7). In parentheses is the number of *gargles*.

1977-1978	AOCJ	BOAG	AOYR	PCAO				
AOCJ (70)		0.29	0.43	0.30				
BOAG (52)			0.56	0.36				
AOYR (52)				0.70				
PCAO (17)								
1978-1979	AOCJ	AOYR	PCAO	WYAO	CABO	AOCR		
AOCJ (54)		0.21	0.33	0.22	0.11	0.20		
AOYR (52)			0.62	0.80	0.77	0.78		
PCAO (40)				0.44	0.34	0.32		
WYAO (23)					0.53	0.56		
CABO (31)						0.53		
AOCR (26)								
1979-1980	AOCJ	PCAO	COAW	POTA	AOJJ	JACO	GOWA	YOWA
AOCJ (22)		0.39	0	0.15	0.11	0.28	0.36	0.51
PCAO (58)			0.65	0.55	0.71	0.50	0.35	0.69
COAW (30)				0.54	0.85	0.38	0.32	0.60
POTA (83)					0.82	0.34	0.49	0.65
AOJJ (65)						0.57	0.60	0.66
JACO (34)							0.51	0.55
GOWA (42)								0.69
YOWA (32)								

## ARE THERE FLOCK SPECIFIC DIALECTS?

Microgeographic variation occurs in *gargles*, the syllables and *gargle* types of birds being different from those in other nearby populations as close as 5.7 km (Ficken and Weise 1984). We now examine whether flocks in the same general area (D7 feeder and F9 feeder, 383 m distant) differ in the occurrence of *gargle* types. Because several flocks visit each feeder (but there is little mixing of individuals between F9 and D7), we could only test for differences between feeders and could not test isolated flocks.

Considerable variation occurred in the coefficients of association of *gargles* of different individuals at the same feeder (Table 4). We calculated means and standard deviations for the index at D7 feeder:  $0.44 \pm 0.16$  for 1977 to 1978,  $0.45 \pm 0.23$  for 1978 to 1979,  $0.45 \pm 0.21$  for 1979 to 1980. This means that about half of the *gargles* of an individual are of types shared with another specific individual. Considerable variation occurs from year to year in the frequency of use of *gargle* types of the same individual (Table 5).

We examined the coefficients of association of *gargle* types for birds occurring at two different feeders (Table 6). All the coefficients for one year at the same feeder were compared with those for the same year at the other feeder, using the Mann-Whitney *U*-test. There was significantly greater

sharing among birds at the same feeder as compared with sharing among birds at different feeders in 1977 to 1978 ( $P < 0.05$ ) but not in 1978 to 1979 ( $P > 0.05$ ). Our records show that in 1978 to 1979 there was more interchange of birds between the feeders.

No correlation occurs between a coefficient of association between two individuals and an index of *gargle* sharing for the same two individuals ( $\rho_s = 0.109$ ,  $n = 28$ ,  $P > 0.05$  for 1979 to 1980 at D7;  $\rho_s = -0.65$ ,  $n = 6$ ,  $P > 0.05$  for 1977 to 1978). We interpret these results as indicating that birds that are members of the same fall-winter flock do not share more call types among themselves than they do with the members of other flocks in the same general area.

## DISCUSSION

Why do chickadees *gargle*? Clearly the production of this vocalization is correlated with winning an agonistic encounter. It is hypothesized

TABLE 5. Coefficients of association for similarity of *gargle* types for same individuals in different years.

	1979-1980 vs. 1978-1979	1979-1980 vs. 1977-1978	1977-1978 vs. 1978-1979
PCAO	0.54	0.58	0.39
AOCJ	0.56	0.15	0.15
AOYR	—	—	0.92

TABLE 6. Coefficients of association for comparison of sharing of *gargles* by individuals at two different feeders. In parentheses is the number of *gargles*.

F9 feeder	D7 feeder					
1977-1978	AOCJ (70)	BOAG (52)	AOYR (52)	PCAO (17)		
AJGO (42)	0.10	0.12	0.12	0.12		
TARO (20)	0	0.13	0.04	0.30		
1978-1979	AOCJ (54)	AOYR (52)	PCAO (40)	WYAO (22)	CABO (31)	AOCR (26)
COAY (27)	0.33	0.57	0.36	0.22	0.50	0.48
AOJJ (32)	0.19	0.76	0.44	0.74	0.75	0.69
BOAW (26)	0.40	0.67	0.29	0.46	0.19	0.23
ROBA (23)	0.16	0.63	0.11	0.36	0.39	0.13
CBAO (29)	0.70	0.60	0.52	0.27	0.45	0.45

that *gargling* indicates to the opponent that the calling individual is willing to continue the conflict. If the opponent does not immediately leave after the first *gargle*, the gargler may escalate the conflict. When a bird *gargles*, the recipient likely ascertains that the gargler is a more dominant bird.

The pattern of call-sharing by birds in a restricted area and the presence of dialects might simply be an epiphenomenon of call acquisition. For example, if *gargles* were learned from flockmates, local dialects might be expected because chickadees are quite sedentary following juvenile dispersal (Weise and Meyer 1979). However, the large repertoires might not be expected in the absence of a direct selective advantage for large repertoire size.

Avian song repertoires in individuals vary from one in some species to over 100 in other species (Krebs and Kroodsma 1980). The Black-capped Chickadee in which each individual has at least 13 *gargle* types would be a moderately diverse vocalizer. Of course comparisons among species are difficult because of variation in criteria used to distinguish song types. We used a "fine-grained" approach in differentiating different types (see p. 500). In examining the problem of repertoire size it is important to understand the functional significance of the vocalization (Krebs and Kroodsma 1980 review the problem of repertoire size). In some species large repertoires might be favored by selection because the vocalizations are given in different contexts (i.e., Smith et al. 1978); this is probably not the case in *gargles*. Also, in some species females' selection of males with larger repertoires might lead to larger repertoire size. However, in chickadees *gargles* given in sexual contexts are quite different from

agonistic *gargles* (Ficken et al. 1985). We deal with two remaining hypotheses (see Krebs and Kroodsma 1980 and Slater 1981): (1) that diversity of call types may decrease habituation of the listener, and (2) that diverse vocal repertoires may enhance fitness by increasing the ability to share call types with particularly dominant individuals or those who share nearby territories. The antihabituation hypothesis seems unlikely in accounting for the diversity of repertoires because the *gargle* is given relatively rarely as compared with song. Also, when birds give a short bout of *gargles* invariably they are all of the same *gargle* type, contrary to the prediction of the antihabituation hypothesis.

Sharing of call types might evolve if an individual new to an area gained an advantage in competitive situations by sharing vocalizations with the residents. If the newcomer's calls were different, asymmetric contests might develop because prior residents would signal their status and newcomers would be losers (Craig and Jenkins 1982). Large repertoire size would evolve as a result of counter-selection on residents to reduce the incidence of matching (Craig and Jenkins 1982). Craig and Jenkins (1982) predicted that: (1) sharing per se is advantageous in winning contests for all birds, or that (2) newly arrived birds gain from sharing but more dominant ones actually gain by not being matched and should evolve more complex repertoires including some nonshared vocalizations. Although extensive call-sharing occurs in chickadees, no correlation was found between dominance and the use of the most common *gargle* types (those that might be expected to be most frequently shared if all birds including the dominants benefitted from sharing). Dominants also do not have more



diverse repertoires than more subordinate individuals, nor do they appear to have more different *gargle* types. In chickadees each individual seems to have some *gargle* types which are very uncommon and may only be shared very rarely. However, we have no evidence that dominants show less sharing than subordinates. The temporal distribution of major call types may indicate that birds tend to give *gargles* similar to those of other members of the flock within a restricted time period. The most likely explanation for large repertoires in chickadees is that sharing is advantageous, but the nature of the advantage is not clear. These calls are important in territorial encounters and birds that were together in winter flocks are likely to be territorial neighbors; thus sharing of *gargles* may be advantageous during the breeding season as well as during the nonreproductive season.

Flock specific dialects were noted in breeding groups of the Yellow-rumped Cacique (*Cacicus cela*) by Feekes (1977) who suggested a password hypothesis in which the flock specific calls aid in recognition of group members vs. strangers. Since chickadees live in flocks most of the year, there might be selection for dialects in chickadee calls by which flock members could be recognized. Mammen and Nowicki (1981) found differences in the fine structure of the *dee* note in the *chick-a-dee* call in different flocks. *Gargles* are evidently not flock specific but more sharing may occur among individuals in the same area than in nearby areas.

Chickadees in the same general area, even though they are members of different flocks, share many *gargles*; birds using primarily different feeders share fewer *gargles* and members of different demes share even fewer *gargles* (Ficken and Weise 1984). For *gargles* of chickadees, we favor the social adaptation hypothesis of Payne (1981) for call-sharing as an explanation for both large repertoire sizes and for dialects. Payne (1981) suggests that local differences in vocalizations may arise when birds that share the vocalizations of an established territorial male may be more successful than others. As Craig and Jenkins (1982) pointed out, dialects can simply be an outcome of selection for sharing; birds in a local area will show a high degree of sharing, with differences occurring among populations. The chickadee system of a number of discrete syllables that are recombined in many ways seems adapted for generating a great diversity of call types (Ficken and Weise 1984).

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