DIALECTS IN A CALL ASSOCIATED WITH PAIR INTERACTIONS IN THE BLACK-CAPPED CHICKADEE

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ABSTRACT.—Calls of Black-capped Chickadees (*Parus atricapillus*) occurring during intrapair interactions were studied at three sites in southeastern Wisconsin. These vocalizations were given by both sexes in early phases of courtship and by males during copulation, and they also occurred later in the breeding season. The ending of this call exhibited a dialect pattern, being very different at two sites 22 km apart. Playback experiments showed that males responded more strongly to their own dialect than to the foreign one. Hand-raised birds that heard no chickadees other than their siblings after about 14 days of age produced aberrant calls, suggesting that learning is involved in the acquisition of these vocalizations. This is the first report of microgeographic variation in an avian vocalization associated only with intrapair associations and not involved with male-male interactions, as is the case with song. *Received 19 December 1983, accepted 24 August 1984.*

SONG dialects occur in many species, and much attention has focused on their evolution (reviewed by Mundinger 1982). Dialects occur in the calls of a few species, but most are macrogeographic, not microgeographic like the song dialects of many species (Mundinger 1982). However, we have observed microgeographic variation in the Gargle, a call of the Black-capped Chickadee (*Parus atricapillus*). Gargles are given most often by males and usually are associated with agonistic behavior such as aggressive encounters during the nonbreeding season and territorial interactions (Ficken 1981, Ficken and Weise 1984).

Gargles also occur in intrapair interactions throughout the reproductive season, and in this context are preceded by a very high-pitched vocalization. Dixon et al. (1970) presented sonagrams and described this call as the solicitation call, noting that it often was followed by "Sleh-poor" (corresponding to what we have termed the Gargle). We follow Smith's (1972) designation in the closely related Carolina Chickadee (*P. carolinensis*) of the initial high-pitched component as "Variable Sees" rather than using the functional designation of "solicitation calls" because Variable Sees occur in contexts other than copulation (Ficken et al. 1978).

Here we describe the characteristics, usages, and geographic distribution of these calls in our study area in Wisconsin and the results of experiments involving playback of calls from two different populations. Finally, we discuss some evolutionary implications of the microgeographic pattern of these calls.

METHODS

The descriptive study.—We recorded vocalizations at three sites in southeastern Wisconsin (Ozaukee Co.): (1) Grafton, near a winter feeder in a suburban area, including a wooded tract along the Milwaukee River, from November through March 1977–1981; (2) Harrington Beach State Park, a wooded area along the shore of Lake Michigan, during May 1982; and (3) The University of Wisconsin–Milwaukee Field Station, Saukville, a site described in Weise and Meyer (1979), throughout the year from 1970 to 1980. Harrington Beach is 22.1 km northeast of the Field Station, while Grafton is 9.8 km southeast of the Field Station. The chickadees at the Field Station were aged, sexed, and individually color banded by C. M. Weise. Birds at other sites were not banded.

We made most of the recordings with a Nagra III tape recorder at 19 cm/s, with a Sennheiser MKH 104 omnidirectional microphone, but we occasionally used a Uher 4000 L tape recorder and a Soundspot 644 microphone. The calls associated with pair activity were infrequent and difficult to record unless we were very close to the birds (<10 m), as they are of low amplitude. Calls were analyzed with a Kay 6061 B Sona-Graph at an intermediate bandwidth setting (150 Hz). The syllables in Gargles are discrete, and we assigned a letter or letter-number designation to each type (Ficken and Weise 1984).

Playback experiments.—We selected 2 study sites, the

Field Station and Harrington Beach, and located territories of 12 males at each. We conducted the experiments on 3 days between 2 May and 10 May 1983. These dates were selected because the calls occur most frequently during this restricted period due to their association with copulation. Variable Sees terminating in Gargles recorded in spring from males at their own site and the other site were played back to each chickadee. Six birds at each site were played resident and then foreign calls, and 6 others received the opposite order. The calls, equalized for volume, were played back on a Nagra III tape recorder using a Nagra DH speaker. The experimental procedure was as follows: 2 min of silence during which location and vocalizations of chickadees were noted, 2-min presentation of the first stimulus call (10 times at 10-s intervals), 5 min of silence (the last 2 min were the baseline for the next playback so that the baseline and playback periods were of equal length), and playback of the second stimulus call in the same manner as the first.

We used two independent assessments of responsiveness: the increase in number of songs (the whistled "Fee-Bee"; Ficken et al. 1978) during playback (number of songs during the baseline was subtracted from that during playback; only 3 of 24 birds sang during the baseline) and latency of approach to within 20 m of the speaker. The latter was measured by the number of playbacks until approach; all birds that approached remained for the duration of that playback. In the analysis we scored approaches: (1) = approached on playback calls 2–4, (2) = calls 5–7, (3) = calls 8–10, and (4) = never approached.

Hand-reared birds.—We hand-raised 4 broods taken from the nest at 14–15 days of age, 1–2 days prior to fledging. Each brood was raised and left together but was visually and acoustically isolated from the other broods. Members of each brood were housed indoors in individual cages in visual and auditory contact and under natural photoperiod. They were never exposed to the intrapair calls of free-living chickadees, although they were exposed to the vocalizations of some other species.

Two of the broods were obtained from nests at the Field Station, 1 brood from Grafton, and 1 brood from Glendale, Milwaukee Co., 30 km southeast of the Field Station. We recorded Variable Sees from 1 adult bird in Field Station brood I, 2 in Field Station brood II, 2 in the Grafton brood, and 1 in the Glendale brood.

RESULTS

We first give an overview of courtship in chickadees and then discuss the role of the particular vocalizations. Dixon et al. (1970) and Ficken et al. (1978) have described courtship of Black-capped Chickadees.

Behavior of the pair.—Chickadees probably form pairs by midwinter while associated in winter flocks (Ficken et al. 1981); the pair-formation process is unknown but probably takes place gradually. One posture that we noted only in the fall and early winter and never observed in agonistic contexts may be involved in pair formation. The body feathers were very fluffed, the wings were trailed, and Variable Sees were given. The sex of the free-living birds was unknown. The captive birds that performed this behavior were males. During December and January we saw no indications of sexual activity, but beginning in February Variable Sees were sometimes given, although no copulations were observed until May.

Copulations usually are limited to a short period just preceding and during egg-laying (early to mid-May in our study areas in Wisconsin), unless the first nesting fails. Our observations are in general accord with those of Dixon et al. (1970). We observed the complete copulatory sequence 8 times. The sequence showed some variation, and either sex initiated sexual activity by uttering Variable Sees, often while quivering the wings. The male then continued Variable Sees, ending in a Gargle just as he mounted the female. All copulations were preceded by these calls.

Chickadees continued to utter Variable Sees throughout the breeding cycle. Both sexes gave Variable Sees accompanied by wing quivering near or at the nest-hole entrance during the incubation and nestling periods. Usually both members of the pair were in close proximity (<4 m), although occasionally a seemingly lone bird gave them. The calls also were uttered by the parents while foraging after the young had fledged and were in family groups. Thus, this vocalization complex occurs in diverse circumstances but always in the context of pair association; the same is true of the Carolina Chickadee (Smith 1972). We do not know the sexes of the birds giving Variable Sees during the winter, but in the spring both sexes gave them, as in the Carolina Chickadee (Dixon et al. 1970, Smith 1972).

Call structure.—The intrapair vocalizations of the chickadee are complex, involving high-pitched Variable Sees that may terminate in only 2 stereotyped Gargle syllables or may then continue and end with a complete Gargle.

Variable Sees from the Field Station population were described in Ficken et al. (1978). They are high-pitched notes with a narrow fre-
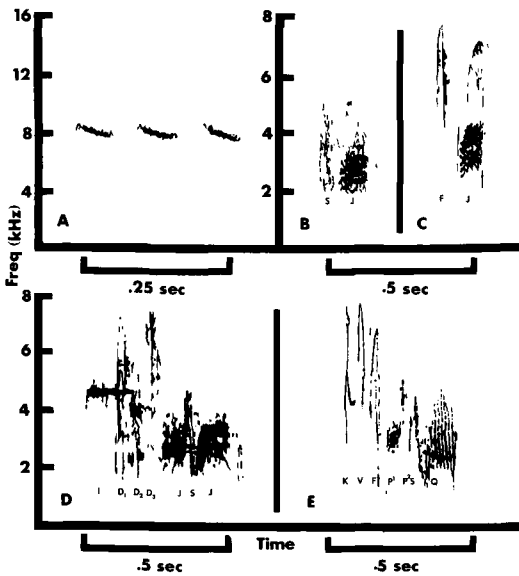
Fig. 1. (A) Variable Sees. Two Gargle syllables following Variable Sees at (B) the Field Station and (C) Grafton. Gargles following Variable Sees at (D) Harrington Beach and (E) the Field Station.

quency range (Fig. 1A). The notes often are given in a long series, and the number of repetitions is highly variable. The calls often (but not always) include 2 syllables found in Gargles. In 34 vocalizations from the Field Station recorded during courtship, all 9 individuals included the 2 syllables S and J (Fig. 1B). SJ is a common ending of agonistic Gargles in this population, although many other syllable combinations may terminate agonistic Gargles (Ficken and Weise 1984). However, these syllables sometimes were omitted during copulation (of 11 calls from 3 individuals, 4 lacked these 2 Gargle syllables). Thus, if the 2 Gargle syllables do occur in the call from the Field Station, they are invariably an S syllable followed by a J.

At Grafton all recordings were made during the nonreproductive season. Seven recordings from 3 different males ended, as did Field Station Variable Sees, with 2 Gargle syllables; however, in this case the syllables were FJ. The F syllable is much higher-pitched than the S of Field Station birds (Fig. 1C). At Harrington Beach we recorded 11 Variable Sees, all associated with copulation from 3 individuals. None included the 2 Gargle syllables, although they all terminated in complete Gargles.

In summary, birds from 2 areas (Field Station and Grafton) differed in the 2 Gargle syllables of the call. Birds from the third site (Harrington Beach) lacked these syllables, but they were recorded only in May when such syllables did not invariably occur at the other sites sampled.

Complete Gargles terminated the Variable See sequence in all copulations, and this call also often terminated Variable Sees given at other times. We describe these Gargles in 2 populations, Field Station (Fig. 1E) and Harrington Beach (Fig. 1D). At Harrington Beach the precopulatory Gargles of 3 males were identical in their syllabic composition (5 from one male, 1 from another, and 3 from the third). The calls consisted of 7 syllables, which we arbitrarily coded I, D1, D2, D3, J, S, and J. I, S, and J also occur at the Field Station in agonistic Gargles, but the other syllables were never found in a sample of 3,738 agonistic Gargles from the Field Station, and the ending JSJ never occurred at the Field Station (Ficken and Weise 1984). We also recorded 18 Gargles in agonistic encounters at territorial boundaries involving these 3 males from Harrington Beach. Because of the great variation in agonistic Gargles even from a single male, this sample size is very small, but it may be significant that none of the agonistic Gargles was similar to the precopulatory Gargles.

The syllabic composition of sexual Gargles from the Field Station is presented in Table 1. We recorded precopulatory Gargles from 3 males, and although some variation occurred in syllabic composition, all included the combinations KVF and P_1P_2S. The 3 individuals recorded in the nonbreeding season had very similar Gargles; all but 1 (from a female) began with KVF and all included P_1P_2S. No agonistic Gargles from the Field Station began with KVF, although the endings of these Gargles were very similar to the sexual ones. The individual syllables (K, V, F) also occurred in agonistic Gargles but never in that particular combination (KVF). Thus, there seem to be some differences in syllable composition between agonistic and sexual Gargles in the same population.

Gargles used in intrapair interactions at the Field Station are much more stereotyped than the agonistic ones, and some syllable combinations are specific to the intrapair context. Each male has at least 13 particular syllable combinations (Gargle types) in its repertoire of agonistic Gargles, and many different syllable

TABLE 1. Syllabic composition of sexual Gargles of birds at the UWM Field Station. All are preceded by Variable Sees ending in SJ. Numbers in parentheses are numbers of calls recorded. Calls given in May were precopulatory; others were not.

Bird	February–March
1♂	KVFP$_1$P$_2$SJ (8)
2♂	KVFP$_1$P$_2$SQ (3)
	KVFP$_1$P$_2$S (2)
	KVFP$_1$P$_2$SJ (4)
3♀	VP$_1$P$_2$SJ (1)
	May
4♂	FP$_1$P$_2$SJKVFS (3)
5♂	KVFP$_1$P$_2$SJKVFS (2)
6♂	KVFP$_1$P$_2$SJ (2)

TABLE 2. Results of playback experiments of sexual calls at two sites.

Study site	Playback of resident calls		Playback of foreign calls	
	Number of songs[a]	Approach latency[b]	Number of songs[a]	Approach latency[b]
Field Station				
Bird A	13	8	0	—
B	9	4	2	—
C	19	—[c]	15	—
D	7	7	0	—
E	21	8	5	—
F	17	—	0	—
G	15	—	0	—
H	12	—	0	—
I	9	2	12	9
J	11	7	0	—
K	8	9	0	—
L	7	10	0	—
Harrington Beach				
M	21	4	0	—
N	19	6	0	—
O	17	2	0	—
P	13	5	13	7
Q	15	7	0	—
R	5	—	0	—
S	13	—	3	10
T	14	3	0	—
U	14	2	0	—
V	17	10	0	—
W	10	8	0	—
X	5	—	0	—

[a] Increase in songs over baseline.
[b] Number of playbacks before approach to <20 m.
[c] No approach.

combinations may compose the beginning (Ficken and Weise 1984). In contrast, sexual Gargles usually started with KVF. As is the case with agonistic Gargles, microgeographic variation occurs in the syllabic composition.

Playback experiments.—The results of the playback experiments are compiled in Table 2. As no significant differences occurred in order of presentation in either song responses or approach latency (Mann-Whitney U-test, two-tailed, $P > 0.2$ for Harrington Beach, $0.2 > P > 0.1$ at Field Station), we combined the two samples that differed in order for each site. The number of songs was significantly greater during playback of the resident dialect than during the foreign one at both the Field Station (Wilcoxon matched-pairs signed-ranks test, one-tailed, $n = 12$, $T = 1$, $P < 0.005$) and Harrington Beach ($n = 11$, $T = 0$, $P < 0.005$). The approach responses also were significantly greater to resident calls at both sites (Harrington Beach $n = 9$, $T = 2$, $P < 0.005$; Field Station $n = 8$, $T = 0$, $P < 0.005$). The approaches were by males, accompanied by the female in a few cases. All males that approached first increased their singing rates.

Hand-reared birds.—Variable Sees and Gargles were first heard in each of the 4 broods of hand-raised birds at 56–59 days of age. Since dispersal occurs about 20 days after fledging, i.e. at about 36 days of age (Weise and Meyer 1979), the first Variable Sees were given after the birds normally would have dispersed. Adult captive birds gave these calls as they wing-quivered and faced each other, and these birds also were similar to free-living chickadees in uttering the calls during the reproductive season (March to

late summer), as well as occasionally in the fall. After an especially intense period of many Variable Sees by one hand-reared male and female, the female laid six infertile eggs.

The Variable Sees were aberrant in the adult hand-raised birds. The calls were more variable in pitch than those of free-living birds (Fig. 2A), and the syllables in Gargles terminating the Variable Sees were less definite and not as temporally discrete (Fig. 2B–E) as those of free-living chickadees. Most of the syllables were very different from those in Gargles of free-living birds from the populations from which the captives were obtained. However, the general form of some of the trilled syllables was similar to that of syllables that often terminate the Gargles of free-living chickadees. The Gargles associated with Variable Sees of the 4 captive broods were very different, including the
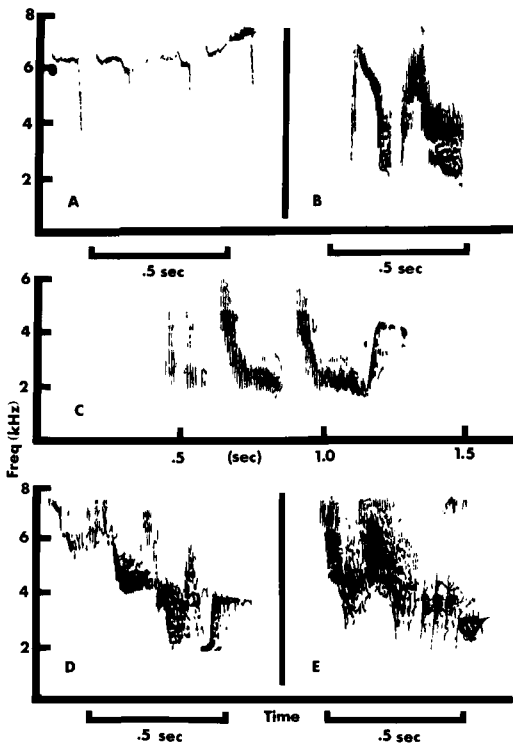
Fig. 2. (A) Variable Sees of hand-reared birds as adults. Gargles terminating Variable Sees of hand-reared broods from (B) Glendale, (C) Field Station I, (D) Field Station II, and (E) Grafton.

2 broods from the Field Station, which were reared separately. However, the Gargles of each individual were very stereotyped in general syllable form, and little variation occurred among members of the same brood that were reared together. Learning is indicated in the development of these Gargles, as the calls of hand-reared birds were convergent with the calls of brood members and were not similar to those of the populations from which they were obtained.

DISCUSSION

Black-capped Chickadees have dialect patterns in several calls. For example, Mammen and Nowicki (1981) showed that flocks in the same area differed in one aspect of the Chick-a-dee call, and Nowicki (1983) demonstrated flock-specific recognition of these calls. Microgeographic variation occurs in Gargles used in agonistic situations (Ficken and Weise 1984) as well as those described here, which function in intrapair situations. Whereas the calls of many passerines are believed to be innate (Marler 1963), chickadees may show more microgeographic variation in calls than most passerines due to their greater reliance on learning in the development of calls.

Considerable discussion has been generated concerning the evolutionary significance of song dialects. Andrew (1962) suggested that dialects are an epiphenomenon of song learning, a view expressed more recently by Wiens (1982) and Mundinger (1982). On the other hand, Nottebohm (1969) proposed that dialects in the Rufous-collared Sparrow (*Zonotrichia capensis*) function in assortative mating among individuals in the same deme, affecting the genetic structure of the population. This view has been supported by the studies of Baker and his co-workers (Baker 1974, 1975, 1982; Baker and Mewaldt 1978; Baker et al. 1981a; Tomback and Baker 1984) in White-crowned Sparrows (*Zonotrichia leucophrys*). Mundinger (1982) pointed out that dialects are the products of cultural evolution (song learning) and consequently cannot have adaptive functions. However, whatever their evolutionary origins, dialects still may have important consequences for the genetic structure of local populations (Mundinger 1982). In the chickadee the Variable See system is probably crucial for sexual activity. Population differences in the structure of the calls may mean that birds are more likely to respond sexually to members of their own dialect group.

For assortative mating it would be crucial for birds to respond selectively to the vocalizations of their dialect group. Results of playback responses are sometimes difficult to interpret (Tomback et al. 1983). For example, Baker (1982) noted that birds in one population of White-crowned Sparrows responded more strongly to playback of dialects from an adjacent area rather than to their own, although responses to a distant alien dialect were very weak. However, another population responded most strongly to its own songs (Tomback et al. 1983). There is evidence that females respond most strongly to songs from their own dialect area (Baker et al. 1981a), but Petrinovich and Patterson (1981) reported that females injected with testosterone sang dialects different from their mates.

It has usually been assumed that if a male responds to playback of song on his territory,

he is being aggressive toward a territorial intruder or, as Wasserman (1977) suggests, to a possible competitor for his mate. The results of our playback experiments clearly show males respond more to their own dialect of sexual calls than to an alien one, indicating that they can discriminate between the two, presumably based on the terminal Gargle, as the Variable Sees from the two populations are very similar. The male may respond in anticipation of attacking a rival for the female because this call occurs in sexual contexts. Males should react very strongly in such a situation to reduce the chances of cuckoldry. However, as females also may give these calls, males might be approaching to seek a sexually active female. In our field tests the female sometimes accompanied her mate if he approached the speaker, and if he did not approach she did not respond (except in one case). The playback experiments are significant because females also give these calls and we measured male responses.

Payne (1981, 1983) and Baker et al. (1981b) stressed that dialects in song may arise through strong sexual selection involving male-male competition. Evidently this is not the case in the intrapair calls of chickadees, because these calls are never used among males. Females may exert selection on the characteristics of the vocalization, but as females sometimes give them as well, male choice of the female call may also operate.

Dixon et al. (1970) first described the sexual calls of Black-capped Chickadees and noted that although the calls occurred infrequently and during a restricted part of the year, they were critical to reproductive success. They suggested that natural selection would favor only a little variation in the form of the signal. We found remarkable stereotypy in the sexual Gargles for each population, although the agonistic Gargles in a population are highly variable (Ficken and Weise 1984). It also may be important that the agonistic and sexual Gargles are so different. Although both share the same syllables (within the same population), sexual Gargles have unique syllable combinations that may reduce the possibility of confusion concerning the message of the calls. Following agonistic Gargles, the recipient usually moves away; if it does not, it is attacked by the individual giving the call. During sexual Gargles the two birds remain in close proximity.

In chickadees there seems to be a two-step process in courtship involving these calls with dialect properties. First, during initial pair bonding the Variable Sees ending in two Gargle syllables may show some populational differences, and birds might only respond to others from their dialect area, as evidenced by Grafton and the Field Station birds having slight call variants. Second, copulation always is preceded by a complete Gargle with population-specific characteristics, and we speculate that it would be very unlikely for sexual behavior to proceed among birds of such different dialect groups as Harrington Beach and the Field Station. Assortative mating might be an indirect outcome of the dialect patterns.

Sexual calls very similar to those of the Black-capped Chickadee also are found in the Mountain Chickadee (*P. gambeli,* Dixon et al. 1970). Calls of this type in the Mountain Chickadee are longer and of higher frequency than in the Black-capped Chickadee (Dixon et al. 1970); they also end with an "aggressive call" associated with copulation (which probably corresponds with the Gargle) in the former species. Descriptions of the sexual calls of several other parids indicate that similar calls ending in Gargles may be widespread in the genus [e.g. Carolina Chickadee, Brewer 1961, Smith 1972; Marsh Tit (*P. palustris*), Morley 1949; Boreal Chickadee (*P. hudsonicus*), McLaren 1975].

Dialects occur in the calls of chickadees associated with pair interactions, and the phenomenon may be more widespread. The sexual or "soliciting calls" of other avian species have been largely ignored as attention concerning dialects focuses on song. We doubt that the dialect pattern in the sexual calls of chickadees is unique among birds, and such calls of other species merit further study. Species in which sexual calls are given only during courtship, and not also after young are present, may demonstrate less learning of these calls than is the case with Black-capped Chickadees, simply because of the lack of opportunity for learning.

Research to KMA. Contribution No. 63 of the University of Wisconsin-Milwaukee Field Station.

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