SONG DEVELOPMENT BY BLACK-CAPPED CHICKADEES (*PARUS ATRICAPILLUS*) AND CAROLINA CHICKADEES (*P. CAROLINENSIS*)

DONALD E. KROODSMA, DANIEL J. ALBANO, PETER W. HOULIHAN,
AND JUDITH A. WELLS
*Department of Biology, University of Massachusetts,
Amherst, Massachusetts 01003, USA*

ABSTRACT.—Do songs of songbirds, which learn to sing, provide reliable clues to genetic identity in zones of secondary contact? How do some songbird species maintain such highly stereotyped songs throughout extensive geographic ranges? These two questions were addressed with a study of song development by Carolina and Black-capped chickadees (*Parus carolinensis* and *P. atricapillus*). In one hand-reared, mixed group in the laboratory, male Carolina Chickadees produced better imitations of a tape-tutored Black-capped Chickadee *fee-bee* song than did two male Black-capped Chickadees. In another mixed group, a male Black-capped Chickadee produced a better imitation of tape-tutored Carolina Chickadee song elements than did the Carolina Chickadee males themselves. Black-capped Chickadees in an additional experiment were tutored with normal *fee-bee* songs and with *fee-fee, bee-bee,* and *bee-fee* songs; these males also produced highly abnormal songs, although songs of males within groups converged on one another, reinforcing ideas that social interactions are crucial for the song learning process. These data thus reveal that song in secondary contact zones of these chickadees is probably not a good indication of genotype. The feat of Black-capped Chickadee song stereotypy in nature, together with other features of their singing behavior (e.g. social and hormonal determinants of singing, subsong by both sexes but loud songs only from males), remain both puzzling and fascinating. *Received 21 January 1992, accepted 14 November 1992.*

SONGS OF closely related bird species, especially in allopatry, are usually unmistakable to human listeners. Thus, throughout most of its geographic range, the Black-capped Chickadee (*Parus atricapillus*) utters a remarkably stereotyped *fee-bee* song (actually *fee-bee-ee*; see below), a two-noted whistle, with the first whistle slightly higher in frequency than the second (review in Hailman 1989). Likewise, the song of the congeneric Carolina Chickadee (*P. carolinensis*) is immediately recognizable. It typically consists of an even number of whistles, often four, with each odd-numbered whistle higher in frequency than the immediately following even-numbered whistle (Ward and Ward 1974). Songs of each male and songs from location to location seem more variable than do the songs of the Black-capped Chickadee, yet nowhere in allopatry would one confuse songs of the two species.

Such stereotypy often deteriorates, however, in contact zones with a closely related congener (e.g. Helb et al. 1985). Among species that do not imitate their vocalizations from other individuals (e.g. suboscine flycatchers; Kroodsma

and Konishi 1991), vocal displays can provide good evidence of genetic identity (Johnson and Marten 1988). Because the songs of chickadees and other songbirds are cultural imitations (e.g. Slater 1989), however, the existence of intermediate or hybrid songs does not indicate that birds are genetic hybrids. For some songbirds, plumage differences between sister taxa provide visible genetic evidence of hybridization. Among the buntings (*Passerina* spp.), grosbeaks (*Pheucticus* spp.), and orioles (*Icterus* spp.) of the Great Plains, for example, birds of both parental and hybrid plumage may sing either intermediate songs or pure songs of either species, so that the learned song by itself is not a reliable cue to the presence or extent of hybridization (Kroodsma 1974, Emlen et al. 1975, Rising 1983, respectively). Sibling species such as the Black-capped and Carolina chickadees present a greater conundrum, because plumage markers provide no reliable indices of hybridization (Robbins et al. 1986). Although the whistled songs are the most distinguishing feature for these two species, the usefulness of songs in assessing genetic backgrounds of individuals depends on

TABLE 1. Treatment groups for individual Black-capped and Carolina chickadees. Group 1 tutored with Black-capped Chickadee song and group 2 with Carolina Chickadee song. Groups 3 and 4, which were subsets of groups 1 and 2, were formed to study song changes in a second year of singing. Groups 5, 6, and 7 consisted of pure groups of additional Black-capped Chickadees tutored with normal *fee-bee*, as well as *fee-fee*, *bee-fee*, and *bee-bee*.

	Black-capped Chickadee		Carolina Chickadee	
Group	Male	Female	Male	Female
1a	G, I		A, B, C, F, H, J	D, E, K
1b			L, M, N	
1c			1 male[a]	2 females
2	X	O, Q, S, V, Z	R, T, W, Y	P, U
3	G		B, H, R	
4	X		Q, S, V, Z	
5	3 males	1 female		
6	2 males	2 females		
7	1 male	3 females		

[a] Individuals in some groups not identified by letter because they are not discussed individually in the text.

the relative abilities of individuals to learn the vocalizations of each parental form.

To test the song learning capabilities of these two chickadee species, we collected nestlings of each species and raised them in mixed groups (see Table 1). One group was tutored with a Black-capped Chickadee song, and the other group was tutored with a Carolina Chickadee song. Puzzled by our results and by the results of Shackleton and Ratcliffe (1993), we raised an additional three groups of Black-capped Chickadees, and tested their ability to learn normal, conspecific songs in the laboratory. Our results indicate that both Black-capped and Carolina chickadees are fully capable of singing a far greater variety of whistled songs, including the songs of the other species, than one would have imagined by listening to these birds in allopatric populations. Behavioral hybridization clearly can occur without genetic hybridization, and how the Black-capped Chickadee maintains such a highly stereotyped song in nature remains somewhat of a mystery.

METHODS

Mixed-species experiment.—The nestling Carolina Chickadees were 10 to 14 days old when they were collected from four nests on lands adjacent to the Tyler Arboretum, Delaware Co., Pennsylvania, on 11 June 1989. The birds thus were well developed and were provided ample opportunity to hear local Carolina Chickadee songs. In this portion of Pennsylvania, Black-capped Chickadees migrate and overwinter, and an occasional singing male Black-capped Chickadee establishes a territory here in the early spring and typically leaves by mid-May and fails to

breed (W. J. Smith pers. comm.). The collecting locations for Carolina Chickadees were about 41 km south of the contact zone with Black-capped Chickadees (F. B. Gill pers. comm.). Nestlings were flown to Amherst, Massachusetts.

The Black-capped Chickadees came from three nests: two from Amherst, and one from the Berkshire Mountains of western Massachusetts. Both sites were several hundred kilometers northeast of the contact zone with the Carolina Chickadee. The Black-capped Chickadees were collected between 5 and 21 June 1989, when the young were 8 to 14 days old. These young, too, had heard local conspecific chickadee songs during their nestling days.

In the laboratory the chickadees were hand-reared on the standard diet recommended by Lanyon (1979). They were maintained on long days (15L:9D) until early September, and then days were gradually reduced to 11L:13D. During early January, day lengths again were increased, so that by March the birds were on long days (15L:9D). Some birds (see below) experienced an additional cycle of short and long days so that we could obtain songs from a second singing season.

The caging and grouping of the birds reflected our desire to simulate sympatric conditions by raising these chickadees in mixed groups. Two main groups were established, with individuals of the two species divided among the groups. Group 1, which was to be tutored with the *fee-bee* song of the Black-capped Chickadee, initially consisted of 15 Carolina Chickadees and 4 Black-capped Chickadees, all within auditory and visual contact, in a single room. At first we paired some individuals within cages, but soon discovered that the Carolina Chickadees were highly aggressive and killed the Black-capped Chickadees. After the loss of two Black-capped Chickadees, we reduced this main group to nine Carolina Chickadees and two Black-capped Chickadees (group 1a); five Carolina Chickadees (birds A–E) were in adjacent cag-

es on one shelf, and facing them about 1.5 m across the room were alternating cages of Carolina Chickadees (F; H; J and K together) and Black-capped chickadees (G, I). Two subgroups of three Carolina Chickadees apiece were placed in two other rooms. One group (1b) consisted of three males (L–N), with cages arranged linearly on a shelf. We illustrate no songs from the other group (group 1c, 2 female and 1 male Carolina Chickadee) because we recorded no whistled songs from them.

Group 2, which was to be tutored with Carolina Chickadee songs, consisted of six Carolina Chickadees (P, R, T, U, W, Y) and six Black-capped Chickadees (O, Q, S, V, X, Z). Two rows of six cages (Birds O–T and U–Z), with rows about 2 m apart and no adjacent cages containing individuals of the same species, were placed in a single room. All individuals in this room were within visual and auditory contact, though visual contact through several wire cages to a distant bird in the same row would have been difficult.

These groups of chickadees were housed in rooms that also contained caged birds of other species. As part of another experiment, Chestnut-sided Warblers (*Dendroica pensylvanica*) were housed on other shelves in the rooms containing the chickadees. All birds heard Chestnut-sided Warbler songs broadcast over loudspeakers during their hatching year, and most also heard singing warblers the next spring, during their first singing season. In a sense, the experiment described here is a test not only of whether the chickadees learn heterospecific chickadee songs or learn from other chickadees in a group, but the experiment also evaluates the ability of the chickadees to distinguish congeneric songs from songs of an unrelated species.

Two tutor tapes were prepared. For group 1a–c, we used an unedited sequence of eight Black-capped Chickadee songs recorded from a single individual in Amherst, Massachusetts. To record these songs, we used a Nagra IV-S and a Sennheiser 106 microphone in a 60-cm parabolic reflector. All eight songs in this sequence were highly similar (see Figs. 1–3). As analyzed on a Kay Elemetrics DSP5500 (see below), the range of frequencies for the eight *fee*'s was 3.84 to 3.93 kHz (CV = 0.7%) and for the eight *bee*'s was 3.34 to 3.38 kHz (CV = 0.4%); the range of durations for the two elements was 0.35 to 0.38 s (CV = 2.9%), and 0.41 to 0.42 s (CV = 1.2%). This 30-s, eight-song sequence was repeated 44 times on a tutor tape. The second tutor tape was constructed from an unedited sequence of nine Carolina Chickadee songs recorded from an individual in Ohio (Cornell LNS cut no. 1; illustrated in Fig. 4). Ranges of frequencies and durations for the four whistled notes were: note 1 (3.97–4.10 kHz, CV = 1.2%; 0.25–0.26 s, CV = 2.3%), note 2 (3.62–3.70 kHz, CV = 0.7%; 0.21–0.25 s, CV = 6.3%), note 3 (6.40–6.55 kHz, CV = 0.9%; 0.24–0.25 s, CV = 2.5%), and note 4 (3.27–3.36 kHz, CV = 1.0%; 0.21–0.25 s, CV = 7.1%). Although the first note of these

songs is lower in frequency than the first note of most Carolina Chickadee songs, it is within the range of natural variation (Ward 1966) and is common in Ohio (S. L. Gaunt pers. comm.). This 30-s nine-song sequence also was repeated 44 times on a tutor tape. The tutor tapes were played once daily over loudspeakers to the respective groups on a total of about 45 days during June and July 1989.

Birds initially were recorded during March–June 1990. We used a Tandberg reel-to-reel tape recorder (mono series 15 or stereo 3300 or 10×) or a Nagra (IV-S) together with Realistic condenser microphones. Using an electronic stepper, we usually recorded, in turn, 1-min samples from selected pairs of birds in a given group during the first 90 min of light in the morning. Thus, in a group of 10 birds, each pair of birds would be recorded for 1 min out of every 5. On other occasions, we recorded selected birds continuously for as many as 90 min.

After the first singing season, we formed two subgroups of birds so that we could test for the ability of these chickadees to modify songs during a second singing season. The first group consisted of four males: Carolina Chickadees B and H from group 1a, and R from group 2, and Black-capped Chickadee G from group 1a. The five surviving Black-capped Chickadees (females Q, S, V, Z and male X) from group 2 formed a second subgroup. Because relatively little singing had occurred after two months of long days during this second season, on 29 November 1990 we implanted silastic tubes with estradiol into two female Black-capped Chickadees (S and Z) and silastic tubes with testosterone into the other seven birds.

Recorded songs were examined on Kay Elemetrics DSP5500 continuous spectrum analyzer. Tapes were scanned, and each whistled song was studied for its frequency and temporal characteristics. Temporal and frequency parameters for 10 or more renditions of most types were measured using a 256- and 1,024-point transform size (corresponding to 117 and 29 Hz analog filters), respectively. Frequency was measured from a power spectrum display, so that reported frequencies are the frequencies at which the greatest energy was concentrated.

Most whistled songs from the males could be classified readily into regularly repeated song types, and coefficients of variation for those song types were low (see below). Sometimes, however, the males regressed to more variable whistles (see also Margoliash et al. 1991). These more variable whistles, which we did not classify as regular song types, suggested that the males maintained an ability to change their whistled songs, much like adults are able to change some nonsong vocalizations (Mammen and Nowicki 1981, Nowicki 1989).

Birds in this first experiment were sexed by laparotomy or during perfusion (for some related neuroanatomical studies) at the conclusion of the experiment. Because we found that only males gave loud whistles and gargles, we used primarily the vocali-
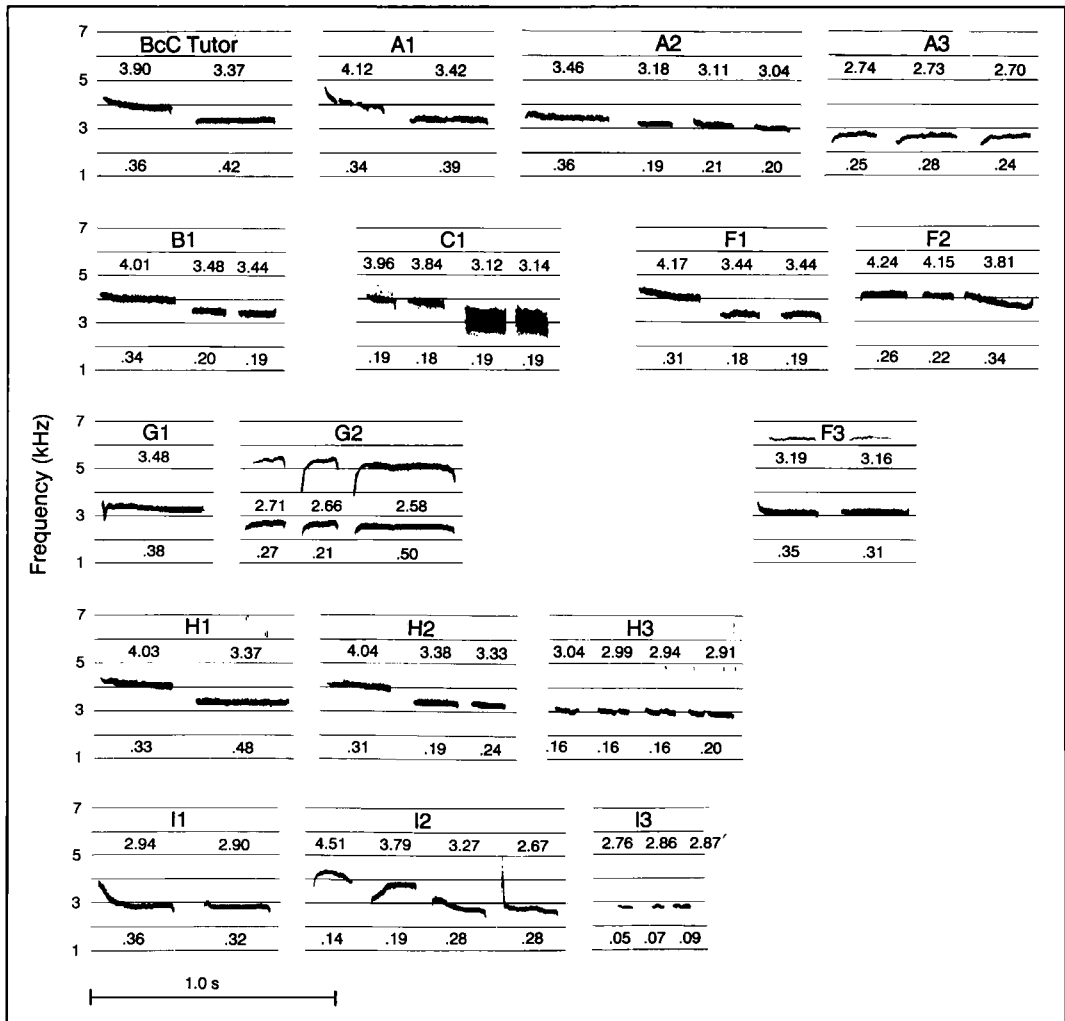
Fig. 1. Sonagrams of songs developed by five Carolina Chickadee males (A, B, C, F, H) and two Black-capped Chickadee males (G, I) in group 1a. Birds tutored with Black-capped Chickadee tutor songs (upper left). Different song types within repertoires of individuals are numbered (e.g. bird A had repertoire of three song types [A1, A2, and A3]). Mean frequency of greatest energy (kHz) indicated above song elements and mean duration (seconds) is below. Total number of renditions examined for each song type as follows: A1 (104), A2 (20), A3 (6), B1 (69), C1 (75), F1 (97), F2 (225), F3 (169), G1 (25), G2 (25), H1 or H2 or both (54), H3 (21), I1 (174), I2 (356), and I3 (28).

zations, double-checked with laparotomy on several birds, to sex birds in the following experiment.

Follow-up Black-capped Chickadee experiment.—Dissatisfied with the number of singing Black-capped Chickadee males in this first experiment, and increasingly puzzled by their song development, we hand-reared an additional 12 birds during 1992 (groups 5, 6, 7; Table 1). Because of the remarkable stereotypy of the *fee-bee* song throughout the range of this species, we wanted to test if males could learn the "correct" song from an array of four songs that contained

all normal components. The subjects were collected as 10- to 14-day-old nestlings on 14 and 15 June from two nests near Amherst, Massachusetts, and tape tutoring began on 24 June when the birds were about three weeks old. The tape consisted of a repeated sequence of four songs; one song was the normal *fee-bee*, and the other three contained normal but rearranged elements, as in *fee-fee, bee-bee,* and *bee-fee.* The mean frequency and duration for the *fee* were 3.90 kHz and 0.36 s; for the *bee,* they were 3.36 kHz and 0.41 s.
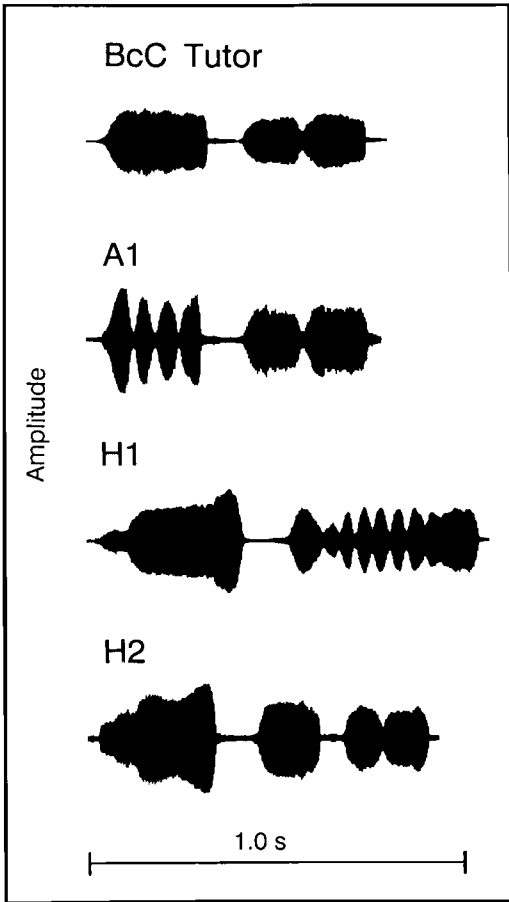
Fig. 2. Oscillograms of a *fee-bee-ee* Black-capped Chickadee tutor song and examples of songs developed by two Carolina Chickadees in group 1a, illustrating how amplitude modulation in *bee-ee* is faithfully copied (as in last-whistled notes of A1 and H2) or exaggerated (as in first note of A1 and last note of H1).

Fig. 3. Sonagrams of songs developed by three Carolina Chickadee males (L-N) in group 1b, illustrating convergence on each others' songs, but less faithful copying of tutored Black-capped Chickadee song. Total renditions: L1 (100), M1 (135), and N1 (3).

Housing conditions for the birds were as follows. Three separate mixed-sex groups of four birds apiece were established in early July: one group with one male, one with two males, and the other with three males. After an initial attempt to house each group in an aviary, so that both vocal and physical interaction would be permitted, we separated the birds, each to its own cage, because the aggression was too high, and birds were being defeathered. Tutoring continued throughout early July and into mid-August, with the birds being exposed thousands of times to each song variant on the tutor tape. Day length was reduced to 11 h during October and early November, and day length was gradually increased from 11 to 15.5 h between 28 January and 23 February.
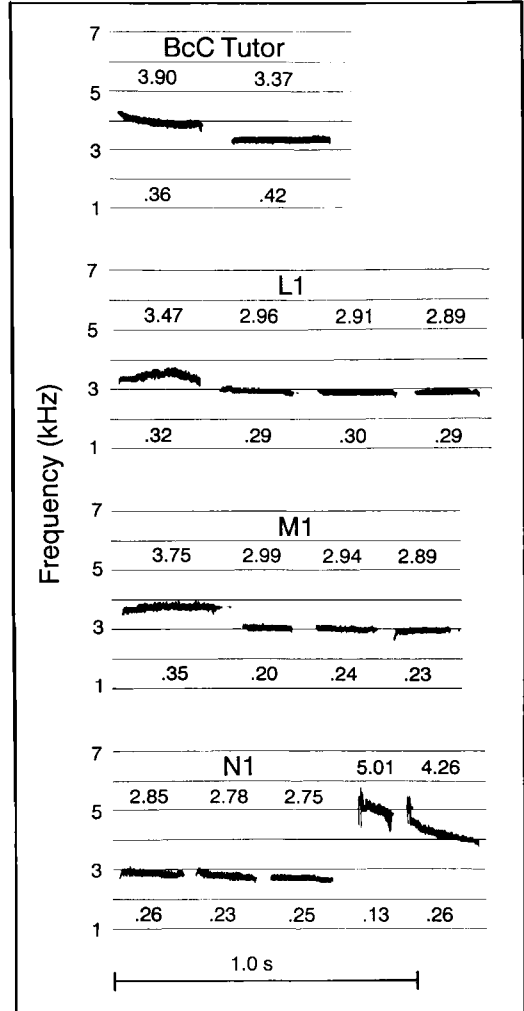
Throughout the year, we recorded vocalizations from the birds under a variety of conditions.

RESULTS

For comparison, we first provide a description of songs of the Black-capped and Carolina chickadees in allopatric populations and then a brief description of vocal behaviors in contact zones. We then describe the song development by males in the mixed species groups and in the pure Black-capped Chickadee groups.
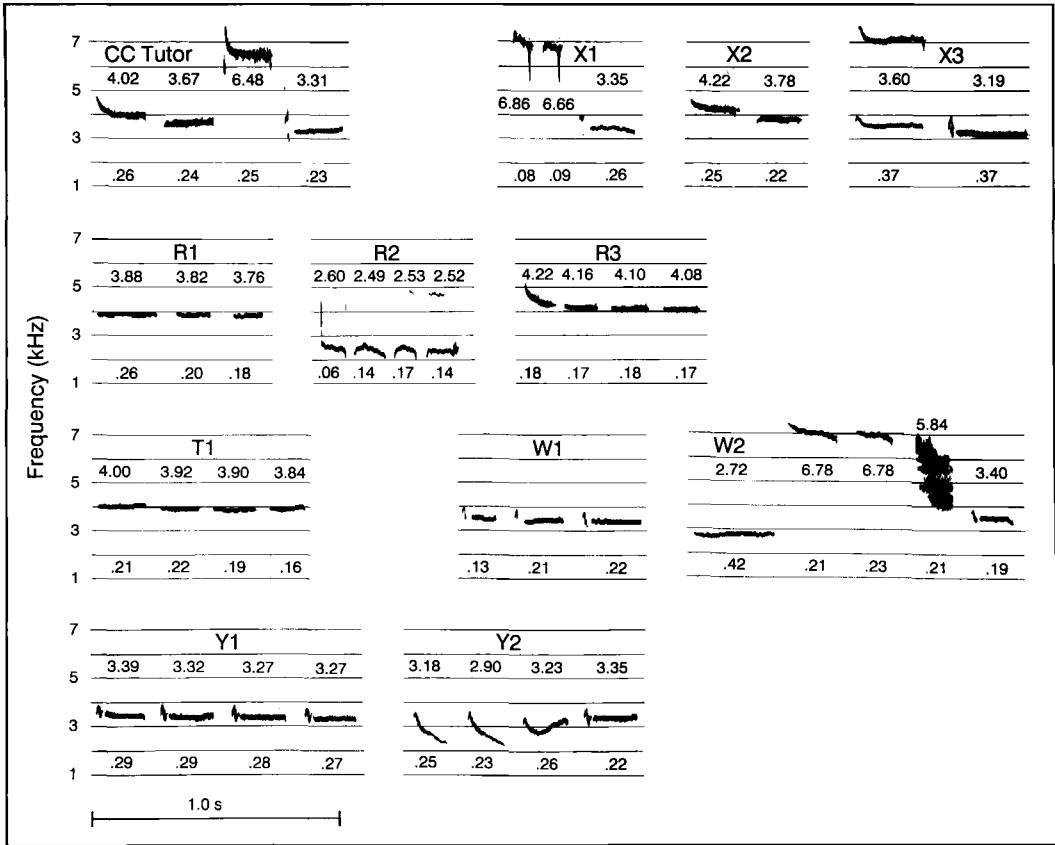
Fig. 4. Sonagrams of songs developed by four Carolina Chickadee males (R, T, W, Y) and one Black-capped Chickadee male (X) in group 2 that had been tutored with a Carolina Chickadee song (upper left). Songs of Carolina Chickadee males converged on one another, and best copy of Carolina Chickadee tutor song was by Black-capped Chickadee male X. Total renditions: R1 (85), R2 (23), R3 (25), T1 (98), W1 (14), W2 (25), X1 (100), X2 (195), X3 (178), Y1 (212), and Y2 (25).

NATURALLY-OCCURRING SONGS OF
CHICKADEES

The *fee-bee* song of the Black-capped Chickadee is remarkably invariant throughout a large portion of its geographic range. The songs typically consist of two whistled components, each of which is about 0.4 s in duration (Fig. 1). The first whistle is usually slurred downward, perhaps through 200 Hz from start to end, and the second whistle then begins immediately about 400 Hz lower. A brief drop in amplitude usually (always?) occurs at the midpoint of the second whistle, thus making *fee-bee-ee* a more appropriate rendering of the song than *fee-bee*, though this feature is not often mentioned by authors (even if illustrated, as in Dixon and Stefanski

1970:fig. 1C). These basic features of the Black-capped Chickadee song are evident in illustrations and descriptions from locations as distant from one another as Utah (Dixon and Stefanski 1970), Alberta (Hill and Lein 1987), Missouri (Robbins et al. 1986), Wisconsin (Ficken et al. 1978, Ficken 1981), Ontario (Ward and Ward 1974, Weisman et al. 1990), New York (Odum 1942), Massachusetts and Pennsylvania (Ward and Ward 1974), and, indeed, much of the North American continent. Ward and Ward (1974) heard this basic song west to British Columbia, Washington, and California. Weisman et al. (1990) could find no evidence of geographic variation in pitch interval, the ratio of the frequency of the two whistles. We have heard the amplitude modulation in every song to which

we have carefully listened in New England, and this same feature can be heard "very clearly in the songs of many Chicago [Illinois] birds" (D. Margoliash pers. comm.).

Other Black-capped Chickadee song forms occur, both as rare or atypical songs at the localities described above and as typical songs in some portions of the geographic range. Out of 156 Black-capped Chickadee recordings in an Ontario study, for example, 5 contained only *fee, fee-fee*, or some variation other than the basic *fee-bee* (Weisman et al. 1990). Monotonal songs, in which all whistles are on the same frequency, might be the normal song on Martha's Vineyard, Massachusetts (two to three whistles; Bagg 1958), in portions of Washington state (three to four whistles; Dawson and Bowles 1909), and near Anchorage, Alaska (about five whistles; Desfayes 1964).

Each male Black-capped Chickadee can apparently sing his *fee-bee* song form at different frequencies. All four wild-caught males in an Ontario study by Ratcliffe and Weisman (1985), for example, sang two types of *fee-bee* songs in the laboratory. The most common song in each male's repertoire averaged 0.04 to 0.39 kHz higher than the respective whistles in the other song. Songs of four wild-recorded males in Alberta were transposed by even greater frequencies, by 0.26 to 0.59 kHz, and shifted songs occurred in 14 of 167 naturally-occurring song bouts (Hill and Lein 1987). Unlike the laboratory-recorded birds, which sang the lower-frequency songs interspersed among the higher frequency songs (Ratcliffe and Weisman 1985), these wild males sang their rarer songs in continuous bouts. Additional recordings from Ontario revealed that 19 of 156 three-song samples from free-living males contained at least one *fee-bee* shifted downward in frequency (Weisman et al. 1990), and extended recordings from individuals eventually revealed a considerable variety of frequencies on which a male could sing his song (Horn et al. 1992).

The typical song of the Carolina Chickadee consists of four whistled notes, with the first and third far higher in frequency than the second and fourth. For a sample pooled from nine regions along the eastern seaboard, Ward (1966) calculated the mean high and low frequencies to be 6.0 to 6.4 kHz and 3.4 to 3.9 kHz, respectively. Mean durations of whistles from the nine sample locations ranged from 0.17 to 0.26 s.

Songs of the Carolina Chickadee seem far less stereotyped, both among locations and within and among males at a given location, than do those of the Black-capped Chickadee. Ward (1966) revealed that in five of nine regions along the eastern seaboard, from New Jersey and Pennsylvania south to Florida, only one-fourth to one-half of all recorded songs conformed to the "high-low-high-low" (HLHL) form. Males at each given location sang the same songs, so that "dialectal" patterns existed. In some populations, males sang a HLHL pattern, but with the first whistle only slightly higher in frequency than the second whistle (e.g. Kansas [Smith 1972]; Ohio [tutor song in Fig. 4]). Smith (1972) also documented considerable variability within and among males in her populations of eastern Pennsylvania. In addition to the standard HLHL song, with high and low notes averaging 6.0 to 7.5 kHz and 3.0 to 4.0 kHz, males used "song variants" with other frequency patterns (e.g. HLLL, LLL), which Smith classified as a separate display. These variants differed structurally from and were rarer than the standard HLHL patterns, and they seemed to have a different pattern of usage than did the typical HLHL pattern. Regardless of how one classifies these whistled vocalizations, males clearly sing many variations.

Songs of birds in contact zones between the two species reveal two important phenomena. First, many chickadees clearly have repertoires of different song forms. Fifteen of 29 individuals recorded in a Missouri contact zone used more than one song type, even though taping sessions with each individual lasted only a few minutes (Robbins et al. 1986). Second, individuals in these contact zones are frequently bilingual, with song repertoires containing songs of both species (Brewer 1963, Johnston 1971, Ward and Ward 1974, Merritt 1978, Robbins et al. 1986). Although "It seems probable that the vocal anomalies [in contact zones] are the result of interbreeding" (Merritt 1981:59), one must know the genetic background of particular singers before such a statement can be accepted. Even though birds in a Missouri zone are morphologically intermediate between the parental types (Robbins et al. 1986), suggesting that hybridization in the contact zone is highly likely (see also Rising 1968), such observations do not provide information needed to relate vocal behaviors to genetic background.

SONG DEVELOPMENT IN MIXED-SPECIES GROUPS

Both males (B, F, G, H, I, R, W, X, Y) and females (D, K, Q, U, V) produced "subsong" beginning at approximately three weeks of age. Individuals either sat motionless on a perch or actively moved about the cage, uttering relatively long, continuous, subdued "warbling." This subsong often could be elicited by the hum of a fan (or distant vacuum sweeper) in the background. Although both sexes produced this subsong, only males produced loud whistled song at one year of age. These whistled songs were, among all males, highly unlike songs of birds in nature.

Group 1 (tutored with Black-capped Chickadee songs).—Six of the nine Carolina Chickadees and both Black-capped Chickadees in group 1a were males, and all eight males sang whistled song components at one time or another. The whistled songs of one Carolina Chickadee male (J), however, remained highly variable and he never sang a loud, stereotyped whistled song like the other males; he was the only male who had been caged with a female (K), and it seems likely that his caging condition influenced his song development. His variable whistles resembled song I2 (Fig. 1) of his cage neighbor, a Black-capped Chickadee male. Six males (A, B, C, F, H, I) sang loud stereotyped whistled songs when one year old, but Black-capped Chickadee male G sang only in his second "year," and only after receiving a testosterone implant.

Four of the five Carolina Chickadees that sang developed a whistled song much like that of the Black-capped Chickadee tutor song. Two of their songs (A1 and H1; see Fig. 1) were nearly identical in overall form to the tutor song, and consisted essentially of two whistles of the appropriate frequency and duration. The amplitude displays of these two songs (Fig. 2; A1 and H1) revealed that these males also produced an amplitude modulation similar to that found in the *bee-ee* of the *fee-bee-ee* tutor song. Although the *bee-ee* of song A1 closely matched that of the tutor songs, other whistled components, such as the *fee* of A1 and the *bee* of H1, usually contained repeated amplitude modulations. Song H2 was similar to H1, except that the amplitude break in the *bee-ee* portion of the tutor song was greatly exaggerated, thus producing two distinct whistles, the combined duration of which was appropriate for a single *bee-ee*. One or both of these *bee* notes were sometimes am- plitude modulated (see Fig. 2; H2). This exaggerated amplitude break in the *bee-ee* was also present in songs B1 and F1 (see Fig. 1). Given that all chickadees in other experimental groups lacked these amplitude modulations, no amplitude modulations of this sort occur in songs of wild Carolina Chickadees, and the two-parted nature of most of these songs, we conclude that these songs from the four Carolina Chickadees A, B, F, and H clearly were derived, either directly or indirectly, from the tutor song. Fine details of the songs revealed that the birds also were matching one another in learning their final song forms.

In addition to imitating heterospecific chickadee songs, one male Carolina Chickadee (H) imitated a Chestnut-sided Warbler song (not illustrated). The chickadees were exposed to two categories of the warbler song, the "accented-ending" and "unaccented ending" (Lein 1978), and this male chickadee produced a good rendition of an accented-ending song.

The song (C1) of the fifth singing Carolina Chickadee seemed the most divergent, primarily because it incorporated some nonwhistled notes into the second half of the song. Both the frequency and combined duration of the first two whistles, however, were similar to the *fee* of the *fee-bee-ee* tutor song.

The songs of the two male Black-capped Chickadees in this room were less like the Black-capped Chickadee tutor songs than were the songs of the Carolina Chickadees. Some of these abnormal Black-capped Chickadee songs were similar to songs of Carolina Chickadee males in the room (compare I1 with F3, G2 with A3, I3 with H3), suggesting some interspecific vocal learning. Perhaps most "normal" were song G1, which consisted of a single note with the frequency and overall duration of the tutored *bee*, and song I1, which contained two whistles of appropriate duration, though of a frequency far lower than that of the tutor song; none of these notes of the two Black-capped Chickadees contained the amplitude modulation of the tutored *bee-ee*. The most distinctive, complex, and frequently used song was I2. This song consisted of a stereotyped series of different whistled notes, with the second and fourth notes illustrated in Figure 1 often repeated. Usually the song started on the highest whistle and progressed to the lowest, but often a note much like the second, which swept up in frequency, would be appended to the end of the song.

The subgroup (1b) of three Carolina Chickadee males (L, M, N) that was removed from the main group showed less influence of the Black-capped Chickadee tutor song (Fig. 3). Two of the males that were in adjacent cages used nearly identical songs (L1 and M1), a HLLL pattern with "the high note . . . only slightly higher than the low notes" (Smith 1972:105). This pattern was described by Smith for a rare song variant from Tyler Arboretum in Philadelphia, near where these Carolina Chickadees had been collected. The third male (N) rarely sang, but his one recorded song type contained a series of low-frequency whistles like those found in the songs recorded from males L and M. The songs of these three males, thus, had converged on one another and were more similar to each other than they were to the songs of males in the main group, even though the males in the two groups had heard the same tutor song.

Group 2 (tutored with Carolina Chickadee songs).— Males in this group sang less frequently than did the males in group 1. One male Carolina Chickadee (Y) was an early and persistent singer, and with the accelerated light schedule he had developed loud, stereotyped songs by 6 March. He usually sang just before and after the lights came on in the morning. Males R, T, and W, also Carolina Chickadees, developed stable songs by the end of March but, despite hours of listening and taping, relatively few songs were recorded from these males. No dawn chorus of songs occurred, and the best singing from male W was recorded during a late afternoon, when a loud cage-washing machine was being used in the next room. By 4 June, none of the six Black-capped Chickadees in the room had sung and, in an attempt to elicit more vocal behavior from these birds, we removed the six Carolina Chickadees. Eight days later we recorded abundant midday, but not early morning, singing from the only male Black-capped Chickadee (X).

Even though this group was tutored with a Carolina Chickadee song, none of the Carolina males developed the HLHL tutored pattern typical of Carolina Chickadees in nature. Males R and T clearly converged on one another (compare R1 and T1 in Fig. 4), as did males W and Y (compare W1 and Y1). The fourth note of the tutor song, with two brief notes just before the main whistle, was clearly the basis for W1 and Y1 and also for the last note of W2 and Y2. Male W was the only Carolina Chickadee to show

evidence of using a high-frequency whistle, around 6.8 kHz, similar to that of the tutor song.

Intriguingly, even though the Black-capped Chickadee male (X) was surrounded by Carolina Chickadee males singing nontutored songs during March, April, and May, and even though he had been tutored with heterospecific song, he provided the best copy of the tutor song. During the first singing season, this male used two different songs (X1 and X2 of Fig. 4). In both frequency and temporal measures, X2 was a good match of the first two whistles of the tutor song. Song X1 clearly contained the fourth whistle of the tutor song, but the high-frequency sounds that preceded the low whistle were more like the "tee" call (Smith 1972) than like the whistle of the tutor song. This male Black-capped Chickadee thus produced a fairly accurate rendition of the two parts of the tutor song.

Singing in year 2.—Songs were recorded from all five males, but none of the four females during the second period of long days (i.e. the second "year"; see Table 1). One of these five males (G) sang for the first time during year 2 and was discussed above. Of the four nonsinging females, Q and V had been implanted with testosterone, and S and Z with estradiol.

Two of the five singing males did not change substantially their songs between years. Male B, for example, continued with his B1; the median frequency and duration of the first note in the song during the second year were 4.01 kHz and 0.32 s, similar to that for the first year (Fig. 1). Male H produced the same three songs of Figure 1 and the same Chestnut-sided Warbler imitation.

Male X, the only male Black-capped Chickadee in group 2, altered his songs significantly between years (Fig. 4). Song X2 remained largely intact, though the frequency of songs measured in year 2 seemed to be about 100 Hz lower than those in year 1. The first notes of X1 were replaced with a single whistle (see X3); the fundamental frequency of this new note was appropriate for a Black-capped Chickadee *fee*, but the second harmonic, which was 4 to 14 dB (median = 8 db, $n = 14$) higher than the fundamental, was similar to that of the Carolina Chickadee tutor song.

The other singing male was a Carolina Chickadee (R) from group 2 that had been moved to an entirely new acoustic and social environment, with three group 1 males (B, G, H). Some

TABLE 2. Means and coefficients of variation (CV) of frequencies (in kHz) for two songs of male X (illustrated in Fig. 4; $n = 123$ for all parameters).

	Mean (range)	CV
Song X2		
High note	4.08 (4.00–4.24)	1.1
Low note	3.68 (3.58–3.81)	1.2
Song X3		
High note	3.56 (3.40–3.83)	2.2
Low note	3.26 (3.14–3.42)	1.7

features of his singing in year 2 might have been stimulated by the new environment, but none of the characteristic group 1 songs were unambiguously copied. By year 2, this male had perfected a song (R3) that had first appeared in variable form during year 1. Song R2 was not recorded during year 2. The durations of whistled notes in song R1 seemed more variable than they had been during year 1; some songs began with relatively long whistles (0.38 s), but others consisted of a series of five to seven whistles of about 0.16 to 0.18 s (3.89 to 3.62 kHz).

Variability in songs of laboratory-reared chickadees.—To determine if a hand-raised male Black-capped Chickadee varied the frequency of his songs like wild birds do, we recorded and analyzed frequency relationships of the two notes in 123 X2 and 123 X3 songs contained in a 90-min sequence during the second season of singing (Table 2). The frequency ranges for the four notes (0.23–0.43 kHz) were within the ranges found among wild birds (0.04–0.59 kHz; Ratcliffe and Weisman 1985, Hill and Lein 1987). The distribution of frequencies around the mean appeared normal, indicating that the chickadee did not sing each song on several discrete frequencies. Two aspects of this male's singing, however, indicated that he was not singing in the rigid fashion typical of males from nature. In nature, males tend to sing several renditions of the *fee-bee* song on a given frequency before going to another frequency (Horn et al. 1992), but successive songs of laboratory-reared males varied considerably. Furthermore, frequency ratios (high frequency/low frequency) for song X1 ranged from 1.07 to 1.15, and for song X3 from 1.04 to 1.16. Although the frequencies of the two notes within each song were significantly correlated (X2, $r = 0.64$; X3, $r = 0.43$; both $P < 0.001$), the percentage of variation (40 and 18%, respectively) explained by these two cor-

relations was relatively low. The frequency of one whistle in the song, thus, was not rigidly determined by the frequency of the other.

Overall variability in frequency was lower than that for duration in the chickadee songs. Median coefficients of variation for frequency and duration for the 97 nontutor song elements in Figures 1, 3, and 4 were 1.2% (range 0.4–9.5%) and 9.0% (range 0.9–35.2%), respectively. Statistics were based on 10 renditions of each song type, except for A3 ($n = 6$) and N1 ($n = 3$).

SONG DEVELOPMENT IN PURE BLACK-CAPPED CHICKADEE GROUPS

Our results with the second experiment on Black-capped Chickadees were largely consistent with those of the mixed-species experiment. First, both males and females engaged in loud subsong during late June and early July, beginning when they were approximately 25 days old. Again, however, it was only the males who subsequently sang loud vocalizations, whether whistles or gargles, as adults.

Second, expression of loud song and other vocalizations by the males depended less on the time of year (and, therefore, presumably less on hormonal levels) than it did on social situations provided by various physical arrangements of cages within the groups. Group 5 (see Table 1), for example, originally consisted of three males and one female, but the female died during November 1992. For 10 days, from 13 to 22 December, we recorded these males during the first 10 min of each day; on odd days, the males could both see and hear each other through the wire bars of their adjacent cages, but on even days a partition was inserted between the cages so that they could only hear each other. When the males could both see and hear each other, they used several calls, such as the "chick-a-dee," and a few other relatively soft vocalizations, but they produced virtually no loud "gargles" or whistled songs (one male produced a total of six gargles during the 50 min sampled). With partitions in place, however, the males were highly vocal. The most vocal male produced an average of 47 whistles and 40 gargles in each 10-min period (ranges 33–75 and 3–69 for whistles and gargles, respectively), the next most vocal male 19 whistles and 30 gargles (11–31 and 14–52), and the quietest male 7 whistles and 9 gargles (0–27 and 0–26). Thus, after males had been on 11-h day lengths for about 6 weeks,

and with gonads presumably fully regressed, the males were primed to "sing" if provided the right social conditions. How each male responded may have reflected his relative position in a dominance hierarchy among the males.

Third, the responses of the three males in the 10-day experiment were all the more intriguing in light of the relative lack of vocalizing by males in the two mixed-sex groups (6 and 7, Table 1) of four individuals apiece during the winter. No songs or gargles were induced in midwinter, for example, by placing partitions between the cages, and the males in these groups vocalized less in the spring, too. Thus, variability in the rate of vocalizing both within and among the three groups was marked. We suspect that the sex ratio was a factor (recall that, in the mixed-species experiments, Carolina Chickadee male J was caged with a female and did not sing well, and that the Carolina Chickadee male with two females in group 1c did not sing either. However, other factors, such as the dynamics of intrasex dominance hierarchies, also could be important.

Fourth, although males in nature sing one basic song pattern (the *fee-bee-ee*), albeit on different frequencies, these males used from one to three different whistled vocalizations. "Song" repertoires, therefore, were larger than typically found among wild males.

Fifth, the songs were highly abnormal. The normal *fee-bee-ee* song was not learned by any of the males, nor was the amplitude-modulated *bee-ee* component. The same abnormal songs tended to be shared by males within groups, however, indicating that social interactions among the males influenced their song repertoires. In the group (5) with three males, for example, the most commonly used song consisted of two whistles, very much like the *fee-fee* song that the males had heard from the tutor tape. For the most-vocal male, both whistles were at 4.1 kHz, with durations of 0.30 s and 0.27 s, with 0.18 s between the whistles (based on $n = 30$ songs); the second-most-vocal male sang the first whistle at 4.1 kHz and the second at 4.0 kHz, with durations of 0.36 and 0.26 s, and with 0.16 s between the whistles ($n = 10$); both whistles of the third male also were at 4.1 kHz, and both were 0.29 s in duration, with 0.23 s between the whistles. A second vocalization used by the three males started with a single buzzy component (much like last notes of C1 in Fig. 1) and ended with a whistle; for the

three males, respectively, the frequency and duration of that whistle were 4.4, 4.6, and 4.2 kHz, and 0.16, 0.24, and 0.25 s ($n = 28$, 8, and 4). The two least-vocal males used still another rare whistled vocalization, a single low-frequency whistle, both at 3.5 kHz, with durations of 0.42 and 0.40 s. The two males in group 6 produced a bewildering variety of whistled songs. The most-vocal male typically produced songs consisting of three to seven whistles, ranging from 3.36 to 4.10 kHz, with some songs rising, some constant, and some dropping in frequency. Songs of the second male consisted of one to four whistles, with variations in frequency among successive whistles similar to those of the first male. In the group (7) with one male, the single whistled song type that we recorded consisted of two to three whistles, with successive whistles slightly lower in frequency (3.60, 3.53, and 3.47 kHz; $n = 11$ songs).

DISCUSSION

Heterospecific song learning.—Perhaps the most important, and in some ways the expected (Kroodsma 1988), conclusion from our study is that the learned song of a Carolina Chickadee or Black-capped Chickadee is not necessarily a good indication of the genetic background of the singer. The male Carolina Chickadees in group 1a, which had been tutored with Black-capped Chickadee songs, produced reasonable copies of the Black-capped Chickadee tutor song. The increased segmentation of the *fee* and *bee-ee* in Carolina Chickadee songs may reveal a natural tendency for the Carolina Chickadee to sing briefer whistles (Robbins et al. 1986, this study). The male Black-capped Chickadee (X) in group 2, which had been tutored with Carolina Chickadee songs, also produced copies of heterospecific song elements. Intriguingly, the high-frequency note of X3 apparently was produced as the second harmonic of a suppressed fundamental that lay in the normal range of Black-capped Chickadee whistle frequencies. The heterospecific imitations by male X, together with the strange songs produced by males G and I, reveal a potential for song variety not realized in allopatric populations in nature. The most that laboratory studies of song learning, such as ours, can demonstrate is a potential for certain kinds of behavior; because of the highly unnatural laboratory setting, however, all we can say is that behavioral hybridization can oc-

cur without genetic hybridization, and songs in contact zones do not necessarily provide reliable clues to species.

Although heterospecific song learning clearly is possible, the role that interspecific social dynamics may play in fostering or inhibiting such learning is unclear. In group 1a, the two chickadees that developed songs most unlike the Black-capped Chickadee tutor songs were the two male Black-capped Chickadees (G, I). The five singing male Carolina Chickadees in this group shared basic features of their most commonly used song with one another, and most of these were based on the heterospecific *fee-bee-ee* tutor song, a song that one would have expected the Black-capped Chickadees to learn most readily. In group 2, the four male Carolina Chickadees shared basic features of their most commonly used songs with one another, but they did not copy the conspecific tutor pattern. The single male Black-capped Chickadee, however, copied all four elements from the heterospecific tutor song, and his songs did not converge on those of the Carolina Chickadee males in the room. In each group, then, the best copies of the tutor tape were unexpectedly produced by chickadees of the "wrong" species. Determining whether these results are a consequence of typical social dynamics within a heterospecific "flock" or are an artifact of the small sample in a laboratory setting will have to await further study.

Song repertoires and geographic variation.—The repertoires of the laboratory-reared chickadees were unlike those of wild-type males. Carolina Chickadees in nature use a variety of song types or variants (Smith 1972); the birds in these experiments also developed several song forms, and many of the song types clearly were based, at least in part, on the single tutored song form that the birds heard. Had we provided the Carolina Chickadees with more tutor song types during the first year, additional copying of tutor songs and development of more normal repertoires may have been evident. Perhaps partly as a consequence of the "deficient" tutor experience, many of these birds improvised or invented songs (sensu Marler and Peters 1982), and most of the songs used by the laboratory-reared males were outside the apparent range of normal variation (Ward 1966, Smith 1972, Ward and Ward 1974, Robbins et al. 1986).

In contrast to birds in nature, the laboratory-reared Black-capped Chickadees developed repertoires of two to three strikingly different non-*fee-bee-ee* song forms (see also Shackleton and Ratcliffe 1993). Reports of song repertoires for wild-type Black-capped Chickadees document only the use of the *fee-bee-ee* on different frequencies (Ratcliffe and Weisman 1986, Hill and Lein 1987), and wild-caught birds seem highly attuned to these subtle frequency changes in their songs (Ratcliffe and Weisman 1986, Weisman and Ratcliffe 1989, Weisman et al. 1990). In the laboratory, however, neither of two male Black-capped Chickadees that was tape-tutored only with the normal *fee-bee-ee* (group 1) developed a normal song; nor did any of the six males (groups 5, 6, 7) tutored with the *fee-bee-ee* and three permutations of those components in a follow-up experiment learn normal songs. As in wild birds, the absolute frequency of the whistles in the songs varied, but the frequency relationships of the whistles were not as rigid as are those found among wild birds (Weisman et al. 1990).

These data prompt two related questions about Black-capped Chickadee songs: What constrains males to the *fee-bee-ee* throughout such a large portion of the geographic range, and why do "repertoires" of *fee-bee-ee*'s on different frequencies develop when birds are clearly capable of developing repertoires of very different, highly contrasting song types? The relative lack of geographic variation in the *fee-bee-ee* song contrasts sharply with the dialectal variation found in the "gargle" vocalization (e.g. Ficken and Weise 1984, Ficken et al. 1985, 1987), and such differences within the vocal repertoire of a single species should provide hints as to the functions and selective forces promoting different degrees of variation. The parallels with the geographic variation in the two song forms of certain paruline warblers are intriguing. Song forms of the Blue-winged Warbler (*Vermivora pinus*) and Chestnut-sided Warbler that are used in aggressive contexts, like the chickadee gargle vocalization, also have local dialects. The warbler song forms that are used in less-aggressive situations, and more in male-female interactions, are essentially invariant throughout the geographic range (Kroodsma 1981), much like the geographic pattern in the *fee-bee-ee* song. Ficken's (1981) description of the use of the *fee-bee-ee* and gargle before and during territorial encounters, respectively, closely parallels the descriptions that Lein (1978) and Kroodsma et al. (1989) provided for the "accented-ending"

(AE) and "unaccented-ending" (UE) songs of the Chestnut-sided Warbler. Because of the vocal learning ability of these songbirds, as illustrated especially in the laboratory, one expects dialectal patterns to emerge, unless strong forces constrain the variety of vocal forms that can develop in nature. Given the proposed male-female functions of the geographically invariant songs of warblers (Highsmith 1989, Kroodsma et al. 1989), and given the role that the nonvocal behavior of female Brown-headed Cowbirds (*Molothrus ater*) may play in developing the relatively invariant songs of males (e.g. West and King 1988), perhaps it is female Black-capped Chickadees that enforce the stability of the *fee-bee-ee* song.

Songs and singing.—Ficken (1981:384) once posed the question "What is the song of the Black-capped Chickadee?" Arbitrary distinctions between "calls" and "songs" may unknowingly mislead our thinking, and Ficken (1981), as well as others (e.g. Dixon and Stefanski 1970), have pointed out that the *fee-bee-ee* song of the Black-capped Chickadee does not conform to our notions of the typical oscine song. Rather, two vocalizations of the Black-capped Chickadee, the gargle (a complex series of vocalizations that Smith [1972] subdivided into additional categories) and the whistled song, seem to share some of the usual proposed functions of song for other songbirds. Furthermore, three North American chickadees lack the whistled song entirely (review in Ficken 1981), and similar consternation occurs for some European species as to what vocalization should be regarded as a "song" (see Hailman 1989).

Several related questions arose during these experiments. Whistled songs and garglelike notes often occurred together, as one might have expected from descriptions of how they are used in nature (Ficken 1981). Songs I3 and F1, for example, almost always were followed immediately by a gargle. The "dawn chorus" typically began with gargles in group 1a, the group with a high concentration of males, and then proceeded to whistled songs and gargles. Other birds sang not at dawn, as one expects of a songbird, but later in the day, and one sang especially during operation of a loud cagewasher in the adjacent room.

Another intriguing observation was that the hand-reared chickadees, unlike individuals of other songbirds that we have hand-reared, could not be sexed reliably by the presence or absence

of subsong during the first 50 to 70 days of life. Songbird species in which males can be identified by their abundant subsong include the Marsh Wren (*Cistothorus palustris*), Song Sparrow (*Melospiza melodia*), Swamp Sparrow (*Melospiza georgiana*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), Red-winged Blackbird (*Agelaius phoeniceus*), several *Dendroica* and *Vermivora* wood-warbler species, and others. For some of these species, such as the Song Sparrow, females occasionally sing as adults (Arcese et al. 1988), but subsong is nonexistent or exceptionally rare. Both male and female chickadees, however, produced frequent subsong during their hatching year, but only males produced the loud whistled songs the next year, during their first breeding season.

Another puzzle involved the role of day lengths and hormonal levels required for singing. In other songbirds that have been laboratory-reared, we have routinely used testosterone implants to enhance singing behavior. The Carolina Chickadees, however, did not respond to such hormone treatment. On 26 February, for example, when some of the males in group 1 were already singing, four males (L, M, N in group 1b, and a fourth male in group 1c) and two females were implanted with testosterone. Normally, one would expect an increase in "singing" by males and some attempts at song from females within 7 to 10 days, as happened with the Chestnut-sided Warbler males and females that had been implanted at the same time from the same stock of testosterone and silastic tubes. From the two females and one male (in group 1c), we never recorded whistled songs or attempts at "songs," even though we monitored this group throughout the month following the hormone therapy. Over a month after receiving testosterone, males L and M began to sing fairly regularly, and N sang three songs during taping sessions, but the effects of the exogenous testosterone would have been expected much earlier.

More important than season and its presumed influence on hormonal levels were the social conditions created by various cage arrangements (see also Lanyon 1979). Three male Black-capped Chickadees were very quiet when they could both see and hear each other, but they vocalized profusely when partitions were placed between cages (Indigo Buntings [*Passerina cyanea*] respond similarly to such treatment; D. Margoliash, pers. comm.). A male Carolina

Chickadee (J) with a female in the cage never sang, even after the female was removed. A male Black-capped Chickadee (X) did not sing until all the Carolina Chickadees were removed from the room, at a time when gonads of the other chickadees had already regressed. Another male Black-capped Chickadee (G), who had been surrounded by male Carolina Chickadees during year 1, sang only in year 2, after testosterone treatment and after isolation from other singing chickadees. The dominance of Carolina Chickadees over Black-capped Chickadees, strong enough that interspecific aggressions caused two deaths in this study, might have inhibited Black-capped Chickadee males G and X from singing, though male I in group 1a was the most persistent singer. Clearly, a high testosterone level (as expected from implants) does not necessarily induce copious singing by males (or females), nor does a low testosterone level (as expected in birds with regressed gonads during midwinter) prevent abundant song from occurring.

  Conclusions.—First, Black-capped Chickadees and especially Carolina Chickadees from allopatric areas can learn song elements or entire songs from the other species; the songs of a chickadee in a contact zone, therefore, provide no reliable clue to his genetic background. Second, the unknown forces that maintain the Black-capped Chickadee's stereotyped *fee-bee-ee* song over much of that species' geographic range were absent in the laboratory. Third, several aspects of chickadee song remain puzzling: females subsing but, under laboratory conditions, do not produce loud whistled songs as adults; social dynamics within a group may inhibit song, even under high testosterone levels; visual or total isolation from other chickadees may lead to abundant singing, even if males have regressed gonads; and the functional relationship between whistled song and nonwhistled vocalizations (e.g. "gargles") remains unclear.

LITERATURE CITED

ARCESE, P., P. K. STODDARD, AND S. M. HIEBERT. 1988. The form and function of song in female sparrows. Condor 90:44–50.

BAGG, A. M. 1958. A variant form of the chickadee's "fee-bee" call. Mass. Audubon 43:9.

BREWER, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina chickadees. Auk 80:9–47.

DAWSON, W. L., AND J. H. BOWLES. 1909. Birds of Washington, vol. I. Occidental Publishing Co., Seattle.

DESFAYES, M. 1964. An observation on the song of the Black-capped Chickadee. Condor 66:438–439.

DIXON, K. L., AND R. A. STEFANSKI. 1970. An appraisal of the song of the Black-capped Chickadee. Wilson Bull. 82:53–62.

EMLEN, S. T., J. D. RISING, AND W. L. THOMPSON. 1975. A behavioral and morphological study of sympatry in the Indigo and Lazuli buntings of the Great Plains. Wilson Bull. 87:145–179.

FICKEN, M. S. 1981. What is the song of the Black-capped Chickadee? Condor 83:384–386.

FICKEN, M. S., R. W. FICKEN, AND K. M. APEL. 1985. Dialects in a call associated with pair interactions in the Black-capped Chickadee. Auk 102:145–151.

FICKEN, M. S., R. W. FICKEN, AND S. R. WITKIN. 1978. Vocal repertoire of the Black-capped Chickadee. Auk 95:34–48.

FICKEN, M. S., AND C. M. WEISE. 1984. A complex call of the Black-capped Chickadee (*Parus atricapillus*). I. Microgeographic variation. Auk 101:349–360.

FICKEN, M. S., C. M. WEISE, AND J. A. REINARTZ. 1987. A complex vocalization of the Black-capped Chickadee. II. Repertoires, dominance and dialects. Auk 89:500–509.

HAILMAN, J. P. 1989. The organization of major vocalizations in the Paridae. Wilson Bull. 101:305–343.

HELB, H.-W., F. DOWSETT-LEMAIRE, H.-H. BERGMANN, AND K. CONRADS. 1985. Mixed singing in European songbirds—A review. Z. Tierpsychol. 69:27–41.

HIGHSMITH, R. T. 1989. The singing behavior of Golden-winged Warblers. Wilson Bull. 101:36–50.

HILL, B. G., AND M. R. LEIN. 1987. Function of frequency-shifted songs of Black-capped Chickadees. Condor 89:914–915.

HORN, A. G., M. L. LEONARD, L. RATCLIFFE, S. A. SHACK-

LETON, AND R. G. WEISMAN. 1992. Frequency variaton in songs of Black-capped Chickadees (*Parus atricapillus*). Auk 109:847–852.

JOHNSON, N. K., AND J. A. MARTEN. 1988. Evolutionary genetics of flycatchers. II. Differentiation in the *Empidonax difficilis* complex. Auk 105:177–191.

JOHNSTON, D. W. 1971. Ecological aspects of hybridizing chickadees (*Parus*) in Virginia. Am. Midl. Nat. 85:124–134.

KROODSMA, D. E. 1981. Geographical variation and functions of song types in warblers (Parulidae). Auk 98:743–751.

KROODSMA, D. E. 1988. Contrasting styles of song development and their consequences among passerine birds. Pages 157–184 *in* Evolution and learning (R. C. Bolles and M. D. Beecher, Eds.). Lawrence Erlbaum Associates, Hillsdale, New Jersey.

KROODSMA, D. E., R. C. BERESON, B. E. BYERS, AND E. MINEAR. 1989. Use of song types by the Chestnut-sided Warbler: Evidence for both intra- and inter-sexual functions. Can. J. Zool. 67:447–456.

KROODSMA, D. E., AND M. KONISHI. 1991. A suboscine bird (Eastern Phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. Anim. Behav. 42:477–488.

KROODSMA, R. L. 1974. Hybridization in grosbeaks (*Pheucticus*) in North Dakota. Wilson Bull. 867:230–236.

LANYON, W. E. 1979. Development of song in the Wood Thrush (*Hylocichla guttata*), with notes on a technique for hand-rearing passerine birds from the egg. Am. Mus. Novit. 2666:1–27.

LEIN, M. R. 1978. Song variation in a population of Chestnut-sided Warblers (*Dendroica pensylvanica*): Its nature and suggested significance. Can. J. Zool. 567:1266–1283.

MAMMEN, D. S., AND S. NOWICKI. 1981. Individual differences and within-flock convergence in chickadee calls. Behav. Ecol. Sociobiol. 9:179–186.

MARGOLIASH, D., C. A. STAICER, AND S. A. INOUE. 1991. Stereotyped and plastic song in adult Indigo Buntings, *Passerina cyanea*. Anim. Behav. 42:367–388.

MARLER, P., AND S. PETERS. 1982. Subsong and plastic song: Their role in the vocal learning process. Pages 25–50 *in* Acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

MERRITT, P. G. 1978. Characteristics of Black-capped and Carolina chickadees at the range interface in northern Indiana. Jack-Pine Warbler 56:171–179.

MERRITT, P. G. 1981. Narrowly disjunct allopatry between Black-capped and Carolina chickadees in northern Indiana. Wilson Bull. 93:54–66.

NOWICKI, S. 1989. Vocal plasticity in captive Black-capped Chickadees: The acoustic basis and rate of call convergence. Anim. Behav. 37:64–73.

ODUM, E. P. 1942. Annual cycle of the Black-capped Chickadee. Part 3. Auk 59:499–531.

RATCLIFFE, L., AND R. G. WEISMAN. 1985. Frequency shift in the fee-bee song of the Black-capped Chickadee. Condor 87:555–556.

RATCLIFFE, L., AND R. G. WEISMAN. 1986. Song sequence discrimination in the Black-capped Chickadee (*Parus atricapillus*). J. Comp. Psychol. 100:361–367.

RISING, J. D. 1968. A multivariate assessment of interbreeding between the chickadees *Parus atricapillus* and *P. carolinensis*. Syst. Zool. 17:160–169.

RISING, J. D. 1983. The Great Plains hybrid zones. Curr. Ornithol. 1:131–157.

ROBBINS, M. B., M. J. BRAUN, AND E. A. TOBEY. 1986. Morphological and vocal variation across a contact zone between the chickadees *Parus atricapillus* and *P. carolinensis*. Auk 103:655–666.

SHACKLETON, S. A., AND L. RATCLIFFE. 1993. Development of song in hand-reared Black-capped Chickadees. Wils. Bull. 105:637–644.

SLATER, P. J. B. 1989. Bird song learning: Causes and consequences. Ethol. Ecol. and Evol. 1:19–46.

SMITH, S. T. 1972. Communication and other social behavior in *Parus carolinensis*. Publ. Nuttall Ornithol. Club 11.

WARD, R. 1966. Regional variation in the song of the Carolina Chickadee. Living Bird 5:127–150.

WARD, R., AND D. A. WARD. 1974. Songs in contiguous populations of Black-capped and Carolina chickadees in Pennsylvania. Wilson Bull. 86:344–356.

WEISMAN, R., AND L. RATCLIFFE. 1989. Absolute and relative pitch processing in Black-capped Chickadees, *Parus atricapillus*. Anim. Behav. 38:685–692.

WEISMAN, R., L. RATCLIFFE, I. JOHNSRUDE, AND T. A. HURLEY. 1990. Absolute and relative pitch production in the song of the Black-capped Chickadee. Condor 92:118–124.

WEST, M. J., AND A. P. KING. 1988. Female visual displays affect the development of male song in the cowbird. Nature 334:244–246.