Patterns and Implications of Aberrant Singing Behaviors of Black-capped (Poecile atricapillus) and Carolina (Poecile carolinensis) Chickadees in Illinois

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Patterns and Implications of Aberrant Singing Behaviors of Black-capped (Poecile atricapillus) and Carolina (Poecile carolinensis) Chickadees in Illinois.

BY

Patrick Caesar Enstrom

THESIS

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Abstract

I studied the singing behavior of the closely related Black-capped (Poecile atricapillus) and Carolina (Poecile carolinensis) Chickadees along their range interface in central Illinois. These sibling species are parapatrically distributed from the Appalachians through the Midwest to Kansas. Where their ranges do overlap, small hybrid zones form and chickadees in these areas frequently sing aberrant songs. The majority of the songs studied were recorded 17 April-16 July 1999 in fifteen counties throughout central Illinois. I measured 8 frequency and duration characteristics of the first two notes of songs that began with two whistled notes. The averages of these characteristics for each song type at each site were classified as Black-capped Chickadee (BCC), Carolina Chickadee (CC) or intermediate on the basis of a discriminant function analysis. I developed a set of objective spectrographic criteria (OSC) that used the frequency, also duration, and basic structural characteristics of the entire song to classify them as BCC, CC, or aberrant. Based on the distribution of intermediate and aberrant song types I located four contact zones in central Illinois between these chickadees. The largest was located in Bond, Fayette, and Montgomery counties. There were smaller contact zones in Shelby, Douglas, and Champaign counties. A comparison among the distributions of BCC, CC and aberrant chickadee singing now and during a previous study in Illinois (1954-59) revealed that there has been little or no change in these two species’ distributions in the past 40 years. The stability of the distributions of the song types associated with each species most
likely has resulted from the fact that the factors that determined the relative
distributions of these species (e.g., habitat availability) have remained stable.
The greatest diversity of song types was present in the largest contact zone. I
found three unique dialects within the contact zones, one each in Bond, Fayette,
and Shelby counties. The Vandalia dialect (Fayette Co.) is probably at least 40
years old (Brewer 1959). I used the song types present at each site to sort the sites
into eight repertoire categories based on the overall combination of song types
present. Repertoire analysis revealed that bilingual singing was widespread and
that individuals that sang both CC and aberrant song types that contained high
frequency (>6kHz) whistled notes or both BCC and songs containing only low
frequency (≤ 5kHz) whistled notes were concentrated in specific, mutually
exclusive areas. The presence of patterns in the distribution of aberrant song types
and repertoire constitution in these contact zones suggests that the interaction of
BCC and CC has led to the development of unique song cultures in at least some
contact zones.
Acknowledgments

I thank Eric Bollinger for his guidance, patience, and faith. I also thank Paul Switzer for sharing his lab space with me and thousands of chickadee songs and his input throughout this project. I would like to thank Kipp Kruse for his input and effort on my behalf. I thank Eastern Illinois University and the Department of Biological Sciences for aiding in the funding of this project. I thank those land owners of Illinois that allowed me access to their land. I thank Bud Fischer for logistical support. I thank my brother David for helping to instill within me a love of birds and of nature in general. I thank Paula and Joe for their generosity and hospitality which was instrumental in the completion of this project.
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Abstract

I recorded the songs of chickadees at 185 sites in 15 Illinois counties in order to map the contact zone between Black-capped (*Poecile atricapillus*) and Carolina (*Poecile carolinensis*) Chickadees. These sibling species are parapatrically distributed from the Appalachians in the east through the Midwest to Kansas. Where they overlap, small hybrid zones form and chickadees in these areas frequently sing aberrant songs. These aberrant songs are closely associated with the genetic contact zones. Analysis of frequency, duration, and other characteristics of the songs I recorded using discriminant function analysis and a set of objective spectrographic criteria revealed that aberrant singing behavior occurred in at least four distinct contact zones in Illinois. The largest was located in Bond, Fayette and Montgomery counties. Smaller contact zones occurred in Shelby, Douglas, and Champaign counties. A comparison among the distributions of Black-capped, Carolina, and aberrant chickadee song types now and during a previous study in Illinois in 1954-59 revealed that there has been little change in these two species' distributions in the past 40 years. The stability of the distributions of the song types associated with each species most likely has occurred because the factors that determine the relative distributions of these species (e.g., habitat availability) have remained stable.
Introduction

Hybrid or contact zones occur where related taxa, whose distributions are largely parapatric, overlap and interbreeding occurs leading to the development of populations with mixed ancestry (Futuyma 1986). Morphological, genetic, and behavioral traits may be affected by interactions occurring in hybrid zones (Robbins et al. 1986, Hewitt 1989). The shape and stability of hybrid zones depends on the spatial relationships of habitat types, and the specific adaptations, behavioral interactions, and genetic compatibility of the taxa (Hewitt 1989, Rohwer and Wood 1998). In addition to genetic hybridization, hybridization of cultural traits may also occur between species or even within a species when they have culturally transmitted traits (Chilton and Lein 1996, Martens 1996.) The production of hybrid songs in birds is an example of the hybridization of a culturally transmitted trait (Emlen et al. 1975).

Black-capped (Poecile atricappilus) and Carolina (Poecile carolinensis) Chickadees are closely-related sibling species that are extremely similar in behavior and ecology (Brewer 1963). It is believed that they diverged approximately 2 million years ago (Gill et al. 1993), and are currently parapatrically distributed from the Appalachians in the east through the Midwest to Kansas. Narrow contact zones occur in some places along this boundary. Illinois is one of nine states where Black-capped and Carolina Chickadees co-occur (Tanner 1952, Brewer 1963, Rising 1968, Johnston 1971, Merritt 1978,

The songs of Carolina Chickadees (CC) and Black-capped Chickadees (BCC) are similar. The typical songs of each species are comprised of pure whistled tones that alternate between relatively high and low frequencies. The song of BCC consists of two-whistled notes with frequencies below 5 kHz (Fig. 1). Very little variation in BCC song exists over of the species’ extensive range, which covers most of northern North America (Kroodsma et al. 1995, Kroodsma et al. 1999). Deviations from the BCC norm are minor, with the most frequent being the addition of a second low note. Only in a few isolated BCC populations on the periphery of its range are there consistent, substantial deviations from the species’ typical song. However, even these deviations are minor compared to the variation occurring among CC populations (Ward 1966, Kroodsma et al. 1999).

Carolina chickadee songs usually contain four whistled notes, but can sometimes have more (Ward 1966). Regardless of note number, CC songs have the general form of alternating high and low whistled notes (Fig. 1.2 A) (Ward 1966). The most common CC song has two, 2-note phrases each with a high and a low note. The second phrase is usually sung at a lower frequency than the first (Fig. 1.2 A) (Smith 1972). Carolina songs in Illinois frequently contain non-whistled elements and one dialect type always includes them (Fig. 1.2 B) (Brewer 1963, Ward 1966, Smith 1972).
In this study, I mapped the location of the current distributions and contact zones of BCC and CC in Illinois based on the distributions of their song types. I compared this to the areas of sympatry and distributions described and mapped by Brewer (1963). Brewer established the distribution of these species in Illinois and the areas of contact between them in 1954-59 by mapping the distributions of whistled songs typical to each species, bilingual individuals, and “hybrid” song types. He described two contact zones in Illinois; one in Bond County and one in Fayette County. East of Vandalia he found that their distributions were alloparapatric, separated by 15 or more miles in some areas during the breeding season (Brewer 1963).

Methods

I recorded chickadee vocalizations at a total of 185 sites in 15 Illinois counties: Bond, Champaign, Clinton, Coles, Douglas, Effingham, Fayette, Iroquois, Madison, McCoupin, Montgomery, Moultrie, Piatt, Shelby, and Vermilion (Fig. 1.3). The majority of the songs were collected from 17 April –16 July 1999. Additional songs were collected in March 1997, and 1 June-20 July 1998. Each site was sampled once, unless no songs were recorded on the initial visit. In that case, the site was revisited. Most sites were within or near the Illinois contact zone as mapped by Brewer in 1954-1959 (Brewer 1963). These sites were most commonly riparian areas within an agricultural landscape and were chosen for accessibility, their location near Brewer’s contact zones, and their proximity to the boundaries of BCC and CC distributions based on Breeding Bird Survey maps (Sauer et al. 1999). In addition, samples of song types were collected 14 March-8
April 2000 from CC and BCC populations at sites distant enough from populations of the heterospecific chickadees (i.e., > 50 km away) to make their influence unlikely (Sattler 1996).

Collection of song at a site was initiated by the broadcast of a bait tape containing alternating bouts of CC and BCC songs from a hand held cassette recorder. These bouts were approximately 30 seconds long and contained 15 songs. The bait songs were taken from the Birds of eastern North America compact disc (Elliot et al. 1997). I entered woodlots that I had access to on foot and moved through them playing the bait tape until I heard a chickadee. I then continued playing the tape until I was close enough to record the chickadee(s). Sites that I could not gain foot access to were sampled from roadways adjacent to the woodlots. If I had not made contact with a chickadee after 30 min I would leave the site and move to the next one.

I typically recorded chickadees from 10 m away but the distance varied with terrain and wind conditions. Once I was within recording range of a chickadee, I stopped playing the bait tape and recorded five songs. Next, I played one more bout of each species' song and recorded five more songs. I continued to alternate between playing the bait tape and recording blocks of five songs until the 0.5 h sampling period had expired. All songs were recorded with a Merantz-PMD 222 recorder and a Senheiser parabolic microphone. If the chickadees were only giving calls, I recorded several examples and then tried to elicit song by playing the bait tape continuously until a chickadee began singing or the sampling period had expired. If a bird initially sang only a few songs and then stopped, I
would begin playing the bait tape again if its silence lasted for more than 1 min. If
the chickadee began singing again I resumed alternating between recording and
playing the bait tape. Songs were digitized on an Apple G3 power Macintosh and
the Canary program, version 1.2.4 (Chariff et al. 1995).

Both chickadee species sometimes use low amplitude, song-like
vocalizations that have functions other than loud territorial song (e.g., quiet fee-
bees) (Brewer 1963, Smith 1972, Ficken et al. 1978). In addition, juvenile
chickadees sing songs that are significantly lower in amplitude and oddly
constructed when compared to adult song and are easily distinguished from them
(Smith 1972, Ficken et al. 1978, Kroodsma et al. 1995). Therefore, to ensure that
all songs analyzed were the fully developed, territorial songs of adult chickadees,
only the songs of chickadees that sang loudly and consistently were analyzed.

I classified songs into song types by grouping songs unified by frequency,
duration, and note characteristics (McGregor and Krebs 1982). If a male had song
types that were very similar in all ways except for the addition or deletion of a
note or phrase these songs were classified as the same song type for analysis
(Sattler 1996). I considered a phrase to be a group of notes that occurred together
consistently within or among song types.

I classified all of the song types present at a site as BCC, CC or aberrant
based on a set of objective spectrographic criteria (OSC) (Table 1.1). The OSC
used frequency, duration, and note number to classify the songs. The OSC were
developed using published characteristics of CC and BCC songs as well as those
of CC and BCC songs I collected in Illinois (March 2000) (Ward 1966, Ficken et
al. 1978, Kroodsma et al. 1999, Lohr pers. comm.). Aberrant songs were ones classified as neither CC nor BCC that had unique features or features of both species. The aberrant song types were presumably the result of contact between BCC and CC. For songs that began with a phrase that contained (or were comprised entirely of) two whistled notes the following measurements were taken from spectrograms of five renditions of each song type; maximum frequency, phrase frequency range, note one frequency range, total phrase duration, latency to second note onset, offset frequency of note one, and onset frequency of note two (Robbins et al. 1986). If the quality of the recordings at a site were of very low quality they were not included. The pitch interval between notes one and two was calculated by dividing the offset frequency of note one by the onset frequency of note two. The mean values (based on the 5 renditions) of these eight variables were used in discriminant function analysis (SAS 1998). Song types for which I did not have at least 5 useable copies from a site were not measured or analyzed using the discriminant function.

Presumed BCC songs were collected March 2000 from areas >50 km northwest of areas where I had recorded chickadees singing songs other than the BCC song type only. I collected presumed CC songs in areas >50 km south and southeast of areas where I had found chickadees singing only the BCC song type. I termed these "parental" songs because they were expected to be from populations of entirely CC or BCC. The parental songs were subjected to a discriminant function analysis using the 8 variables described above (SAS 1998). The two functions that resulted (denoted as D1 for BCC and D2 for CC) were
then used to generate two discriminant function scores for each potential contact zone song type. Potential contact zone song types were ones that had been collected within a 50 km band centered around the line of contact. The ratio of D1 and D2 for each song type was used to classify these song types as CC, BCC or intermediate. The parental CC samples collected to develop the discriminant function had D1/D2 ratios of 0.965-0.985 and the BCC parental samples ranged between 1.012 and 1.030. Thus, songs that had D1/D2 ratios between 0.991 and 1.010 were classified as intermediate, and considered to potentially be the result of contact between BCC and CC. In some cases the discriminant function and the OSC did not agree in the classification of a song type for an individual or site. In such cases, I used the OSC to classify song bouts because these criteria took into consideration characteristics of the entire song whereas the discriminant function was applied to measurements from only the first two notes. For many of the song types, the first two whistled notes comprised only half or less of the song’s total length.

To establish the locations of hybrid zones, I mapped the sites where evidence of cultural interaction was present. I used the presence of the any of the following at a site as an indication of cultural interaction between these species; 1) the presence of individuals singing both CC and BCC songs at the same site, 2) bilingual individuals, 3) songs having intermediate discriminant function scores, 4) songs incorporating characteristics of both species’ songs or 5) aberrant song types. I generated a line of contact by mapping sites at which only either BCC or CC song types occurred and then drawing a line equidistant between the BCC and
CC sites closest to each other. This line approximates the division between BCC-dominated and CC-dominated regions in Illinois.

Results

I found that both Black-capped and Carolina Chickadee song types, and therefore almost certainly both species co-occur in 15 counties in Illinois during the breeding season. The line of contact I developed ran from an area near St. Louis on the Mississippi River to central Iroquois County on the Indiana border (Fig. 1.3). A line of contact based on Brewer’s figure 1 (1963), is very similar to the one developed in this study (Fig 1.3). In southwestern Illinois the apparent difference in these two contact lines may be due to the small number of sites sampled for each study in that region. BCC have moved into the Champaign-Urbana area in Champaign County, presumably from the north or west. Brewer found that these species were allopatric east of Vandalia in central Fayette County (Fig. 1.3). There are now at least three areas east of Vandalia where there is evidence of cultural interaction between these species (Shelby, Douglas and Champaign counties) (Fig. 1.4).

There are actual contact zones in Bond, Fayette, Shelby, Douglas, Champaign and Montgomery counties (Fig. 1.4). Individuals with at least one song type that was classified as a CC and one classified as a BCC were considered bilingual. Six bilingual singers occurred in the largest contact zone in Bond, Fayette and Montgomery counties. The largest contact zone encompassed the contact zones described by Brewer in Bond and Fayette counties. The other three contact zones in Shelby, Douglas, were Champaign counties were relatively
small. Aberrant song types occurred in each of the four contact zones. I recorded 31 song types that were intermediate or aberrant in the contact zones (Fig. 1.5, App. I). Of the 190 contact zone songs that were analyzed using the discriminant function, 89 had CC ratios, 49 had BC ratios, and 52 had intermediate ratios (Fig. 1.6). The majority of these intermediate songs were distributed within the contact zones (Fig. 1.7). The intermediate song bouts that fell outside of the zone were almost all of song type 16, which was also common in the contact zones. There were two instances where songs classified as intermediate by the discriminant function were classified as parental songs by the OSC. These were bouts of BCC song in which the songs were shorter than normal. These two bouts were from poor quality recordings making the judgement of the beginnings and ends of notes difficult. This probably explains the shorter duration of each and probably the intermediate scores. There were nine aberrant song types that were classified as intermediate by the discriminant function (App. I: types 4, 12, 13, 14, 15, 18, 19, 20, 21, and 22). Each of these songs began with a two-note whistled phrase that was nearly identical to song 16 in frequency and duration characteristics. Song type 16 has been recorded in other studies both within and on the Carolina sides of other BCC/CC contact zones (Sattler et al. 1996).

Discussion

Because a genetic survey was not part of this study, I did not know the genetic ancestry of any of the birds from which I recorded song. However, I believe the song-based contact zone generated by this study accurately reflects the distribution of the genetic contact zones between these chickadee species in
Illinois. Sattler (1996), for example, established that bilingual singing and aberrant songs were tightly associated with contact zones between these species and exhibited a narrower cline width than did some genetic markers used to identify hybrids.

There are some differences in the distribution of Black-capped and Carolina Chickadees as estimated by this study of chickadee singing patterns and the one carried out in Illinois in 1954-59 by Brewer (1963). For example, Brewer reported that these species were not sympatric in Illinois east of Vandalia. However, I found evidence of contact in three counties east of Vandalia (Shelby, Douglas and Champaign counties). The contact in Champaign County appears to be due to recent movement of Black-capped Chickadees into the area around Champaign and Urbana most likely from the north, west, or both. These differences between the contact zones are probably due to some movement of chickadees (e.g. Champaign County), the larger number sites sampled in this study, and differences in methodology.

There were a number of methodological differences between this study and Brewer’s. I followed chickadees for a half-hour, recording vocalizations and using playback of both chickadee species to elicit responses. Brewer found singing chickadees without playback and noted the types of songs they sang. He did not have the benefit of measuring and studying spectrograms of the chickadee songs. Analyzing the spectrograms allowed me to identify some aberrant and intermediate songs that were not obviously so to the ear. Black-capped Chickadees seem to song match with other males by singing their songs on about
the same frequency as playback (Hill and Lein 1987). Mountain chickadees, a close relative of BCC and CC, also match song types (Wiebe 1995). I believe the stimulus of the playback songs I played made it more likely for me to be exposed to and record a chickadee’s entire repertoire, especially if contact zone chickadees tried to song match. It is likely that had I followed chickadees for longer time periods some individuals would have sung song types that I did not record for them. This also means that the distribution of aberrant and bilingual singing and consequently the contact zone may be underrepresented in some areas. Brewer’s map (Fig. 1, 1963) showed 37 sites whereas my study included 151 sites plus 34 parental sites. This difference in site numbers and, therefore, resolution may also explain some of the differences between the studies. For example, I found a pocket of aberrant song types in Shelby County. This pocket may have been there in the 1950s because Brewer did not sample this area.

The Illinois contact zone mostly passes through intensively farmed areas. Therefore, source populations of the parental chickadee species are not always adjacent to the woodlots that often comprised the only chickadee habitat in the contact zone. Due to the apparent low fitness of hybrid chickadees, hybrid chickadee populations are thought to rely on emigration of Carolina and Black-capped Chickadees to maintain their numbers (Saway 1990, Sattler 1996). BCC usually only disperse a few km from their natal areas and CC may be even more sedentary (Ward 1966, Weise and Meyer 1979). This limited dispersal means that isolated areas that harbor hybrid zone populations of chickadees may receive few parental immigrants from populations of Carolina and Black-capped Chickadees.
If dispersal of parental types is infrequent into a small population of hybrid chickadees, that population may be unstable and potentially short-lived. If a small hybrid population becomes extinct, a population comprised of one of the parental species could replace it. This new parental population may then receive dispersing members of the heterospecific chickadee species leading to the reestablishment of a hybrid population dependent on the support of parental individuals and the cycle could be repeated. Thus, studies sampling these areas may draw different conclusions depending on when they are conducted. If these scenarios of genetic and cultural turnover occur, they could explain some of the small-scale differences between this and Brewer’s study.

Finally some changes in the contact zone may be the result of habitat changes outside the contact zone. A loss of habitat on one side or the other of the zone could decrease the number of Carolina or Black-capped Chickadees dispersing into the hybrid zone. Over time the hybrid population would become swamped by the species with which it maintained contact and a new hybrid zone could be established towards the side where the habitat had been lost. This scenario could result in the presence of islands of aberrant songs within what have become basically unmixed parental populations. The occurrence of song 16 outside of the contact zones may be an example of this phenomenon. This song type is present at least 20 km within the distribution of CC from the line of contact in Illinois. If the contact zone shifted northward, this song type may have been adopted by some of the CC populations as they replaced the hybrid zone populations.
Overall, however, the Illinois contact zone between Black-capped (*P. atricapillus*) and Carolina (*P. carolinensis*) Chickadees has moved very little over the past 40 years. The stability of the contact zone suggests that the ecological, physiological, genetic, and/or behavioral factors that interact to influence the distribution of these species have not changed significantly in Illinois during this time period. A general trend of northward movement of Carolina chickadees has been reported (Peterjohn 1989, Sattler 1996). However, I did not find evidence of the expansion of Carolina song culture to the north as would seem likely if their range had expanded northward in Illinois. The Bond/Fayette/Montgomery hybrid zone has probably increased in size since Brewer's study, possibly due to an increased influx of CC into the former contact zone. If there were enough chickadees present in the contact zones, perhaps their dialect could be adopted by the CC as they expanded north. If an influx of CC into the largest contact zone had created a CC-dominated population perhaps dispersal by these CC, using the contact zone song cultures, into BCC areas would create new contact zones.
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Table 1.1. The objective spectrographic criteria used to classify song bouts as Black-capped Chickadee (BCC), Carolina Chickadee (CC) or aberrant. The pitch interval is the ratio of the offset of the first note divided by the onset frequency of the second in kilohertz (kHz).

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<th>Characteristic</th>
<th>BCC</th>
<th>CC</th>
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<td>Maximum song frequency (kHz)</td>
<td>≤ 5</td>
<td>6-11</td>
</tr>
<tr>
<td>Pitch Interval (note 1/note 2)</td>
<td>1.10-1.30</td>
<td>1.23-2.02</td>
</tr>
<tr>
<td>Total note number per song</td>
<td>2</td>
<td>3-20</td>
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<tr>
<td>Non-whistled elements</td>
<td>never</td>
<td>frequently</td>
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<tr>
<td>Phrases with a note in both the 4-5 kHz range and &gt; 6kHz</td>
<td>never</td>
<td>usually</td>
</tr>
<tr>
<td>Phrase duration (ms)</td>
<td>&gt;800</td>
<td>variable</td>
</tr>
</tbody>
</table>

(mean = 600ms)
Figure 1.1. A spectrogram (top) of a Black-capped Chickadee song plotting time in milliseconds (ms) versus frequency in kilohertz (kHz). A waveform plotting song power in micropascals (uPa) of pressure versus time is on the bottom. The amplitude modulation in the middle of the second note is a highly stereotyped feature. The number above song in all spectrograms corresponds to the number of each song type in Appendix I.

Figure 1.2. Two examples of Carolina Chickadee song; A) This is an example of the Carolina Chickadee song that is the most common in Illinois. B) An example of Carolina Chickadee song dialect from southern Illinois in which the fourth note is a rapid buzz.
Figure 1.3. The sites where I found only Black-capped Chickadee (BCC) song (open circles) and Carolina Chickadee (CC) song (crosses). The sites where Brewer found only BCC song (black circles) and CC (black squares) also shown. My line of contact is represented by the solid line and a line of contact based on Brewer’s study is represented by the dashed line.
Figure 1.4. The locations of the four contact zones between Black-capped and Carolina Chickadees in Illinois, as determined by this study.
Figure 1.5. Some of the aberrant song types present in the Illinois contact zones. The numbers above each spectrogram are the song numbers listed for these song types in Appendix 1.
Figure 1.6. The distribution of parental (light) and potential hybrid (dark) song bouts into sixteen categories based on their discriminant function scores. The D1/D2 ratio was developed based on parental songs with D1 being for Black-capped Chickadees and D2 being for Carolina Chickadees (see text for more details).
Figure 1.7. The distribution of intermediate songs (asterisks) based on the discriminant function results. Most occurred in the largest contact zone in Bond, Fayette and Montgomery counties.

**Abstract**

I studied the singing behavior of the closely related Black-capped (*Poecile atricapillus*) and Carolina (*Poecile carolinensis*) Chickadees along their range interface in central Illinois. The majority of the songs studied were collected 17 April – 16 July 1999 in fifteen counties throughout central Illinois. The songs collected at a site were segregated into song types based on similarities in the structure of their constituent notes and phrases. I developed a set of objective spectrographic criteria (OSC) that used the frequency, duration, and basic structural characteristics of each song type to classify them as Black-capped Chickadee, Carolina Chickadee or aberrant. The greatest diversity of song types was present in the largest contact zone that encompassed parts of Bond, Fayette, and Montgomery counties. I found three unique song dialects, one each in Bond, Fayette, and Shelby counties. The Vandalia dialect (Fayette Co.) is probably at least 40 years old (Brewer 1959). I used the song types present at each site to sort them into repertoire categories based on the overall combination of song types present. Repertoire analysis revealed that bilingual singing was widespread and that individuals which sang both CC and aberrant song types containing high frequency (>6kHz) whistled notes or both BCC and songs containing only low frequency (<5 kHz) whistled notes were concentrated in specific, but mutually exclusive, areas. The presence of patterns in the distribution of aberrant song types and repertoire constitution in these contact zones suggests that the interaction of
Black-capped and Carolina Chickadees has led to the development of unique song cultures in at least some contact zones.

**Introduction**

Cultural hybrid or contact zones result from the sympatry of individuals from different variants of a cultural tradition of a learned trait such as the songs of passerine birds (Order Passeriformes, Suborder Passeri). The cultural entities interacting in hybrid zones may be dialect types within a species or the songs of distinct species (Bjerke 1982, Emlen 1975, Martens 1996). Interactions in passerine hybrid zones can lead to the presence of aberrant or intermediate song types and bilingual individuals (Brewer 1959, Emlen et al. 1975, Robbins et al. 1986, Martens 1996).

Passerines always learn their songs (Clayton 1989). The fact that song is learned gives it the potential to be an indicator of behavioral and cultural interactions between groups with different cultural traditions (Clayton 1989, Martens 1992). Song is usually the most complex vocalization of a passerine species and is given exclusively or most frequently by males (Ficken 1990). The timing and duration of song learning varies among species (Kroodsma et al. 1995, O’Loghlen 1995). Song learning is often completed during the first breeding season, however, in some species modification of songs may occur between the first and second breeding season or throughout life (Derrickson 1984, Kroodsma et al. 1999b).

Black-capped (BCC) and Carolina (CC) Chickadees are closely related sibling species that are extremely similar in behavior and ecology (Brewer 1963, Kroodsma et al. 1995). The construction of their songs and calls and the contexts in which each type of vocalization is used seem to be homologous (Haftorn et al. 1998). The songs
of these species in their contact zones have been well studied and have proven to be indicative of areas where hybridization is occurring between them (Sattler 1996).

The song of the BCC (Fig. 2.1 A) is highly stereotyped over nearly all of its extensive range which encompasses most of northern North America (Kroodsma et al. 1999a). Their songs do not have regional, dialectical variants, which occur in many other species of passerines including CC (Ward 1966, Kroodsma et al. 1999a). CC song is less stereotyped than BCC song, however, a general song form does predominate throughout its range. The most common CC song (Fig. 2.1 B) can be broken down into two phrases each of which is similar to a BCC song in that both are basically comprised of a high whistle followed by a lower whistle. The second CC phrase is usually given at a lower frequency than the first (Ward 1966, Smith 1972).

The timing of Carolina and Black-capped Chickadee song learning in the wild is unknown, although it has been suggested that post-fledging interactions with adults are important to BCC song learning (Kroodsma et al. 1999a). Captive-raised CC and BCC males exposed to taped songs from adult males in the absence of live adult male tutors or adult females developed aberrant songs (Kroodsma et al. 1995), supporting the notion that interactions with adults are important for song development in these chickadees.

This study documents the patterns of singing behavior occurring in the four BCC and CC contact zones that occur in Illinois (Chapter 1). In this chapter, I describe the song types that were present and map their distributions and propose their possible origins and functions.
Methods

I recorded samples of chickadee vocalizations at 185 sites in fifteen Illinois counties: Bond, Champaign, Clinton Coles, Douglas, Effingham, Fayette, Iroquois, Madison, McCoupin, Montgomery, Moultrie, Piatt, Shelby, and Vermilion. The majority of the songs were collected from 17 April –16 July 1999. Additional songs were collected in March 1997, June–20 July 1998, and 14 March–8 April 2000. Each site was sampled once, unless no songs were recorded on the initial visit in which case the site was revisited. Most sites were within or near the Illinois contact zone as mapped by Brewer in 1954-1959 (Brewer 1963). These sites were most commonly riparian areas within an agricultural landscape and were chosen for accessibility and their location near Brewer’s contact zone. In addition to the 151 sites, samples of song types were collected from CC and BCC populations at 34 sites distant enough from populations of the herterospecific chickadee (i.e. > 50 km away) to make their influence unlikely (Robbins et al. 1986, Sattler 1996).

Collection of song at a site was initiated by the broadcast of a bait tape containing alternating bouts of CC and BCC songs from a hand held RCA cassette recorder. The bait songs were taken from Elliot et al. (1997). I entered woodlots that I had access to on foot and moved through them playing the bait tape until I heard a chickadee. I then continued playing the tape until I was close enough to record the chickadee(s). Sites that I could not gain foot access to were sampled from roadways adjacent to the woodlots. If I had not located a chickadee after 30 min, I would leave the site and move to the next one.
I typically recorded chickadees from approximately 10 m away but the distance varied with terrain and wind conditions. Once I was within recording range of a chickadee, I stopped playing the bait tape and recorded five songs. Next, I played one more bout of each species’ song and recorded five more songs. I continued to alternate between playing the bait tape and recording blocks of five songs until the 0.5 h sampling period had expired. All songs were recorded with a Merantz-PMD 222 recorder and a Senheiser parabolic microphone. If the chickadees were only giving calls, I recorded several examples and then tried to elicit song by playing the bait tape continuously until a chickadee began singing or the sampling period had expired. If a bird initially sang only a few songs and then stopped, I would play the bait tape again if its silence lasted for more than 1 min. If the chickadee began singing again, I resumed alternating between recording and playing the bait tape. Songs were digitized on an Apple G3 power Mac and the Canary program, version 1.2.4 (Chariff et al. 1995).

Both chickadee species sometimes use low amplitude, song-like vocalizations which have functions other than loud, territorial song, (e.g., quiet fee-bees) (Brewer 1963, Smith 1972, Ficken et al. 1978). In addition, songs of juvenile chickadees are significantly lower in amplitude and oddly constructed when compared to adult song (Ficken et al. 1978, Smith 1972, Kroodsma et al. 1995). To ensure that all the songs that I analyzed were the fully developed territorial songs of adult chickadees, only the songs of chickadees that sang loudly and consistently were analyzed.

I classified songs into song types by grouping ones unified by frequency, duration, and note characteristics (McGregor and Krebs 1982). If a male had songs
that were very similar in all ways except for the addition or deletion of a phrase, these songs were classified as the same song type for analysis (Sattler 1996). I considered a phrase to be a group of notes that occurred together in the same order consistently within song types (McGregor and Krebs 1982). In order to document dialect patterns that might have existed in the contact zone, I grouped similar song types together and mapped their distributions. Dialects were considered to be a group of song types that shared distinctive features and were unique to a locality (Lemon 1975).

I classified all of the song types present at each site as BCC, CC or aberrant based on a set of objective spectrographic criteria (OSC) (Table 2.1). The OSC used frequency, duration, and note number to classify the song bouts. I considered a song bout to be all of the individual songs that had been grouped into the same song type at a site. The OSC was developed using known characteristics of CC and BCC songs as well as those of CC and BCC songs I collected in Illinois (Ward 1966, Kroodsma et al. 1999a, Lohr pers. comm.). Aberrant songs were considered those that shared features of both BCC and CC songs or exhibited unique characteristics.

After individual song bouts had been classified as BCC, CC, or aberrant, I then classified all sites on the basis of the repertoires of the male chickadees present (Table 2.2). When more than one male was present the repertoires of all of the males were considered in order to classify the site as BCC, CC, or aberrant. I mapped the distributions of the seven repertoire categories in order to discern more general patterns of song culture in the contact zone.
Results

Of 208 song bouts, 46 were classified as BCC, 96 as CC, and 66 as aberrant based on the OSC. These 66 aberrant bouts represented 31 song types sung by chickadees in the Illinois contact zones (Appendix I). The classification of the aberrant song bouts into types suggested that dialect patterns existed within the contact zones. The “Vandalia” dialect consisted of eight aberrant song types (Fig. 2.3) distributed between six sites in central Fayette County (Fig. 2.4). These songs were united into a dialect by the presence of a three note whistled phrase that was modified in some cases. The first note of the phrase was a quickly descending, whistled note beginning at approximately 9 kilohertz (kHz), the second a mid-frequency whistled note at ~5 kHz, and the last a whistled note at ~4 kHz. These songs also tended to have clicks incorporated into their phrases. The Vandalia song types were also unified by geography as all occurred within 15 km of Vandalia, Illinois.

There was, however, in the ways the Vandalia songs were constructed. For example, there was a male in Fayette County that sang song types 22, 23, 24, and 25 (Fig. 2.4 B-E). A comparison of the phrases that comprised each song revealed that phrases 3-5 of song 22 were the same phrase type as phrase 2 of song 23 and phrases 1 and 5 of song 24, although song 24 had an introductory note added to phrase 1. This phrase, shared by songs 22, 23, and 24, was used in conjunction with other phrase types unique to each of these 3 songs. On the level of individual notes, phrases 2-6 of song 21 seem to be the result of the deletion of the mid-frequency note of phrases 3 and 4 of song 24.
The “Greenville” song dialect consisted of two basic aberrant song types (Fig 2.5) and was limited to north-central Bond County (Fig. 2.4). These songs contained pure whistled notes that were all below 5 kHz. The Greenville dialect songs began with a two-note phrase that was very similar to song type 4 (Fig. 2.6). Most of Greenville aberrant songs included a very short duration, broad frequency note (a “click”) prior to the third note and fifth note (if present). A comparison of songs 13 (Fig. 2.5) and 16 (Fig. 2.7) suggests that Greenville songs may be the result of a compression of the frequency ratio between notes three and four in song 16. There are variants of song 16 in which the third note is a pure whistle with a click proceeding; these are very similar to the ones that occur in the Greenville dialect.

Monotonal song types (Fig. 2.8) were made up entirely of relatively low (<4 kHz) frequency whistled notes, with pitch intervals near 1.0 for notes one and two. They had a broader distribution than either the Vandalia or Greenville aberrant song dialects and may not represent a unified dialect (see discussion) (Fig. 2.9). The “Shelby” aberrant song dialect contained phrases with three notes in which the beginning of the second note of the phrase was a trill (Fig. 2.10). These song types were limited to three sites in northeastern Shelby County (Fig. 2.11).

The most widely distributed aberrant song type was song 16 (Fig. 2.7). This song began with two whistled notes that had frequency characteristics very similar to those of a BCC song, but this phrase was consistently shorter in duration than a BCC song. The first phrase of song 16 also occurs alone as song 4, basically a truncated BCC song (Fig. 2.6).
Song 35 (Fig. 2.12) was collected in the contact zone at one site in western Douglas county. It is most likely an example of the “hi-lo” call described for BCC and a close relative of BCC and CC, the Willow Tit (*Parus montanus*) (Haftorn et al. 1998). Like the hi-lo call, the high notes of this vocalization are chevron shaped and may be derived from the introductory note of the “chick-a-dee-dee” call.

Inspection of some of the aberrant songs suggested that they are combinatorial in nature. Combinatorial songs occur if sets of note types or phrases are combined in different ways that create unique song types (Ficken 1990). Song types 4 (Fig. 2.6) and 16 (Fig. 2.7) suggested combinatorial singing behavior because song 4 occurs as a stand-alone song and as the first two notes of song 16. Similarly, song types 18 and 34 (Fig. 2.13) are from the same site within the Bond County contact zone. The last three notes of song 18 occur at the end of the first two phrases in song 34.

Figure 2.14 shows the distribution of sites with only BCC (repertoire category 1) or CC (repertoire category 2) song types in their repertoires based on the OSC. Individuals in these two repertoire categories did not co-occur at any of the sites I sampled. The closest proximity of these two repertoire types occurred in Champaign County where they were separated by only a few km and may co-occur in places. Repertoire categories 3-8 basically occurred in areas between categories 1 and 2 (Fig. 2.15). Repertoire category 3 (bilingual) occurred in Bond, Douglas, Fayette and Montgomery counties. Category 4 sites (modified bilingual) occurred in Bond, Champaign, and Shelby counties. Repertoire category 5 (CC & aberrant) was concentrated in Fayette County, but also occurred in Shelby, Douglas, and Champaign counties. Category type 6 was limited to one site in northern Bond County and three
in Montgomery County. The distribution of the low aberrant repertoire category 7 was limited to three sites within the distribution of the Greenville dialect and these males sang only Greenville aberrant song variants (Fig. 2.15). Repertoire category 8 (high aberrant) was limited to Fayette and Shelby counties; these songs were ones in the Vandalia and Shelby dialects, respectively. Repertoire types 5 (CC and aberrant) and 8 (high aberrant) occurred in close association in Fayette and Shelby counties (Fig. 2.15).

Discussion

The derivation of some of the aberrant song types seems straightforward. The Vandalia and Shelby three note, aberrant song phrases seemed to be based on variation that is present in the songs of Carolina chickadees. In some cases this link is very clear (Fig. 2.16), which illustrates how the three note phrases common to the Vandalia song types were most likely created by the modification of the first phrase of the most common CC song type (Fig. 2.1A). The middle frequency notes present in most of the song types in the Vandalia dialect can clearly be seen in song 38 (Fig. 2.17), which was collected in a population of CC in Vermilion county. This type of song is part of a CC dialect which I found in Champaign, Vermilion and Iroquois counties. This song type also occurred in the contact zone in Champaign and Shelby counties.

The construction of song 16 suggests a combination of the features of BCC songs (phrase 1) with those of CC songs (phrase 2) (Fig. 2.7). Songs of this general type have been identified in previous studies of CC/BCC contact zone singing and were most common near contact zones (Robbins et al. 1986, Sattler 1996) This is also true in Illinois (Fig. 2.18). Song type 4 sounded very much like a somewhat truncated
BCC song and seemed to be identical to the first phrase of song 16. Song type 4 was only used by males that also sang song type 16 (2.19). These males sang song type 4 loudly and frequently, suggesting that it was not the result of incomplete attempts to sing song 16 by unmotivated singers.

Brewer reported aberrant singing behavior in Bond County and around Vandalia in Fayette County. He described one song that occurred in Vandalia with the mnemonic “fee-be-deekee-deekee”. This seems to be very similar to song type 22 of the Vandalia dialect (Fig. 2.3 B). Thus, aberrant singing behavior and perhaps even specific song types have probably existed around and in Bond and Fayette counties for at least 40 years. The presence of dialect types in these areas suggests that at least some aberrant song types are representative of unique song cultures that have resulted from long-term interactions between Black-capped and Carolina Chickadees. Aberrant song types have been documented for other chickadee contact zones (Sattler 1996). However, distinct suites of aberrant song types constituting discrete cultural units (dialects) have not been noted. The major dialect types (i.e., Vandalia and Greenville) both occur in the largest contact zone. The presence of these dialects may be due to the size and perhaps age of the Bond/Fayette/Montgomery contact zone. If this contact zone has existed for a long period of time it may have allowed the sustained interaction of BCC and CC song traditions, perhaps helping to promote the unique song dialects. The size of the contact zone could have aided in its persistence. Its size may be the result of relatively large amounts of suitable habitat for chickadees in the this region.
There are several hypotheses for the development and presence of aberrant singing behaviors in contact zones. The two major hypotheses are (1) that they have been culturally selected for or (2) that they are epiphenominal.

Hypothesis no. 1: The aberrant songs have characteristics that have encouraged their perpetuation in contact zone areas.

This could explain the presence of song types that either incorporate characteristics of both species or posses unique characteristics that may allow them to operate as effective signals to both CC and BCC. These types of songs would maximize the efficiency of a chickadee's singing output in areas where the cultural background of the chickadees encountered is variable. The song types that began with a relatively low frequency, two-note whistled phrase (suggesting a shortened BCC song), followed by phrases that were either typical Carolina phrases or ones derived from them may fit this pattern and support this hypothesis (e.g., song types 16, 18, 19, 20, 21, 22, App I.).

Playback experiments in CC and BCC populations distant from the contact zones could test the effectiveness of the song types that seem to incorporate features of each species’ song types relative to conspecific and heterospecific chickadee song. However, if these songs proved to be more effective than heterospecific song it may not necessarily mean they have become established in the contact zone because of their broader effectiveness as chickadee signals. It may be that their construction is the result of the conflicting song models that co-occur in contact zone. These songs may have occurred irrespective of their effectiveness as signals to the chickadees of variable cultural backgrounds potentially encountered in the contact zones.
The Vandalia song types may trigger responses from chickadees regardless of their cultural background because of their unique structural characteristics. Responses of chickadees from outside of the contact zone may not be because these songs are similar to the songs of either CC or BCC. The repetitious construction and broad frequency coverage of the Vandalia songs is shared with the chick-a-dee call, gargle (rasp) call (Fig. 2.20), and the hi-lo (Haftom et. al. 1998) calls of chickadees (Fig 2.12). These similarities between Vandalia phrases and different types of chickadee calls may make the Vandalia aberrant songs effective in encounters with chickadees of variable cultural backgrounds, if not as songs, then perhaps as aggressive calls.

Hypothesis no. 2. The aberrant songs are epiphenominal.

Cultural drift due to the accumulation of errors during the song learning process may have contributed to patterns of singing behavior present in the Illinois contact zones (Bjerke 1982). Especially in the smaller contact zones the aberrant songs may be due to cultural drift within a small, isolated population of one of these species (Kroodsma et al. 1999a). In some parts of the contact zone, chickadees are limited to small isolated pockets of habitat. Therefore, since chickadees generally do not disperse great distances, these populations would be expected to receive few immigrants, perhaps contributing to the development of aberrant song types (Weise and Meyer 1979). The immigration of BCC between populations is believed to be one factor promoting the remarkable stereotypy of their song over the majority of their range due to an averaging of songs between sub-populations (Kroodsma et al. 1999a). Another possible cause of aberrant songs is the influence of conflicting song models due to the possible influence of chickadees singing BCC, CC and aberrant song types (Bjerke
Post fledging interactions may also explain the presence of some aberrant song types if chickadee song learning includes interactions with chickadees after dispersal from the natal area. Males from populations singing one of the parental songs may disperse into the contact zone and develop aberrant songs in addition to or exclusively while attempting to match the songs of males in the contact zone.

There are many questions that this study has raised that can only be answered by playback and aviary experiments. For example, what is necessary for a full species response to song in the contact zone individuals and more specifically ones that use one of the aberrant song dialects? Is the low BCC-like introductory phrase of song types 16, 18, 19, 20, 21, 22 effective as a signal to populations of BCC and CC away from the contact zone? Are the click-whistle phrases present in many of the Greenville song types adequate to elicit full responses from CC? How do populations of BCC and CC respond to the Vandalia song types with complex repeating phrases? What is the exact timing of chickadee song learning? Will CC or BCC that have been taken just prior to fledging learn aberrant song types if housed with adults of Vandalia or Greenville dialects? There are varying degrees of selection for the different genetic loci studied in hybridizing CC and BCC (Sattler 1996). Does a similar phenomenon occur for their vocal repertoires? These chickadees share most if not all of the same basic vocalization types. Hybrid singing is limited to areas closely associated with the genetic hybrid zone. Is this true of all of their vocalizations? How do chick-a-dee calls vary in and near the hybrid zone? Gargle dialects occur and are limited to small areas. Is there a unique gargle complex in these hybrid zones and how similar is it to those
of adjacent populations of either population? How do pair-limited call types (e.g. sexual gargles) vary in relation to contact zones?

In conclusion, the total of 31 aberrant song types occurring in the Illinois contact zones represents the greatest diversity in singing behavior documented thus far for these species in their mutual hybrid zones (Brewer 1963, Robbins et al. 1986, Sattler 1996). The presence of unique song types and of dialects in the contact zone that combine the characteristics of both BCC and CC song types indicates that in areas of sympathy the song cultures of these species have interacted leading to singing behaviors that are unlike those of either parental species.
Literature Cited


Haftorn, S., W. Huang, C. K. Griswold, and J. P. Hailman, J.P. 1998. Independent discoveries of a new apparently homologous call in the
Willow tit *Parus montanus* and Black-capped Chickadee *Parus atricapillus*. Ibis 140:174-176


Table 2.1. The objective spectrographic criteria used to classify song bouts as Black-capped Chickadee, Carolina Chickadee or aberrant. The pitch interval is the ratio of the offset of the first note divided by the onset frequency of the second in kilohertz (kHz).

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>BCC</th>
<th>CC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum song frequency (kHz)</td>
<td>≤ 5</td>
<td>6-11</td>
</tr>
<tr>
<td>Pitch Interval (note 1/note 2)</td>
<td>1.10-1.30</td>
<td>1.23-2.02</td>
</tr>
<tr>
<td>Total note number per song</td>
<td>2 (rarely 3)</td>
<td>3-20 (usually 4)</td>
</tr>
<tr>
<td>Non-whistled elements</td>
<td>never</td>
<td>frequently</td>
</tr>
<tr>
<td>Phrases with a note in the 4-5 kHz range and &gt; 6kHz</td>
<td>never</td>
<td>usually</td>
</tr>
<tr>
<td>Phrase duration (ms)</td>
<td>&gt;800</td>
<td>variable (mean = 600ms)</td>
</tr>
</tbody>
</table>
Table 2.2. The eight categories of site repertoire classification and the criteria that defined each.

<table>
<thead>
<tr>
<th>Category</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) BCC(^{\text{\textbullet}}) only</td>
<td>The only songs present were classified as BCC on the basis of the OSC.</td>
</tr>
<tr>
<td>2) CC(^{\text{\textbullet}}) Only</td>
<td>The only songs present were classified as CC on the basis of the OSC.</td>
</tr>
<tr>
<td>3) Bilingual</td>
<td>Both song types classified as CC and BCC on the basis of the OSC were present. Aberrant song types may have also been present.</td>
</tr>
<tr>
<td>4) Modified bilingual</td>
<td>At least one song type was present within which all of the whistled elements were less than or equal to 5.25 kHz. In addition there was at least one song type within which there occurred a phrase with one whistled note above 6 kHz. Aberrant song types may have also been present.</td>
</tr>
<tr>
<td>5) CC and aberrant</td>
<td>Song type(s) which was classified as CC on the basis of OSC and DF are present as was a song type(s) which was classified as aberrant by the OSC.</td>
</tr>
<tr>
<td>6) BCC and aberrant</td>
<td>A song type that was classified as BCC by the OSC and DF is present in the repertoire as is a song that was classified as aberrant by the OSC and DF if the DF was applicable.</td>
</tr>
<tr>
<td>7) Low frequency aberrant</td>
<td>Only aberrant song types in which all whistled notes were below 5 kHz are present.</td>
</tr>
<tr>
<td>8) High frequency aberrant</td>
<td>Only aberrant song types were present and each type had a peak frequency above 5 kHz.</td>
</tr>
</tbody>
</table>

\(^{\text{\textbullet}}\)BCC=Black-capped Chickadee, \(^{\text{\textbullet}}\)CC=Carolina Chickadee, \(^{\text{\textbullet}}\)OSC=objective spectrographic criteria (see text), \(^{\text{\textbullet}}\)DF=discriminant function analysis (see text).
Figure 2.1. A) The song of the Black-capped Chickadee; the top box is a spectrogram that plots time in milliseconds (ms) vs. frequency in kilohertz (kHz). The bottom box is a waveform that shows the relative strength of the signal in micropascals (uPa) of pressure over time. The frequency modulation in the middle of the second note is typical.

B) A spectrogram of the most common song form of the Carolina Chickadee in Illinois. The numbers on these and all later spectrograms denote the number of each song type in Appendix I.
Figure 2.2. The Illinois contact zones of Carolina and Black-capped Chickadees, as determined by the distribution of bilingual chickadees and ones singing aberrant song types.
Figure 2.3. The eight song types (A-I) that comprise the "Vandalia dialect". The number and letter combinations on the spectrograms correspond to the designation of each song in Appendix I.; detailed information about each can be found there. The numbers within the spectrograms below the songs correspond to the phrase number of each.
Figure 2.4. Distribution of the "Vandalia" (black dots, songs 21-28) and "Greenville" (black x's, songs 12-15) aberrant song dialects.
Figure 2.5. Two variants of the “Greenville” dialect song type.

Figure 2.6. Song type 4.

Figure 2.7. An example of song type 15, a possible aberrant song type.

Figure 2.8. An example of the monoton, song type with a pitch interval of ~1.
Figure 2.9. The distribution of song type 9.

Figure 2.10. An example of the “Shelby” aberrant dialect.

Figure 2.11. Distribution of song type 32.
Figure 2.12. Two phrases of “song type” 35, which is most likely a chickadee “hi-lo” call and not a song. Each vocalization was comprised of four to six identical phrases.

Figure 2.13 Song types 18 and 34, both from the same site in Bond Co., showing combinatorial singing behavior on the phrase level. The last three notes of song 18 are nearly identical to the three note units which punctuate the first two phrases of song 34.
Figure 2.14. Distributions of repertoire category 1 sites with only Black-capped Chickadee song present (black dots) and category 2 sites with only Carolina Chickadee song types present (stars).
Figure 2.15. The distributions of repertoire categories 3 (bilingual), 4 (modified bilingual), 5 (Carolina Chickadee & aberrant), 6 (Black-capped Chickadee & aberrant), 7 (low frequency aberrant) and 8 (high frequency aberrant).
Figure 2.16. These two songs were collected from a single male from the Shelby contact zone during one sampling period. The first phrase of the second song is the introductory phrase of the most common CC song. The song on the left shows how the three note phrase of the Vandalia dialect was probably created.

Figure 2.17. A variant of the Carolina Chickadee dialect common to Champaign, Vermilion, and Iroquois counties.
Figure 2.18. The distribution of song type 4.

Figure 2.19. The distribution of song type 16.
Figure 2.20. An example of a Carolina Chickadee rasp (gargle). Those of the Black-capped Chickadee are a very similar class of vocalizations.
Appendix I

Spectrograms of song types recorded during this study in 1998-2000, primarily in central Illinois. Vertical axes are in kilohertz (kHz) and horizontal axes are time (either seconds, S, or milliseconds (ms).

1) A typical Black-capped Chickadee song recorded at San Christ State Park in Sangamon County, April 2000.

2) A three-note Black-capped Chickadee song recorded at two sites in Fayette County and one in Montgomery County, June 1999.

3) A song comprised of two Black-capped Chickadee songs sung back to back, this example was recorded June 1999 in Fayette County. This song was also recorded at a site in Montgomery County.

4) A truncated Black-capped Chickadee like song that only occurred at sites where song 16 was also present. It was recorded at seven sites in 1998 and 1999; three sites in Bond, three in Fayette, and one in Shelby County.

5) Recorded at one site in Fayette County, July 1998.

6) Recorded at one site in Champaign County, May 1999.

7) Recorded at one site in Fayette County, June 1999.

8) Recorded at one site in Douglas County, July 1999.

9) Recorded at a total of eleven sites, four in Fayette, two in Champaign, and five in Bond. This example is from Bond County, June 1999.

10) Recorded at one site in Bond County, June 1999.

11) Recorded at one site in Fayette County June 1999.

12) Recorded at seven sites in Bond County June-July 1999.
13) Recorded at two sites in Bond County, June 1999.

14) Recorded at three sites in Bond County, June 1999.

15) Recorded at one site in Bond County, June 1999.

16) a\&b, This song type was widespread and occurred in Bond, Champaign, Clinton, Coles, Douglas, and Shelby counties. Both 16a and 16b were recorded in Bond County, June 1999. There were other variants of this song that included an additional phrase of the same type as the second phrase.

18) Recorded at one site in Fayette County, July 1998. Song 18 was sung by the same male that sang song 34; these songs shared the three note phrase that was the last phrase of song 18.

19) Recorded at one site in Bond County, May 1999.

20) Recorded at one site in Shelby County, May 1999.

21) Recorded at three sites in Fayette County, two in June 1998 and one in June 1999.

   21a) A close-up of one of the last five phrases of song type 21.

22) Recorded at one site in Fayette County, June 1999.

   22a) A close-up of the first phrase of song 22. This phrase is very similar to song type 4 and the first two notes of songs 16, 18, 19, and 20.

   22b) The second phrase of song 22.

   22c) A close-up of the fifth and the sixth phrases of song 22.

23) Recorded at one site in Fayette County, June 1999.

   23a) A close-up of the middle and last phrases of song type 23.

24) Recorded at two sites in Fayette County, June 1998 and 1999. Also recorded in March 2000, in Fayette County.
24a) A close-up of the first phrase of song type 24.

24b) A close up of the fourth and the fifth phrases of song type 24.

24c) A close-up of the fifth (last) phrase of song type 24.

25) Recorded at one site in Fayette County June 1999.

25a) A close-up of the second and third phrases of song type 25.

26) Recorded at one site in Fayette County, July 1999.

26a) A close-up of a phrase from song type 26.

27) Recorded at one site in Fayette County, July 1999.

27a) A close-up of one of the first three phrases of song type 27.

28) Recorded at one site in Fayette County, July 1998.

28a) A close-up of three of the phrases of song type 28.

29) Recorded at one site in Fayette County, July 1999.

29a) A close-up of a phrase from song type 29.

30) Recorded at one site in Fayette County, July 1998.

30a) A close-up of a phrase from song type 30.

31) Recorded at one site in Fayette County, July 1999.

31a) A close-up of a phrase from song type 31.

32) Recorded at three sites in Shelby County, two in July 1998 and one in June 1999.

33) Recorded at one site in Shelby County, June 1999. The second note of the first phrase, which was composed of three notes, begins with a rolled trill.

34) Recorded in Shelby County, June 1999.

35) Recorded at one site in Douglas County, July 1999. This is probably not a song; it seems structurally similar to the “hi-lo” call described for Black-capped Chickadees.
36) The most common Carolina Chickadee song type in Illinois. This example was recorded in Clinton County, June 1999.

37) This Carolina Chickadee dialect occurs in Champaign, Iroquois, Shelby and Vermilion counties. This example was recorded in Vermilion County, March 2000.

38) A variant of song 37 recorded in Vermilion County, March 2000.

39) Two variants of song type 37 sung by the same male in Shelby County, June 1999.

40) Possibly a variation of song type 37. The double clicks following the second and third whistled notes are very similar to those of song type 21. This song was recorded in Bond County, June 1999.

41) A variation of song type 37 recorded in Shelby County, June 1999.

42) One of several Carolina Chickadee song types occurring in southern Illinois that contained a non-whistled buzz or trill. Note four in this song is a broad frequency buzz. This song was recorded in Jackson County, March 2000.

43) Another example of a Carolina Chickadee song type containing non-whistled elements. This song was sung by one male in Clark County, April 2000.

44) An unusual Carolina Chickadee song recorded in Perry County, March 2000. This was sung by one male who also sang two more typical Carolina Chickadee songs that were shared with neighboring chickadees. The series of low notes after each whistled note is acoustically more complex than the clicks that were present in song type 21 for example.

45) An example of a rasp (gargle) call. This call was given by a Carolina Chickadee in Johnson County, March 2000.