Morphology and Variation in the Gargle Call in a Chickadee Hybrid Zone in Central Illinois

Shannon Marie Regan
Eastern Illinois University

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MS in Biological Sciences
Graduate Degree Program

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Date

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Morphology and Variation in the Gargle Call in a Chickadee Hybrid Zone in Central Illinois

BY Shannon Marie Regan

THESIS
SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science in Biological Sciences IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY CHARLESTON, ILLINOIS

2017

I HEREBY RECOMMEND THAT THIS THESIS BE ACCEPTED AS FULFILLING THIS PART OF THE GRADUATE DEGREE CITED ABOVE

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ABSTRACT

Black-capped (Poecile atricapillus) and Carolina Chickadees (P. carolinensis) have distributions that span the northern and eastern portions of the United States. The areas where these distributions meet are called contact zones and extend from Kansas to New Jersey. Contact zones often have a narrow range of hybridization and usually within these zones of hybridization we will see a mixture of genetic, morphological, and cultural traits. One focus of this project was to compare morphology and genetics of chickadees within and near the largest Illinois contact zone, which has not been done previously. This contact zone was delineated by Enstrom and Bollinger (2009) based only on song structure and not on genetics or morphology. I placed 150 nest boxes within and on the edges of this contact zone in central Illinois. To examine the extent of hybridization occurring in this area, nestlings and adults were weighed and measured. Blood and tissue samples were also taken for genetic analyses. Results showed that although clutch size was similar across all sites, the hatchability of eggs differed significantly. This would suggest a reproductive depression in areas of hybridization, which is to be expected. I also found that wing chord and tail measurements for most individuals were Carolina-like with only individuals from the northernmost site having black-capped-like morphology.

I also examined a chickadee vocalization known as the “gargle” call. This short and complex call is often used in agonistic situations and sometimes immediately preceding copulation. Gargles were recorded year-round from areas surrounding the nest boxes. Recordings were conducted in one minute intervals, for up to five minutes at a
time. Across sites, I compared the core components of the gargle, such as the start frequency, maximum frequency, minimum frequency, and end frequency.

These results showed a high amount of variation within the call across all sites. Another component examined was the syllabic composition. Although there were three universal syllables found at all sites, there was considerable variability in the overall abundance and patterns of all other syllables. Overall, my results indicate that the individuals within the Illinois contact zone are genetically more similar to Carolina Chickadees than Black-capped Chickadees. More extensive genetic and behavioral studies are necessary in order to determine the extent of hybridization occurring throughout this area.
ACKNOWLEDGEMENTS

I would like to first thank Eric Bollinger for his continuous support, encouragement, positivity, and good humor in my times of struggle and discouragement. I would also like to thank Christopher Langland for his tremendous emotional support and the many hours of manual labor he put into making, and placing, nest boxes with me. I thank Paul Switzer and Ann Fritz for always giving me academic advice (and general life advice) when I needed it. I thank Scott Meiners for patiently helping me with statistics and statistical software. I thank the Illinois Department of Natural Resources, the Kingsbury Park District (Bond County), and the private landowners involved for allowing me to use their land. I thank the friends that I have made here at EIU for showing me that it is okay to have fun once in awhile and always encouraging me to be better, especially Bethany Hoster, Dan Roth, Jordan Pesik, Matt Kneitel, Camden Nix, Sarah Manka, Eric Hine, and Jess Thornton. Lastly, I would like to thank my family for always supporting me no matter how far away from home I move or how many family events I miss out on. Especially my dad and my sister, who have been with me every step of the way—starting with wildlife trips to the forests of northern Wisconsin while we were growing up to helping me move to another state all by myself to begin a “real” job the day after my college graduation. You have all played a huge part in my success and I could not be more grateful.
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ABSTRACT

Contact zones, also known as hybrid zones, form in areas where two closely related parapatric species overlap and hybridize. Individuals in these hybrid zones can often show a mixture of, or intermediate values between, the two species' morphological, genetic, cultural, and behavioral traits. We can see these mixtures in the contact zones of Black-capped (*Poecile atricapillus*) and Carolina Chickadees (*P. carolinensis*). Previous studies in Illinois have focused on vocalizations only to determine areas of possible hybridization, although mixed or aberrant vocalizations do not always indicate the presence of genetic hybrids. This study examined the morphological and genetic composition and reproductive success of chickadees across the largest contact zone in Illinois. I placed 150 nest boxes spanning the contact zone in Bond and Fayette Counties in central Illinois from January 2016 - May 2017. Boxes were placed at four sites; two sites in the center of the contact zone, one on the north edge, and one on the south edge. I monitored nest success in these boxes and took tissue samples and measured and weighed nestlings, along with measuring, weighing, and taking blood samples from the adults.

I found no differences between sites for clutch size, average weight, and total number of nestlings. Hatchability of eggs was significantly different among sites, with the sites outside the presumptive contact zone having a higher hatchability than the sites within it. I also found that morphologically, individuals seem to be more Carolina-like. However, the northernmost site did have 3 of 4 adults with black-capped-like wing-to-tail ratios. The extent of variation, the morphological intermediates, and the decreased hatchability of eggs found throughout these sites
suggests that genetic hybridization may be present in these areas, but that chickadees at the two sites within the presumptive contact zone are much more similar to Carolina than to black-capped chickadees.
INTRODUCTION

Background and geography

Parapatric taxa have separate distributions but share a common border with minimal overlap (Bull 1991). Contact zones, also known as hybrid zones, form in areas where two closely-related, parapatric species do overlap and hybridize (Futuyuma 1986, Bull 1991). These hybrid zones can often show a mixture of morphological, genetic, cultural, and behavioral traits between the species (Kroodsma 1974, Emlen et al. 1975, Payne 1980, McDonald et al. 2001, and Beecher and Burt 2004) and have previously been thought to exhibit intermediate stages in the process of speciation (Mayr 1963). Others, however, have argued that these contact zones are a form of microgeographic variation and, therefore, do not always result in speciation (Moore 1977).

Black-capped (BCCH) and Carolina Chickadees (CACH) have parapatric distributions that span the eastern United States and most of the Midwest. A narrow zone of hybridization is often found along these contact zones, usually no more than a few miles wide (Brewer 1963, Braun and Robbins 1986, Sattler and Braun 2000, Bronson et al. 2005, Enstrom and Bollinger 2009; Figure 1.1). The Black-capped Chickadee range covers the entire northern United States, including Alaska, and most of western Canada. This can also extend southward within the Appalachians into Tennessee and North Carolina (Brewer 1963). The range of the Carolina Chickadee covers the southeastern states, extending from central Texas up through southern Pennsylvania. Brewer (1963) found that the westernmost point you could find these two species together was in Vandalia, Fayette County, Illinois. As you move west through the state of Illinois, the distance between the species increases until it seems there are no chickadees for up
to 25 kilometers. In the Appalachian Mountains, altitude is the major factor for the separation of these species. Tanner (1952) and Brewer (1963) found that Black capped Chickadees will be found nesting at altitudes above 1500 feet whereas Carolina Chickadees will usually be found below that threshold.

Hybridization

In some areas where these two chickadee species come together, studies have found evidence of hybridization (Missouri: Robbins et al. 1986, Ohio: Bronson et al. 2005, Pennsylvania: Reudink et al. 2007, and Virginia: Sattler and Braun 2000). In Illinois, hybridization has been reported by Brewer (1963) and Enstrom and Bollinger (2009), based on aberrant vocalizations and morphological intermediates but not genetic analyses. Most reports of hybridization in their family (Paridae) occur in areas of extensive overlap where at least one of the species is rare (Randler 2006). In contrast, with Black-capped and Carolina Chickadees, previous studies have established that hybridization is common in many areas of contact where neither species is rare (Brewer 1963, Rising 1968, Johnston 1971, Gill 1998, Sattler et al. 2007).

The BCCH and CACH are very similar in morphology and behavior with only slight difference (Rising 1968, Pyle 1997). Despite their extensive similarities they are not sibling species (Gill et al. 1993, Curry 2005). The closest relative of the Black-capped Chickadee is the Mountain Chickadee (Poecile gambeli; MOCH), found from the Rocky Mountains to the west coast. Interestingly, Mountain chickadees and Black-capped chickadees have ranges that overlap but they do not interbreed like we see with BCCH and CACH. Perhaps because of their different foraging behaviors and habitat selections (Hill and Lein 1989). The most closely-related extant species of the Carolina Chickadee is still unknown but some suggest that it may be the Mexican
Chickadee (*P. sclateri*; Curry 2005). BCCH and CACH have very similar preferences for nest sites and foraging areas so interspecific interaction is more common which may increase the likelihood of hybridization.

Previous studies of chickadees within and near the contact zone in Illinois have all been based on the aberrant songs and behaviors of the birds, without the morphological and genetic data support (Brewer 1963, Kershner and Bollinger 1999, Entsrom and Bollinger 2009). Brewer (1963) mapped the contact zone in the early sixties and Enstrom and Bollinger (2009) mapped it again, approximately 40 years later. Both of these studies used aberrant vocalizations to determine the extent and locations of probable hybridization. However, due to the learned component of vocalizations, aberrant songs are not always a reliable indicator of hybridization (Rising 1963, Kroodsma 1974, Emlen et al. 1975, and Beecher and Burt 2004). Therefore, this study examined the morphological and genetic composition of chickadees in the largest contact zone in Illinois.

**METHODS**

*Field Methods*

In the first year of the study, 100 nest boxes were placed throughout Fayette County spanning the contact zone and just outside of it. Fayette County has previously been an area within the contact zone supporting a relatively high density of chickadees (Brewer 1963, Enstrom and Bollinger 2009). There were three sites in total with one north of the contact zone, one in the center, and one in the south. The northern site was located at Ramsey Lake State Park, the central location in Vandalia, IL, and the southern site at Carlyle Lake Wildlife Management Area (Figure 1.2). Ramsey Lake State Park was chosen because it is within typical Black-capped
chickadee range (based on vocalizations, see Enstrom and Bollinger 2009). Ramsey is 21 km from the center of the contact zone whereas Carlyle Lake WMA is within typical Carolina range (based on vocalizations) and is 18 km from the center. Boxes were made with 2 cm-thick plywood, measured 15 cm x 10 cm x 20 cm, with a 0.64 cm hole on the front. They were placed on 2.4 meter metal conduit poles, usually at the edges of woodlots or along hiking trails, and were placed one month prior to the breeding season. I spaced boxes a minimum of 75 meters apart from each other to ensure that there were unlikely to be two boxes within a single territory.

The 2017, I added one more site in Greenville, IL (Bond County), about 24 km west and 3-4 km south of Vandalia, IL (Figure 1.2). This site was added because of minimal box usage in Vandalia during 2016. Greenville was chosen because it also has a high abundance of breeding chickadees (Brewer 1963, Enstrom and Bollinger 2009). Half of the boxes from Ramsey and Carlyle were moved to Greenville to increase the chances of active nests in the center of the contact zone. Fifty more boxes were made and also placed in Greenville during the second year which increased the total number of boxes to 150. After moving old boxes and placing the new ones, there were 100 boxes within the contact zone and 25 at each of the other two sites (Ramsey and Carlyle).

Nest boxes were checked once every ten days. If the nest had eggs, I would return when nestlings were at least seven days old. If the nest did not have eggs, I would check back every three days until eggs were laid or it was determined the nest was not active. Morphological measurements and tissue samples were taken from each nestling. Measurements taken for nestlings were weight (to the nearest 0.1g; small tabletop digital scale), wing chord (to the nearest 0.1mm; stopped wing ruler), and tarsus (to the nearest 0.1mm; Vernier callipers). For
tissue sampling, one secondary pinfeather was plucked from each wing using forceps (Stangel and Lennartz 1988). These pinfeathers were placed in ethanol for transport and lab analysis. Once measurements were finished and feathers were collected, nestlings were placed back into the nest. The laboratory and analytical methods for the genetic portion of this project are still ongoing (Fahad Alshammari, unpublished data).

During the 2017 breeding season and the winter preceding it, nets were placed around feeders and nest boxes to capture adult chickadees. Measurements taken were weight, wing chord, and tail length (to the nearest 0.1mm). Adults were sexed based on the presence of a brood patch or a cloacal protuberance (Pyle 1997).

Analytical Methods

In a hybrid zone, you would usually expect to see a decrease in nest success (Bronson et al. 2003, Grant et al. 2003, Barreto and Burton 2013). In this study, to examine the possibility of decreased nest success, I compared egg hatchability among sites, average clutch sizes, and the percent of nestlings that fledged. One-way ANOVAs followed by pairwise comparisons were used to test for significant differences among or between sites or individuals. To look at the differences in morphology among sites, I used descriptive statistics and ANOVAs to find any differences.

RESULTS

Nest data

The average number of eggs across all sites was 5.64 ±2.03 (n=31; Table 1). Ramsey had the highest average number of eggs at 6.75 ±1.71 (n=4) whereas Carlyle had the lowest 5.30 ±1.50 (n=10; Table 1.1). There were no significant differences found in the pairwise
comparisons. Hatchability among sites was significantly different; Ramsey and Carlyle had high hatchability (>80%) and Vandalia and Greenville had low hatchability (<65%) (F_{1,31}=24.61, p<0.005). Clutch size was similar among sites (F_{3,29}=0.48, p=0.70), as was the average number of nestlings per active nest (F_{3,29}=1.43, p=0.25).

Ramsey had the highest average number of nestlings at 6.0 (±2.58, n=4) and Greenville had the lowest average at 3.40 (±2.56, n=11). Across all sites, 58% (n=19) of all nests successfully fledged young whereas 42% (n=14) did not. 71% (n=10) of the unsuccessful nests were due to either predation or takeover by House Wrens (*Troglodytes aedon*) or Paper Wasps (*Vespidae*). The remaining 28% (n=4) failed due to unknown causes. The percentages of nestlings that fledged at each site were: Carlyle: 40% (n=10), Greenville: 53% (n=15), Vandalia: 75% (n=4), and Ramsey: 100% (n=4).

*Morphological Data*

A total of 22 adults were captured and measured. Of those 22, there were 13 females, 5 males, and 4 unknowns. The 4 unknowns were captured in winter months. There were 6 after-hatch-year birds, 15 second-year, and one adult bird of unknown age. Nine of the adults were captured at Greenville, two at Carlyle, six at Vandalia, and five at Ramsey.

On average, males were heavier than females (F_{1,16} = 11.3, p = 0.004; Figure 1.4). Comparing all individuals across sites, there was no significant difference in weight (F_{3,18} = 0.97, p = 0.43; Table 1). I also captured one individual from Minnesota that was 12.8g, almost 2 grams heavier than any of the individuals at my sites. There were also no differences between tail length (F_{4,18} = 1.55, p = 0.23; Figure 1.4) or wing chord (F_{4,68} = 1.94, p = 0.11; Figure 1.5) across sites. The wing chord/tail length ratios for each site are as follows: Carlyle: 1.13 ± 0.01 (n=5),
Greenville: 1.12 ± 0.04 (n=9), Ramsey: 1.10 ± 0.06 (n=5), and Vandalia: 1.14 ± 0.02 (n=6).

Wing chord/tail length did not differ significantly between sites ($F_{3,18} = 1.18, p = 0.35$).

DISCUSSION

Typically, in the center of a hybrid zone we would expect to see a depression in fitness (Barton and Hewitt 1985, Robbins et al. 1986, Bronson et al. 2005). Therefore, the outer edges should still exhibit some decreased fitness, but not as much. Smaller clutch sizes, lower hatchability, and increased nest failure are possibly good indicators of a decrease in fitness (Bronson et al. 2003). In some aspects, the birds of the central Illinois contact zone do follow the typical trends you would expect to find in any hybrid zone. For example, hatchability was lowest in the center of the contact zone. Also, the Ramsey birds seemed to be heavier than the Carlyle birds whereas the birds within the presumptive contact zone (i.e. Greenville and Vandalia) fell somewhere in between, although across all sites there were no significant differences. This should be expected considering Black-capped Chickadees are typically larger than Carolina Chickadees (Robbins et al. 1986, Sattler and Braun 2000). Lastly, Ramsey successfully fledged all nestlings. The examples above suggest that the Ramsey chickadees may actually be genetically closer to BCCH than the individuals at the other sites.

Originally, based on the knowledge that Ramsey birds sing BCCH songs whereas Vandalia and Greenville birds sings aberrant songs (see also Enstrom and Bollinger 2009) and that hybrid zones are usually quite narrow, we assumed that, genetically, Ramsey birds should be more BCCH-like, Carlyle birds should be more CACH-like, and Greenville and Vandalia birds would be hybrids. Alternatively, we also know that the chickadee hybrid zone is slowly moving northward in most locations (Sattler and Braun 2000, Bronson et al. 2005, Reudink et al. 2007,
but see Enstrom and Bollinger 2009). Therefore, our alternative hypothesis was that Carlyle
birds were likely genetically pure CACH, or close to it, and that the other sites were all genetic
hybrids. Preliminary genetic results from two individuals (using mitochondrial DNA) from
Ramsey indicated that they clustered nearer CACH than BCCH, which further supports the
northward movement of this hybrid zone.

This northern movement could either be due to climate change, selection that opposes
introgression, or the fact that CACH males outcompete BCCH males. In a female mate
preference study, Bronson et al. (2005) found that females of both BCCH and CACH preferred
CACH males over BCCH males. This suggests that CACH males are dominant over BCCH
males, and could account for the northward movement of the hybrid zone (Bronson 2003). Based
on the above example, along with the results we found, it is plausible that this is what is
happening in the Illinois contact zone.

In conclusion, my results indicate that the majority of individuals at our study sites are
probably more CACH-like than BCCH-like. Genetic testing of individuals spanning a larger area
across the contact zone will be necessary in order to fully understand the extent of hybridization
occurring in this location and the extent to which the contact zone has moved northward. In
addition, mate selection within and between these populations would help us determine if the
CACH males are actually outcompeting the BCCH males.
LITERATURE CITED


Table 1.1 Mean number of eggs found across all sites and within individual sites.

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<tr>
<th></th>
<th>Mean</th>
<th>SD</th>
<th>N</th>
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</thead>
<tbody>
<tr>
<td>All Sites</td>
<td>5.64</td>
<td>2.03</td>
<td>31</td>
</tr>
<tr>
<td>Carlyle</td>
<td>5.30</td>
<td>1.50</td>
<td>10</td>
</tr>
<tr>
<td>Greenville</td>
<td>5.60</td>
<td>2.50</td>
<td>13</td>
</tr>
<tr>
<td>Vandalia</td>
<td>5.50</td>
<td>1.73</td>
<td>4</td>
</tr>
<tr>
<td>Ramsey</td>
<td>6.75</td>
<td>1.71</td>
<td>4</td>
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Table 1.2 Mean number of nestlings found across all sites and within individuals.

<table>
<thead>
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<th>Egg Hatchability</th>
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<td>4.06</td>
<td>2.45</td>
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<td>72%</td>
</tr>
<tr>
<td>Carlyle</td>
<td>4.50</td>
<td>2.01</td>
<td>9</td>
<td>85%</td>
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<tr>
<td>Greenville</td>
<td>3.40</td>
<td>2.56</td>
<td>11</td>
<td>61%</td>
</tr>
<tr>
<td>Vandalia</td>
<td>3.50</td>
<td>2.52</td>
<td>3</td>
<td>64%</td>
</tr>
<tr>
<td>Ramsey</td>
<td>6.00</td>
<td>2.58</td>
<td>4</td>
<td>88%</td>
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Table 1.3. Mean weight of adults across all sites

<table>
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<th>Mean (g)</th>
<th>SD</th>
<th>N</th>
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<tr>
<td>All Sites</td>
<td>10.48</td>
<td>0.90</td>
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<tr>
<td>Carlyle</td>
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</tr>
<tr>
<td>Greenville</td>
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<td>0.81</td>
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<tr>
<td>Ramsey</td>
<td>10.76</td>
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<tr>
<td>Vandalia</td>
<td>10.30</td>
<td>0.70</td>
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</tr>
<tr>
<td>Minnesota</td>
<td>12.80</td>
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<td>1</td>
</tr>
</tbody>
</table>
Figure 1.1 A map of the distributions of the BCCH (north) and the CACH (south) including a line representing the hybrid zone where these two distributions meet.
Figure 1.2. Map of Illinois displaying the sampling sites in relation to the contact zone which was mapped by Enstrom and Bollinger (2009). The northern site is Ramsey, the east-central is Vandalia, the southern is Carlyle, and the western is Greenville.
Figure 1.3. Wing chord and tail measurements (in millimeters) from each individual captured. Each point is labeled with the first letter of the capture site. This graph also includes measurements from one BCCH caught at Maplewood, Minnesota, which is labeled with an "M". Averages for each site are represented by boxes with the standard deviation for both variables. The line separating the species comes from the *Identification Guide to North American Birds* (Pyle 1997).
Figure 1.4. Average size for adult males and females (±SD, n=18; 5 males, 13 females).

Figure 1.5. Average wing chord and tail length between sites (±SD, n=23).
Chapter 2. Analysis of the Gargle Call in Chickadees Within a Contact Zone in Central Illinois

ABSTRACT

Vocalizations of songbirds typically have a significant learned component. In the contact zone between Black-capped (Poecile atricapillus) and Carolina (P. carolinensis) chickadees, individuals often produce aberrant songs. These aberrant songs are indicative of genetic and/or cultural hybridization at some locations. Previous studies in the Illinois contact zones have detailed these aberrant songs extensively. In addition to song, chickadees have a short, complex call, known as a gargle or a rasp, that is often used in agonistic situations. Because of the extensive variation in song that can often be found within contact zones, this study examined if the gargle call also displayed this range of variation, despite its shorter duration and higher complexity.

Gargle vocalizations were recorded at sites spanning the large contact zone within Bond and Fayette Counties in central Illinois. Gargle characteristics (average frequency, max frequency, etc.) were analyzed within individuals and across sites. Composition (syllable types) was also compared. Overall, individuals at our study sites produced gargles with more Carolina qualities than black-capped. I also found almost no intra-individual variation whereas the inter-individual variation was high. There were three syllables found at all sites but the frequency and order of syllable types varied greatly. Thus, the gargle call seems to follow patterns previously found in chickadee song, suggesting that there is a mixture of genetic and cultural hybridization happening within this contact zone.
INTRODUCTION

Vocalizations of songbirds often have a significant learned component. This can result in a broad range of vocalizations, often categorized loosely as songs and calls. In the black-capped chickadee, there is very little variation in the song across most of this species' range (Kroodsma et al. 1999). This species' song consists of two whistled notes ("fee-bee"), the second one always lower in pitch than the first. Within the Carolina Chickadees, we see a slight increase in variation but the song remains distinct. Their songs are usually four whistled notes ("fee-bee-fee-bay"), with the first and third notes higher in frequency than the others.

Contact zones, also known as hybrid zones, form in areas where two closely-related, parapatric species do overlap and hybridize (Futuyuma 1986, Bull 1991). In hybrid zones, the consistency of these songs decreases considerably and sometimes completely different and aberrant songs are produced (Robbins et al. 1986, Enstrom and Bollinger 2009). These variable, aberrant songs are indicative of genetic and/or cultural hybridization (Kroodsma et al. 1995, Brewer 1963, Enstrom and Bollinger 2001). Previous studies in the Illinois contact zones, as discussed above, have detailed these aberrant songs extensively (Kerschner and Bollinger 1999, Enstrom and Bollinger 2009, Brewer 1963).

Besides their song, chickadees have two complex calls that are commonly used: the "chick-a-dee" call and the "gargle" or "rasp" call. The chick-a-dee call is structurally complex and is used year-round and in many different social and environmental situations (Mammen and Nowicki 1981, Clucas et al. 2004). The "gargle" call (sometimes called a "rasp" in Carolina chickadees) is a short and very complex call produced by chickadees in agonistic situations and
by males immediately before copulation (Ficken et al. 1978, Ficken and Weise 1984). Just like the chick-a-dee call, it is produced year-round, especially at bird feeders or other foraging areas. This study examined if the gargle call also displayed the same range of extensive variation as song, despite its higher complexity and much shorter duration.

METHODS

Vocalizations were recorded at sites spanning the contact zone within Bond and Fayette Counties in central Illinois, most of them in areas no further than three miles from the nest boxes (see Chapter 1). Two sites were located on Illinois DNR property; Ramsey Lake State Park (Ramsey, IL) and Carlyle Lake State Fish and Wildlife Area (Vernon, IL). All other sites were located on private and county properties.

Recordings were collected year-round using a Roland R-26 portable recorder (Roland Corp., 2011) with a shotgun microphone. To record gargle calls, I walked around suitable habitat until I heard or saw chickadees. I would then move as close as I could and begin recording for one minute intervals. If the chickadees were not gargling, I would play a bait tape, either a pre-recorded song or “chick-a-dee” call, to elicit an aggressive response (Enstrom and Bollinger 2009). The pre-recorded vocalizations were taken from the Cornell Macaulay Library of Natural Sounds; including ML 41385 (BCCH song from NJ), ML 40796 (BCCH call from NY), ML 94226 (CACH song from MD), ML 84822 (CACH call from MD), and ML 105467 (CACH call from GA)(App I). I would record for 5 minutes or until birds either stop calling or moved too far away. Birds recorded were always within ten meters of the recorder. During fall and winter months, only a “chick-a-dee” call bait tape was played since chickadees do not respond to songs
at this time of year. Once a bird was recorded, I would never return within a hundred meters of that area again. Thus, I feel that recordings are from separate individuals.

Analysis of vocalization characteristics was conducted with Raven Lite© and Raven Pro 2.0© software (Charif et al. 2010, Table 1). When certain parts of a call were not clear (i.e. very high and low frequencies, usually on the extremes) I would only analyze the core portion of the call that was consistently clear. If more than one trill appeared in a call, I would only analyze whichever one came last.

To compare call characteristics across sites, I used a MANOVA followed by univariate analyses to determine which variables had the strongest effects. All gargle analyses include my four sites along with genetically “pure” BCCH and CACH gargles taken from the Cornell Macaulay Library of Natural Sounds for comparison. These BCCH and CACH gargles will also be referred to by the location of the recording. These calls come from various areas spread throughout their respective ranges. The BCCH recordings included gargles from Alaska, Utah, New York, and Quebec. The CACH recordings came from Ohio, New Jersey, North Carolina, Oklahoma, Missouri, and Arkansas (Fig. 1).

The last comparison I made was comparing the amount of shared syllables between three randomly chosen individual gargles from each site (or parental species in the case of the BCCH and CACH gargles) and then overall between sites. To compare shared syllables between sites, I tallied the number of syllables that were found at each site at least once.
RESULTS

Call characteristics

I examined the gargles in two ways. First I compared a series of quantitative characteristics (Table 1). Second, the syllables present in each call were catalogued and compared. In order to examine if there was any intra-individual within sites, I took the first four recordings from each site and analyzed the first four gargles within each of those recordings. Four recordings (i.e. individuals) were also chosen as the maximum for all sites because I only had four BCCH and Carlyle recordings of sufficient quality. Four gargles was also chosen as the maximum because in more than one recording, the maximum number of gargles was four.

There was no significant intra-individual variation found at any of the sites (all analyses, p>0.05). It was also important to see if there was a significant difference between the BCCH gargles and the CACH gargles. An ANOVA showed that the only variable that differed significantly between the two sites was the average trill frequency (F_{1,5} = 9.17, p = 0.03). I also wanted to compare the characteristics found across all of my sites combined with the characteristics of the BCCH and CACH. To do this, I pooled the data from my sites and conducted ANOVAs. Variables that differed significantly between at least two sites are as follows: maximum frequency (CACH-my sites, p = 0.01), minimum frequency (CACH-my sites, p = 0.04), overall frequency (CACH-BCCH, p = 0.03; CACH-my sites, p < 0.001), total call length (BCCH-my sites, p = 0.02; CACH-BCCH, p = 0.05), and number of syllables (BCCH-my sites, p = 0.03). CACH had the highest average maximum frequency, minimum frequency, and overall frequency whereas BCCH had the longest calls and the most syllables on average.
To test for possible relationships between call characteristics (Table 2) across all sites, I again conducted one-way ANOVAs. All variables with a non-normal distribution were log-transformed. These were: start frequency, end frequency, total length, number of syllables, overall average frequency, and pitch interval. I found that location had a significant effect on average trill frequency ($F_{5,52}=2.56, p=0.04$) and pitch interval ($F_{5,39}=3.40, p=0.01$). Tukey’s post-hoc tests revealed the differences in average trill frequency were between CACH and Vandalia ($p=0.04$), with CACH being higher in frequency. For pitch interval, the differences were likely between CACH and Carlyle ($p=0.06$) or Ramsey and Carlyle ($p=0.07$). Carlyle had a greater pitch interval, although these differences were not statistically significant. Location had no effect on any other variables. Because a bait tape was used to elicit stronger responses in shy birds, it was important to test for a possible effect on the calls. I found that the bait tape had no effect on the gargles recorded ($F_{6,38}=1.10, p=0.30$).

**Syllable data**

An example of a gargle from each site can be found in Figures 2-7. There are three syllables that are considered universal because they appeared at every site at least once (A, B, and G). A defining characteristic found in all gargles is a trill or buzz (Fig. 2). Syllables A or B, the fast trill and slow trill, respectively, were found in every call across all sites except one call at Carlyle (Table 3). 74% of all calls contained an “A” trill and 63% contained a “B” trill ($n=35$ different individuals). 43% contained both A and B together while only 0.03% contained neither. It is worth noting that syllable A is almost always a higher frequency than syllable B. Therefore, we would expect to see syllable A come first in the call, as average frequency decreases over time. Syllable B was found as the last syllable in 60% of all calls and A was the last syllable in
29% of all calls. In all of the calls that had A as the last syllable, no B syllable occurred. Of all recordings, B was never the first syllable and A was found to be the first syllable in only one call (Greenville). The middle of the call is defined as any syllable that is not first or last. Syllable A was found in the middle of the call 49% of the time whereas B was found in the middle only 8% of the time.

Comparing shared syllables within sites, I found that Carlyle's individuals had only one syllable that was shared whereas Ramsey had anywhere from 3-7 shared syllables between individuals. All other sites had individuals that shared only 1-2 syllables. Between sites, the most syllable-sharing occurred between BCCH-CACH, Carlyle-CACH, and Ramsey-CACH (Table 4). These sites shared six syllables in total, whereas the other sites shared either five syllables or three syllables. This seems to indicate that CACH shares more syllables than any other sites. This also revealed that Ramsey shares the most syllables (5 or 6) with all sites which seems to suggest there is probably more hybridization occurring in Ramsey than we previously anticipated.

DISCUSSION

Oscines typically learn their songs and sometimes calls from their parents and the adults around them (Clayton 1989, Marler 1990, Nowicki et al. 1998, Beecher and Burt 2004, Weisman and Ratcliffe 2004). This allows for a unique look into the cultural and behavioral interactions (Clayton 1989, Martens 1992). Previous studies have shown that the gargle call exhibits microgeographic variation between populations (Ficken et al. 1978, Baker and Gammon 2006). Considering that this study found a high amount of variation between sites and almost no variation within individuals, it could be argued that the contact zone birds follow this pattern. As
a whole, however, I cannot say for sure. So lack of variation within individuals could be due to the fact that each individual was only recorded one time so although there was no variation in the few short minutes recorded, there may be variation present over longer periods of time. The high amount of unexplained variation between sites may indicate cultural hybridization throughout the contact zone.

In a previous study by Ficken et al. (1984), three universal syllables of the gargle occurred across all sampling stations, which were all located within the Black-capped Chickadee distribution. I also found three universal syllables, two of them similar to the ones found by Ficken et al. (1984)(the fast and slow trill). This suggests that even in areas of probable hybridization and vocal admixture, there must be some aspects of this call that are needed in order to make it a gargle, rather than something else. We also know that the gargle has different dialects, just like we find with the songs of many passerines, including the chickadees within the Illinois contact zone (Brewer 1963, Ficken et al. 1987, Kershner and Bollinger 1999, Baker and Gammon 2006, Enstrom and Bollinger 2009). It seems on the surface that there may be different gargle dialects within the Illinois contact zone but with so much variation in all aspects of these populations, it is possible that these slight similarities between the individuals at my sites and individuals in the Ficken et al. (1984) study, it could just be coincidence or false positives due to limited samples.

Another interesting comparison was the number of shared syllables between individuals within sites and also between individuals across sites (Table 4). There was not much syllable-sharing within sites. Five out of the six sites had individuals that shared three or fewer syllables whereas the sixth site, Ramsey, had seven different shared syllables between individuals. When I
looked at shared syllables across sites, I found that BCCH-CACH shared the most, along with Ramsey-CACH and Ramsey-Vandalia. Considering that BCCH-CACH share the most, this suggests that there may be more universal components of the gargle than the other results seems to indicate. It may just be that even if chickadees have a universal set of syllables found in the majority of gargles, the individual variation appears more in the frequencies, repetitions, or duration of those syllables.

Based on the previous studies of aberrant vocalizations (Brewer 1963, Ficken et al. 1987, Kershner and Bollinger 1999, Baker and Gammon 2006, Enstrom and Bollinger 2009), I assumed there was at least some cultural hybridization in Illinois. When I include the similarities found in morphology and reproductive success, it seems more likely that both genetic and cultural hybridization are occurring or have occurred at my sites. In order to determine the extent of each, there are a few different ways to approach it. The first approach would be a longer duration study with wild populations in which the genetic makeup of the individuals is known. This would allow many more possibilities of recording specific individual behaviors, population dynamics, and an overall larger scope of the mechanisms behind the variation. A possible experiment that could be done is to use decoy chickadees with playback trials to determine how responsive individuals are to gargles that are very different from their own. The second approach would be to examine individuals in a lab and conduct experiments surrounding song and call learning in hybrid chickadees. By doing this, some of the questions surrounding the inter-individual variation within populations may become more clear.
LITERATURE CITED


Table 2.1. A description of each of the call characteristics analyzed. All frequencies are in kilohertz (kHz) and time is in seconds (s).

<table>
<thead>
<tr>
<th>Call Characteristic</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Start Frequency</td>
<td>Starting frequency of the first note in the call</td>
</tr>
<tr>
<td>End Frequency</td>
<td>Ending frequency of the last note in the call</td>
</tr>
<tr>
<td>Max Frequency</td>
<td>Highest frequency exhibited throughout the entirety of the call</td>
</tr>
<tr>
<td>Min Frequency</td>
<td>Lowest frequency exhibited throughout the entirety of the call</td>
</tr>
<tr>
<td>Overall Average Frequency</td>
<td>Average frequency of the call as a whole, calculated by Raven°</td>
</tr>
<tr>
<td>Trill Length</td>
<td>Duration of the last trill in the call</td>
</tr>
<tr>
<td>Average Trill Frequency</td>
<td>Average frequency of the last trill in the call, calculated by Raven°</td>
</tr>
<tr>
<td>Total Length</td>
<td>Duration of the call as a whole</td>
</tr>
<tr>
<td>Pitch Interval</td>
<td>Calculated by dividing the offset frequency of the first note in the call by the onset frequency of the second note in the call (syllable 1/syllable 2)</td>
</tr>
<tr>
<td>Number of Syllables</td>
<td>The number of syllables found in a single gargle call</td>
</tr>
</tbody>
</table>

Table 2.2. Means for each of the gargle components for the first gargle in each recording. Presented as mean (±SD).

<table>
<thead>
<tr>
<th></th>
<th>BCCH</th>
<th>Ramsey</th>
<th>Vandalia</th>
<th>Greenville</th>
<th>Carlyle</th>
<th>CACH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Start Frequency</td>
<td>6.49 (±2.29)</td>
<td>6.85 (±2.14)</td>
<td>5.51 (±3.28)</td>
<td>6.48 (±1.77)</td>
<td>5.99 (±0.95)</td>
<td>7.64 (±2.49)</td>
</tr>
<tr>
<td>End Frequency</td>
<td>2.61 (±0.44)</td>
<td>2.42 (±1.26)</td>
<td>3.13 (±1.06)</td>
<td>3.29 (±1.54)</td>
<td>3.50 (±0.85)</td>
<td>3.49 (±0.73)</td>
</tr>
<tr>
<td>Max Frequency</td>
<td>8.89 (±1.15)</td>
<td>8.35 (±1.18)</td>
<td>8.21 (±1.26)</td>
<td>8.46 (±1.10)</td>
<td>8.11 (±2.02)</td>
<td>9.57 (±1.36)</td>
</tr>
<tr>
<td>Min Frequency</td>
<td>1.96 (±0.54)</td>
<td>2.28 (±0.63)</td>
<td>2.24 (±0.38)</td>
<td>2.16 (±0.45)</td>
<td>2.39 (±0.37)</td>
<td>3.15 (±2.53)</td>
</tr>
<tr>
<td>Overall Average Frequency</td>
<td>5.39 (±0.59)</td>
<td>5.32 (±0.64)</td>
<td>5.23 (±0.69)</td>
<td>5.31 (±0.49)</td>
<td>5.25 (±0.90)</td>
<td>6.59 (±1.17)</td>
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<tr>
<td>Trill Length</td>
<td>0.136 (±0.04)</td>
<td>0.176 (±0.07)</td>
<td>0.168 (±0.07)</td>
<td>0.174 (±0.51)</td>
<td>0.157 (±0.44)</td>
<td>0.278 (±0.10)</td>
</tr>
<tr>
<td>Average Trill Frequency</td>
<td>2.76 (±0.35)</td>
<td>2.65 (±1.31)</td>
<td>2.81 (±1.08)</td>
<td>3.59 (±1.16)</td>
<td>3.41 (±1.79)</td>
<td>4.19 (±1.47)</td>
</tr>
<tr>
<td>Total Length</td>
<td>0.732 (±0.36)</td>
<td>0.536 (±0.16)</td>
<td>0.518 (±0.18)</td>
<td>0.578 (±0.24)</td>
<td>0.514 (±0.15)</td>
<td>0.770 (±0.31)</td>
</tr>
<tr>
<td>Pitch Interval</td>
<td>0.86 (±0.14)</td>
<td>0.67 (±0.20)</td>
<td>0.97 (±0.38)</td>
<td>1.43 (±0.78)</td>
<td>1.46 (±0.55)</td>
<td>0.85 (±0.40)</td>
</tr>
<tr>
<td>Number of Syllables</td>
<td>8.39 (±1.67)</td>
<td>7.67 (±1.15)</td>
<td>7.29 (±2.14)</td>
<td>8.33 (±3.85)</td>
<td>6.17 (±2.23)</td>
<td>6.50 (±3.74)</td>
</tr>
</tbody>
</table>

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Table 2.3. Binomial representation of the 12 most common syllables (found at 3 or more sites) and where they were found. The first three syllables (A, B, and G) were found at least once at every site. The fourth syllable, Q, was found at all sites except for BCCH. They are grouped in terms of whether they appear in one of the parental species and not the other, in both species, or neither.

<table>
<thead>
<tr>
<th>Syllables</th>
<th>BCCH</th>
<th>CACH</th>
<th>VANDALIA</th>
<th>GREENVILLE</th>
<th>RAMSEY</th>
<th>CARLYLE</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>B</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>G</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Q</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>C</td>
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<td>1</td>
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<td>T2</td>
<td>1</td>
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<tr>
<td>L</td>
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</tr>
</tbody>
</table>
Table 2.4. Number of total shared syllables between sites.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Number of Syllables Shared</th>
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</thead>
<tbody>
<tr>
<td>CACH-Ramsey</td>
<td>6</td>
</tr>
<tr>
<td>CACH-BCCH</td>
<td>6</td>
</tr>
<tr>
<td>CACH-Greenville</td>
<td>5</td>
</tr>
<tr>
<td>CACH-Vandalia</td>
<td>5</td>
</tr>
<tr>
<td>CACH-Carlyle</td>
<td>3</td>
</tr>
<tr>
<td>BCCH-Ramsey</td>
<td>5</td>
</tr>
<tr>
<td>BCCH-Carlyle</td>
<td>5</td>
</tr>
<tr>
<td>BCCH-Vandalia</td>
<td>3</td>
</tr>
<tr>
<td>BCCH-Greenville</td>
<td>3</td>
</tr>
<tr>
<td>Ramsey-Vandalia</td>
<td>6</td>
</tr>
<tr>
<td>Ramsey-Carlyle</td>
<td>5</td>
</tr>
<tr>
<td>Ramsey-Greenville</td>
<td>5</td>
</tr>
<tr>
<td>Greenville-Carlyle</td>
<td>3</td>
</tr>
<tr>
<td>Greenville-Vandalia</td>
<td>5</td>
</tr>
<tr>
<td>Vandalia-Carlyle</td>
<td>3</td>
</tr>
</tbody>
</table>
Figure 2.1. Map of the United States showing locations of bait tape recordings taken from the Macaulay Library of Natural Sounds (Cornell Lab of Ornithology).

Figure 2.2. An example gargle from Carlyle with time (in seconds) on the x-axis and frequency (kHz) on the y-axis. This spectrogram contains good examples of a fast trill, slow trill, and a buzz. Syllable sequence: TOMABQA2
Figure 2.3. Example gargle from Greenville. Syllable sequence: T2T2T3TG2IAT2

Figure 2.4. Example gargle from Vandalia. Syllable sequence: JJDT2DG2ZA
Figure 2.5. Example gargle from Ramsey. Syllable sequence: CEFIDAB

Figure 2.6. Example gargle from New Jersey (BCCH). Syllable sequence: O2DG3A2DG3A2
Figure 2.7. Example gargle from Utah (CACH). Syllables sequence: GGGGGIA2B
Appendix

Spectrograms of song exemplars used for bait tapes. Vertical axes are in kilohertz (kHz) and horizontal axes are in seconds (s).


1.

2.