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Persistence of Aberrant Song Types of Chickadees in an Illinois Contact Zone

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ABSTRACT

We studied the patterns and persistence of aberrant song types of the closely related Black-capped (*Poecile atricapillus*) and Carolina (*P. carolinensis*) Chickadees (and probable genetic hybrids) along their range interface in central Illinois. The majority of the songs studied were recorded in 1999 in fifteen counties throughout central Illinois and in 2008 in two of those counties. The greatest diversity of aberrant song types (categorized into two dialects) was present in the largest contact zone located primarily in Bond and Fayette counties. One song type from the dialect in Fayette County has probably existed for at least 60 years and the dialect in Bond County has persisted for at least 20 years. These results suggest that interactions of Black-capped and Carolina Chickadees have led to the development of unique and long-lasting aberrant song cultures in at least one contact zone in Illinois.

INTRODUCTION

Black-capped (BCCH) and Carolina (CACH) Chickadees are closely-related species that are similar in morphology, behavior and ecology (Brewer, 1963; Kroodsma et al., 1995). They are distributed largely parapatrically from Kansas to New Jersey. Typically, narrow zones of sympatry, also referred to as 'contact zones,' occur sporadically along this interface, including in Illinois (Rising, 1968; Merritt, 1978; Grub et al., 1994; Sattler et al., 2007; Enstrom and Bollinger, 2009). Molecular evidence indicates frequent interbreeding in these areas, which are, therefore, genetic hybrid zones as well as cultural hybrid zones in all cases in which a genetic survey was conducted (Robbins et al., 1986; Sawaya, 1990; Sattler and Braun, 2000; Curry, 2005; Reudink et al. 2007).

The songs of BCCH and CACH are similar. The song of the BCCH is highly stereotyped over most of its extensive range, consisting of two whistled notes with frequencies below 5 kHz (Kroodsma et al., 1999). Their songs do not typically exhibit regional, dialectical variants, which occur in many other species of passerines including CACH (Ward, 1966; Kroodsma et al., 1999). CACH song is less stereotyped than BCCH song; however, a general song form does predominate throughout its range. This song can be broken down into two phrases each of which is similar to a BCCH song in that both are basically comprised of a high whistle (above 6 KHz) followed by a lower whistle. The second two-note CACH phrase is usually given at a lower frequency than the first (Ward, 1966; Smith, 1972).

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 (Ward and Ward, 1974; Sattler, 1996; Sattler et al., 2007). Vocal admixture (including bilingually singing birds and aberrant songs with intermediate or atypical characteristics) seems restricted to locations at or near the range interface (Sattler et al., 2007). However, most aberrant song types are probably ephemeral, a likely consequence of the northward shifting contact zones in many locations (e.g., Bronson et al., 2005; Reudink et al., 2007). This study documents the patterns of singing behavior occurring in the largest chickadee contact zone in Illinois, where the range interface has remained largely unchanged for at least 60 years (Enstrom and Bollinger, 2009, Thompson 2021). We describe the persistence of two aberrant song dialects for at least 20 years and likely 60 years for one of these dialects. In addition, we propose their possible origins and functions.

MATERIALS & METHODS

We recorded chickadee vocalizations at 185 sites in fifteen Illinois counties (Enstrom, 2000; Enstrom and Bollinger, 2009). The majority of the songs were collected from 17 April –16 July 1999 and 29 March – 11 April 2008. Additional songs were recorded in March 1997,1 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; Enstrom and Bollinger, 2009). Recordings made in 2008 were restricted to areas near Vandalia (Fayette County) and Greenville (Bond County) within the largest contact zone in Illinois (see Fig. 3 in Enstrom and Bollinger, 2009).

Collection of song at a site was initiated by the broadcast of a bait tape containing alternating bouts of CACH and BCCH songs from a hand-held RCA cassette recorder (Sattler et al., 2007). We played the bait tape as we walked through a site until chickadee vocalizations were detected; the tape was then played continuously until we had moved to within ~10 m of the chickadee(s). If we had not located a chickadee after 30 min, we would leave the site.

Once we were within recording range of a chickadee, we stopped playing the bait tape and recorded five songs.

Next, we played one more bout of each species' song and recorded five more songs. We continued to alternate between playing the bait tape and recording blocks of five songs until the 0.5 h sampling period had expired. Songs were recorded with a Merantz-PMD 222 recorder and a Senheiser parabolic microphone in 1997-2000 and a M-Audio Microtrack II digital recorder and Azden SGM-2X shotgun microphone in 2008. Songs recorded in 1997-2000 were digitized on an Apple G3 power Mac and the Canary program, version 1.2.4 (Chariff et al., 1995); those recorded in 2008 were digitized and analyzed using Raven Pro 1.4 (www.birds.cornell.edu/raven, Charif et al., 2010).

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). We 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, we grouped similar song types together and mapped their distributions (Enstrom, 2000). Dialects were considered to be a group of song types that shared distinctive features and were unique to a locality (Lemon, 1975).

We classified all of the song types present at each site as BCCH, CACH or aberrant based on a set of distinctive spectrographic criteria (DSC) (see Table 1, Enstrom and Bollinger, 2009). The DSC used frequency, duration, and note number to classify the song bouts. We considered a song bout to be all of the individual songs that had been grouped into the same song type at a site. The DSC was developed using known characteristics of CACH and BCCH songs as well as those of CACH and BCCH songs we collected in Illinois (Ward, 1966; Kroodsma et al., 1999; Enstrom, 2000; Enstrom and Bollinger, 2009). Aberrant songs were considered those that shared features of both BCC and CC songs or exhibited unique characteristics.

We also documented the existence of these aberrant songs in March and April 2019 and February and March 2020 (see Thompson 2021). We went to 7 locations within and near Greenville and 3 locations within and near Vandalia to conduct trials documenting response of chickadees to song playback. We began each trial with a 30 second listening period when no playback occurred. After this period, one of 16 exemplars of chickadee song (4 each of either Carolina, Black-capped or aberrant songs from the Greenville or Vandalia dialects – see below) was played for 15 seconds followed by a 30 second listening period during which we documented any chickadee songs or calls that we heard. If no chickadee vocalizations were heard, we repeated this protocol 2 more times with songs from different groups.

RESULTS

Of 276 song bouts recorded in 1997-2000 and 2008, we classified 129 as aberrant based on DSC. These 129 aberrant bouts represented 33 song types sung by chickadees in the Illinois contact zones. We recorded five of these aberrant song types in both time periods in the largest contact zone.

The classification of the aberrant song bouts into types suggested that dialect patterns existed within the largest contact zone. The "Vandalia" dialect consisted of eight aberrant song types (Fig. 1) recorded within 15 km of Vandalia, Illinois in central Fayette County in 1997-2000. Of these, three were still present in 7 of 12 males recorded in 2008 (Fig 2). These songs were united into a dialect by the presence of a three-note whistled phrase that was modified in some cases. The first part of the phrase was a quickly descending note beginning at 8-9 kilohertz (kHz), the second a mid-frequency note at ~5 kHz, and the last a note at ~4 kHz.

The "Greenville" song dialect consisted of two aberrant song types (Fig. 3) and was limited geographically to north-central Bond County. These songs contained pure whistled notes that were all below 5-6 kHz, beginning with a two-note phrase that was very similar to a truncated BCCH song. Most of the Greenville aberrant songs included a very short duration, broad frequency sound (a "click") prior to the third note. One or both of these songs were present in 11 of the 14 males we recorded in 2008 (Fig. 4).

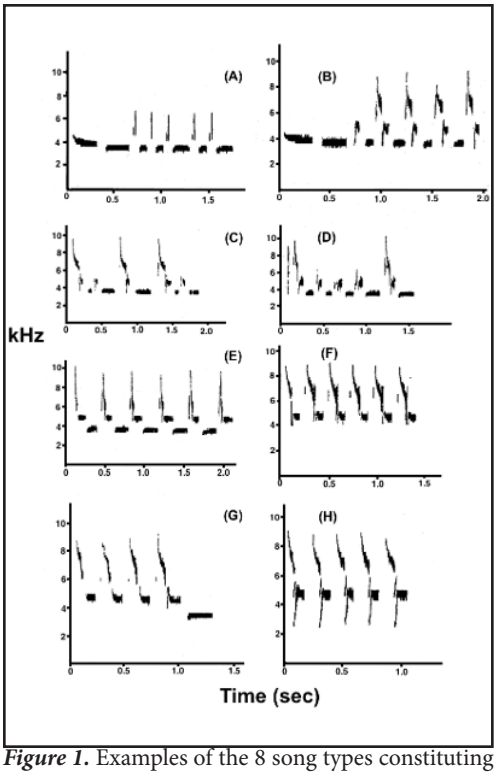

Figure 1. Examples of the 8 song types constituting the Vandalia dialect, recorded in Fayette County in April-June 1999.

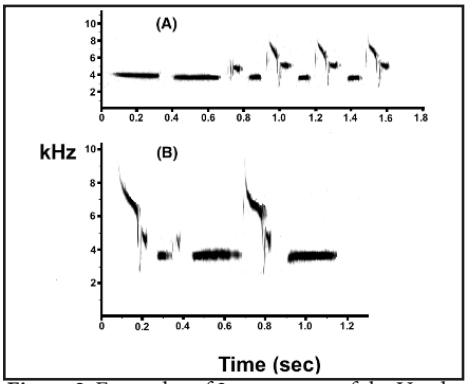

Figure 2. Examples of 2 song types of the Vandalia dialect still present in 2008 (recorded in April 2008). Song type A matches type B from 1999 (Fig. 1B) and song type B matches type C from 1999 (Fig. 1C).

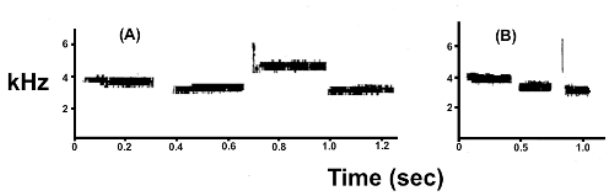

Figure 3. Examples of the 2 song types constituting the Greenville dialect, recorded in Bond County in April-June 1999.

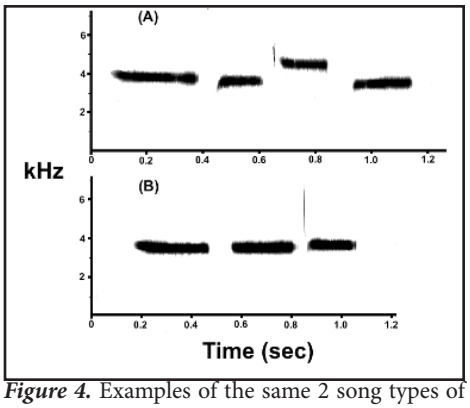

Figure 4. Examples of the same 2 song types of the Greenville dialect seen in Fig. 3, recorded in Bond County in April 2008. Song type B in 2008 no longer has the slightly descending pitch intervals between notes seen in 1999.

In 2019-2020, we documented that 5 of 7 chickadees that vocalized during our trials in the Greenville area produced songs that were easily recognizable as belonging to the Greenville dialect. In addition, 2 of 3 vocalizing chickadees in the Vandalia area produced songs of the Vandalia dialect.

DISCUSSION

Brewer (1963) 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 is a very appropriate mneumonic for one of the most common song types of the Vandalia dialect that was present in both 1998 (Fig. 1B) and 2008 (Fig. 2A). Thus, aberrant singing behavior and probably specific song types have existed in Bond and Fayette counties for at least 60 years. The presence and persistence of dialect types in these areas suggests that at least some aberrant song types represent unique song cultures that have resulted from long-term interactions between Black-capped and Carolina Chickadees. This is also supported by the presence of chickadees singing typical Black-capped songs along the northern border of the contact zone in 1998 (Enstrom 2000). Aberrant song types have been documented for other chickadee contact zones (e.g., Ward and Ward 1974, Robbins et al. 1986, Sattler 1996, Curry 2005, Sattler et al. 2007). 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 and persistence of these dialects may be due to the size and age of the Bond/Fayette contact zone. This contact zone has existed for at least 60 years (Brewer 1959, 1963) and this may have allowed for the sustained interaction of BCCH and CACH song traditions, perhaps helping to promote these unique song dialects. The relatively large size of the contact zone (> 700 km^2) and the limited amount of suitable habitat connecting it to other areas could have also aided in its persistence.

Two hypotheses for the development and persistence of aberrant singing behaviors in contact zones are (1) that they have been culturally selected for, and (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 possess unique characteristics that may allow them to operate as effective signals to both CACH and BCCH. 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. Both Greenville and Vandalia dialects contained song types that began with a relatively low frequency, two-note whistled phrase (suggesting a shortened BCCH song), followed by phrases that were either typical Carolina phrases or ones derived from them. Playback experiments in CACH and BCCH 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 this 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 CACH or BCCH. The repetitious construction and broad frequency coverage of the Vandalia songs is shared with the chick-a-dee call, gargle (rasp) call, and the hi-lo calls of chickadees (Haftorn et. al. 1998). 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; Kroodsma et al., 1999). 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 BCCH 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., 1999). Another possible cause of aberrant songs is the influence of conflicting song models due to the possible influence of chickadees singing BCCH, CACH and aberrant song types (Bjerke, 1982). 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 while attempting to match the songs of males in the contact zone.

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LITERATURE CITED

Bjerke, T.K. (1982). Origin of song traditions in the Redwing *Turdus iliacus*: evidence from field studies. Fauna norv. C. Cinclus, 5, 84-92.

Brewer, R. (1959). Comparative life history of the Carolina Chickadee. Wilson Bulletin, 73, 348-373.

Brewer, R. (1963). Ecological and reproductive relationships of Black-capped and Carolina Chickadees. Auk, 80, 9-47.

Bronson, C.L., Grubb, Jr., T.C., Sattler, G.D. & Braun, M.J. (2005). Reproductive success across the Black-capped Chickadee (*Poecile atricapillus*) and Carolina Chickadee (*P. carolinensis*) hybrid zone in Ohio. Auk, 122, 759-772.

Charif, R.A., Mitchell, S. & Clark, C.W. (1995). Canary 1.12 User's Manual. Cornell Lab of Ornithology, Ithaca, New York.

Charif, R.A., Waack, A.M. & Strickman, L.M. (2010). Raven Pro 1.4 User's Manual. Cornell Lab of Ornithology, Ithaca, New York.

Curry, R.L. (2005). Hybridization in chickadees: much to learn from familiar birds. Auk, 122, 747-758.

Enstrom, P.C. (2000). Patterns and implications of aberrant singing behaviors of Black-capped (*Poecile atricapillus*) and Carolina (*P. carolinensis*) chickadees in Illinois. M.S. thesis. Eastern Illinois University, Charleston, IL.

Enstrom, P.C. & Bollinger, E.K. (2009). Stability in distributions of Black-capped, Carolina, and aberrant chickadee song types in Illinois. Wilson Journal of Ornithology, 121, 265-272.

Grubb Jr., T.C., Mauck, R.A. & Earnst, S.L. (1994). On no-chickadee zones in Midwestern North America: evidence from the Ohio Breeding Bird Atlas and the North American Breeding Bird Survey. Auk, 111, 191-197.

Haftorn, S., Huang, W., Griswold, C.K. & 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

Kroodsma, D.E., Albano, D.J. & Wells, J.A. (1995). Song development by Black-capped (*Parus atricapillus*) and Carolina Chickadees (*P. carolinensis*). Auk, 112, 29-43.

Kroodsma, D.E., Byers, B., Halkin, S., Hill, C., Minis, D., Bolsinger, J., Donelan, E., Farrington, J., Gill, F.B., Houlihan, P., Innes, D., Keller, G., MacCaulay, L., Marantz, C.A., Ortiz, J., Stoddard, P.K. & Wilda, K. (1999). Geographic variation in Black-capped Chickadee songs and singing behavior. Auk, 116, 387-402.

Lemon, R.E. (1975). How birds develop dialects. Condor, 77, 385-406.

McGregor, P.K., & Krebs, J.R. (1982). Song types in a population of great tits (*Parus major*): their distributions, abundance and acquisition by individuals. Behaviour, 79, 126-152.

Merritt, P.G. (1978). Characteristic of Black-capped and Carolina chickadees at the range interface in northern Indiana. Jack Pine Warbler, 56, 170-179.

Reudink, M.W., Mech, S.G. & Curry, R.L. (2007). Structure and dynamics of the Black-capped Chickadee (*Poecile atricapillus*) and Carolina Chickadee (*P. carolinensis*) hybrid zone in southeastern Pennsylvania. Auk, 124, 463-478.

Rising, J.D. (1968). A multivariate assessment of interbreeding between chickadees *Parus atricapillus* and *P. carolinensis*. Systematic Zoology, 17, 160-169.

Robbins, M.B., Braun, M.J. & Tobey, E.A. (1986). Morphological and vocal variation across a contact zone between the chickadees *Parus atricapillus* and *Parus carolinensis*. Auk, 103, 655-666.

Sattler, G.D. (1996). The dynamics of vocal, morphological and molecular interaction between hybridizing Black-capped and Carolina Chickadees. Ph.D. dissertation, University of Maryland, Amherst, MA.

Sattler, G.D. & Braun, M.J. (2000). Morphometric variation as an indicator of genetic interactions between Black-capped and Carolina chickadees at a contact zone in the Appalachian Mountains. Auk, 117, 427-444.

Sattler, G.D., Sawaya, P.L. & Braun, M.J. (2007). An assessment of song admixture as an indicator of hybridization in Black-capped (*Poecile atricapillus*) and Carolina chickadees (*P. carolinensis*). Auk, 124, 926-944.

Sawaya, P.L. (1990). A detailed analysis of the genetic interaction at a hybrid zone between chickadees *Parus atricapillus* and *P. carolinensis* as revealed by nuclear and mitochondrial DNA restriction fragment length variation. Ph.D. dissertation, University of Cincinnati, Cincinnati, Ohio.

Smith, S.T. (1972). Communication and other social behavior in *Parus carolinensis*. Publications of the Nuttal Ornithology Club No. 11. Cambridge, MA.

Thompson, V. (2021). Remapping the chickadee contact zone in Illinois using response to song playback. Undergraduate honors thesis, Eastern Illinois University, Charleston, IL.

Ward, R. (1966). Regional variation in the song of the Carolina Chickadee. Living Bird, 5, 127-150.

Ward, R. & Ward, D.A. (1974). Songs in contiguous populations of Black-capped and Carolina chickadees in Pennsylvania. Wilson Bulletin, 86, 344-356.

Weise, C.M. & Meyer, J.R. (1979). Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee. Auk, 96, 40-55.