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Adaptive Significance of Aberrant Chickadee Song in Illinois

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ABSTRACT

I studied the behavioral responses of Black-capped (*Poecile atricapilus*) and Carolina (*P. carolinensis*) chickadees to playback of Black-capped, Carolina, and aberrant chickadee songs throughout the state of Illinois. These two species are parapatrically distributed throughout the eastern United States, including Illinois. Some areas exist where the ranges of the two species overlap. Individuals in these contact zones often sing aberrant vocalizations. This study focused on the two parental vocalizations (i.e., Black-capped and Carolina song), and two of the most common aberrant vocalizations (the 'Greenville' and 'Vandalia' aberrant dialects), in an attempt to understand the adaptive significance of these aberrant songs. Playback experiments were conducted from March to June in 2011 and 2012 in 28 counties throughout Illinois. During playback trials, behavioral response data were collected and compared among the four different chickadee playback vocalizations; Black-capped, Carolina, and Greenville and Vandalia aberrant dialects. Black-capped and Carolina chickadees displayed their most aggressive responses to conspecific playback. However, contact zone individuals responded aggressively to all playback types. Aberrant vocalizations elicited largely intermediate responses from Black-capped and Carolina Chickadees. We found no differences in behavioral responses to playback when comparing responses of parental populations within 50 km and farther than 50 km from the contact zone. Due to the numerous aberrant dialects and parental songs that exist throughout the contact zones, it may be necessary for contact zone individuals to recognize and respond to most chickadee-like song types in order to establish and defend territories, and to attract mates. Intermediate responses to aberrant vocalizations by parental birds could be due to certain syllabic cues within the aberrant songs that elicit aggressive response.

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INTRODUCTION

Hybrid zones offer a unique opportunity to study speciation and the evolutionary biology of closely-related species. Hybridization among avian taxa has resulted in intermediate behavior (e.g., Payne 1980), plumage (e.g., McDonald et al. 2001), and song (e.g., Emlen et al. 1975), and is expected to occur in one in ten species (Grant and Grant 1992). Examining vocalizations in contact zones can be a functional method for understanding the structures of these areas, and the dynamics of hybridization and interactions between closely-related species. Vocalizations of hybrid individuals have been shown to be highly variable and to differ from parental vocalizations in multiple taxa, including deer (e.g., Long et al. 2006), frogs (e.g., Gerhardt 1974; Doherty and Gerhart, 1983), apes (e.g., Tenaza 2005), and birds (e.g., Emlen et al. 1975; den Hartog et al. 2007).

Many studies have investigated the behavioral responses of contact zone individuals to playback, and have considered the responses as individual and local phenomena, or as having adaptive value (e.g., Emlen et al. 1975, den Hartog et al. 2007). For example, indigo buntings (*Passerina cyanea*) and lazuli buntings (*P. amoena*) sang and responded to heterospecific and conspecific songs equally in a sympatric population in Nebraska (Emlen et al. 1975). These same buntings were interspecifically territorial, defending territories against conspecifics, heterospecifics, and intermediate individuals. Emlen et al. (1975) proposed that these behaviors were a result of individual encounters, and individual behavior is determined by previous experiences with birds with heterospecific plumage or song type. In two species of closely related African doves, males in the hybrid zone did not respond differently to the two parental vocalizations and one hybrid vocalization (den Hartog et al. 2007). However in areas outside the contact zone, males responded more to conspecific than heterospecific vocalizations (den Hartog

et al. 2007). Den Hartog et al. (2007) suggested that intermediate vocalizations within the contact zone function similarly to parental vocalizations that are outside of the contact zone, and they hypothesized that these vocalizations play a large role in maintaining the stability of the contact zone.

We studied the behavioral responses of Carolina (*Poecile carolinensis*) and Black-capped (*P. atricapillus*) chickadees to song playback throughout Illinois. These two small songbird species are very similar in morphology, behavior, and ecology (Mostrom et al. 2002; Smith 2010), and are parapatrically distributed across the eastern United States from New Jersey to Kansas (Mostrom et al. 2002; Smith 2010). Black-capped chickadees (BCCH) occupy a large area throughout most of northern North America. Carolina chickadees (CACH) have a smaller range primarily in the southeastern United States.

At certain areas along the boundary between these two species, contact zones exist where both species coexist (or coexisted in the past). Contact zone interactions between these two species have been documented by multiple studies throughout many states including; Kansas (Rising 1968), Missouri (Robbins et al. 1986), Illinois (Brewer 1963; Kershner and Bollinger 1999; Enstrom and Bollinger 2009), Ohio (Bronson et al. 2005), Pennsylvania (Curry et al. 2007), North Carolina (Tanner 1952), and Virginia (Johnston 1971). These contact zones can range from nonexistent (Grubb et al. 1994), to as large as 50 km wide (Curry et al. 2007). Mixed species pairings in these areas have been documented, and are even considered common (Brewer 1963; Rising 1968; Robbins et al. 1986; Curry et al. 2007).

These documented mixed species pairings have resulted in phenotypic and genetic hybrid individuals (Johnson 1971; Robbins et al. 1986; Curry et al. 2007). Measurements of tail/wing ratios and weights of birds have been used to suggest that both phenotypic hybrids and parental

birds are present in contact zone areas of Virginia (Johnston 1971) and Missouri (Robbins et al. 1986). Hybridization is considered to be extensive in some contact areas (Robbins et al. 1986; Reudink et al. 2007), but rare in others (Merritt 1981). It was also suggested that hybridization between these two species will probably occur when these species are sympatrically associated during a breeding season (Johnston 1971). In Illinois, Brewer (1963) found multiple mixed pairs, but noted that those pairs had lower nest success, and estimated that reproductive success was significantly lower than in conspecific pairs (see also Bronson et al. 2005).

In their traditional ranges, BCCH sing a lower pitched 2-3 note song ("Fee-bee"), whereas CACH sing a higher pitched 4 note song ("Fee-bee, fee-bay") (Mostrom et al. 2002; Smith 2010). However, individuals in contact zones can have complex aberrant song repertoires that vary significantly from traditional parental songs (Brewer 1963; Ward and Ward 1974; Robbins et al. 1986; Enstrom and Bollinger 2009) with high variability in song composition (Robbins et al. 1986). For this study, we define aberrant songs as those given by chickadees that contain parts of either (or both) parental songs, or have characteristics of neither song type. These aberrant songs in Illinois were originally defined by Enstrom and Bollinger (2009) through distinctive spectrographic criteria. Aberrant songs have been documented at multiple areas where the two species overlap (Brewer 1963; Johnston 1971; Ward and Ward 1974; Merritt 1981; Enstrom and Bollinger 2009).

We investigated a historic contact zone in central Illinois that has remained relatively unchanged since it was first documented in the late 1950s (Brewer 1963), despite the northward shifting of contact areas in other locations (Bronson et al. 2005; Curry 2005; Reudink et al. 2007). Aberrant vocalizations in this area have also remained fairly stable since first documented (Brewer 1963; Enstrom and Bollinger 2009). While at least nine aberrant song types have been

documented in Illinois (Enstrom and Bollinger 2009), we chose to focus on the two most common dialects. These two song types are present in and around Bond and Fayette Counties. Individuals near Greenville, in Bond County, sing a three note "fee-bee-bee" that most typically follows the descending pitch of "three–blind–mice". Individuals near Vandalia, in Fayette County, sing an aberrant "fee-bee-ka-bee-ka-bee-ka-bee-ka-bee". Bilingual individuals in this area have also been observed singing other aberrant vocalizations and a typical CACH song (personal observation).

Songs in contact zones of these chickadees have proven to be poor indicators of genotype (Kroodsma et al. 1995), and caution must be used when drawing conclusions about hybridization by only examining vocalizations (Sattler et al. 2007). In the laboratory, Kroodsma et al. (1995) demonstrated that chickadees are able to learn heterospecific songs. In southeastern Pennsylvania, males that sing normal BCCH songs can have CACH mtDNA and microsatellite genotypes that are consistent with hybrid individuals (Curry et al. 2007). In that area, the BCCH song remained the dominant song even though males may be genetically 'pure' CACH (Curry et al. 2007). While hybridization is expected to be extensive (as shown in other chickadee contact zones; Robbins et al. 1986; Curry et al. 2007; Reudink et al. 2007), and mixed pairings in Illinois have been inferred (Brewer 1963), the genetics of Illinois contact zone birds have not yet been determined. Therefore, we are careful to omit the term 'hybrid', and prefer to refer to these birds that sing aberrant vocalizations as 'contact zone' individuals.

The main goal of this study was to investigate the most common aberrant dialects (described above), and attempt to understand the significance of these aberrant vocalizations and their relation to parental songs in all regions of the state. Robbins et al. (1986) suggested that birds will respond more to the song type that is used most frequently in the local population.

Thus, we predicted that BCCH would respond more to BCCH playback than CACH playback, and that CACH would respond more to CACH playback than to BCCH playback. We also predicted that contact zone individuals would respond most to aberrant playback. However, we were not sure what to expect regarding BCCH and CACH responses to aberrant song or contact zone individuals' responses to parental songs. Finally, we collected data from locations farther from the contact zone in the ranges of both parental species to compare with data collected closer to the contact zones to investigate potential familiarity with congeners occurring in individuals that were closer to the contact zones.

METHODS

Data were collected from 15 March - 15 June in 2011 and 2012 during the peak of both species' breeding seasons (Mostrom et al. 2002; Smith 2010) from 28 counties throughout the state: most data were collected at Illinois Department of Natural Resources (IDNR) state parks and state recreation areas. Other locations included county forest preserves (Champaign, Cook, and Lake Counties), city parks, and residential neighborhoods. These localities were chosen due to their ease of access to chickadee breeding habitat.

We collected most parental songs for playback treatments in February 2011. However, to ensure five high-quality songs from each parental species, three songs were selected from the Cornell Macaulay Library of Natural Sounds for their clarity and recording quality; including ML 128911 (CACH from AR), ML 129810 (CACH from AR), and ML 105210 (CACH from TX). Two songs were also used from audio files in an audiobook field guide (Elliott et al. 1997). All aberrant songs were recorded from March to April 2008 by P. Enstrom and S. Wayman in the contact zones in the Greenville and Vandalia areas.

Five exemplars of each of the four song types (Black-capped, Carolina, Greenville, and Vandalia) were used for a total of twenty playback treatments. Multiple exemplars of each song type were used to limit pseudoreplication that occurs in studies using only one exemplar (Kroodsma 1989).

Playback exemplars were created and edited with RavenPro® software (Cornell Laboratory of Ornithology, 2010). This software allowed for removal of background noise from the original recordings, and for the creation of precise time intervals and constant volume for all treatments. Each playback recording consisted of the same song exemplar repeated at three second intervals for one minute, followed by ten seconds of silence. This pattern was repeated four more times for a total of five minutes of song playback for each playback treatment.

Each five minute trial was divided into five one-minute intervals. Data were recorded while maintaining visual contact with the focal individual. We also used an Olympus® WS-700M digital voice recorder (Olympus America Inc., 2009). For each minute, the number of songs, chick-a-dee calls, and gargles (as defined by Mostrom et al. 2002 and Smith 2010), and the individuals' closest approach to the speaker were all recorded.

Once an individual bird was located, the researcher moved to within 10 meters of the individual and played the playback treatment; either a Black-capped, Carolina, Greenville, or Vandalia song. We randomly selected the playback treatment order without replacement, and then repeated this random selection process after each set of twenty individuals. Each individual chickadee was only presented with one treatment. Songs were played with a FOXPRO® Firestorm (FOXPRO Inc., 2009) field speaker that was placed on the ground with the enabled speaker facing upward. The observer stood approximately three meters from the speaker during all trials. Trials were not conducted if there were multiple singing males in the area. Since the

average breeding territory size for CACH is 1.6-2.4 ha (Mostrom et al. 2002) and 1.5-5.3 ha for BCCH (Smith 2010), for subsequent focal individuals we moved greater than or equal to 1 km from the previous trial location in order to yield naïve birds that were not previously exposed to the playback recordings. GPS coordinates were taken at each trial location with a Garmin® eTrex H (Garmin LTD., 2007) handheld GPS unit.

Whereas some hybrid zone playback studies have recorded pre-playback behavior and compared that to playback behavior (den Hartog et al. 2007; Dingle et al. 2010), we did not document pre-playback behavior as we are more interested in behavioral comparisons across song types. Initially, we included a Carolina Wren, CAWR, (*Thryothorus ludovicianus*) vocalization as a control after every ten trials in order to ensure that chickadees were responding to our chickadee vocalizations, and not just to sound emitted from a speaker. We chose this species as it occupies habitats similar to these chickadee species (Haggerty and Morton 1995), and chickadees would presumably recognize this song as a non-threatening familiar individual within the same area. Kershner and Bollinger (1999) used playback of a white-breasted nuthatch (*Sitta carolinensis*) song to establish a baseline level of chickadee aggressive response. Although their results indicated that chickadees were able to distinguish chickadee vocalizations from a non-chickadee species, we wanted to include our own control vocalization that matched our playback and data collection protocols. This control exemplar, also created in RavenPro®, followed the same methodology as the chickadee playback treatments. However, because we saw virtually no aggressive responses after the first seven CAWR trials, we terminated these control trials.

We grouped our data into three response behaviors; total number of vocalizations made during the trial period, the closest approach to the speaker, and the amount of time that an

individual spent within 5 meters of the speaker. Combinations of these categories have been used in studies with chickadees (and other avian species) to measure aggressive response (e.g., Schroeder and Wiley 1983; Brindley 1991; Shackleton et al. 1992; Lovell and Lein 2004; Searcy et al. 2006). We compared mean values of behavioral responses among three types of focal chickadees; BCCH, CACH, and contact zone chickadees. Contact zone individuals were birds in the contact zone areas that sang aberrant, non-parental songs. Songs were determined as aberrant by spectrographic criteria established by Enstrom and Bollinger (2009). We found no focal individuals near the contact zones that sang pure parental songs (per the aforementioned spectrographic criteria). The mean values for each of our four playback treatments were analyzed with a series of single factor analyses of variance (ANOVA) by using the ProcGLM procedure in SAS (SAS Institute, 2010).

GPS coordinates were analyzed with the Near function in ArcGIS (Esri, 2010) to determine which parental individuals (BCCH and CACH) were within 50 km of the contact line, and which were farther than 50 km from the contact line. The three behavioral responses of the parental species were compared with respect to distance group (<50 km and >50 km from the contact line) for each of the four playback treatments with a series of comparisons of means.

RESULTS

BCCH responses – Results of the single factor ANOVAs comparing means of BCCH responses to playback indicate that BCCH individuals responded with significantly more vocalizations to BCCH playback than CACH playback ($P = 0.028$). BCCH birds approached the speaker closer to BCCH playback than to CACH playback ($P = 0.014$). BCCH also approached the speaker closer to Greenville playback than to CACH playback ($P = 0.019$). BCCH closest approach did not differ between CACH playback and Vandalia playback ($P = 0.465$). BCCH closest approach

did not differ between Greenville playback and Vandalia playback (0.130). BCCH spent more time closer to the speaker during BCCH playback than during CACH playback (P = 0.003). BCCH also spent more time closer to the speaker in response to Greenville playback than to CACH playback (P = 0.003) (Figure 1). Thus, overall, BCCH response to aberrant playback was intermediate (not as aggressive as response to BCCH playback, but more aggressive than response to CACH playback) for all three behavioral response categories (Figure 2).

CACH responses – Results of the single factor ANOVA tests comparing means of CACH responses to playback treatments indicate that CACH individuals responded with significantly more vocalizations to CACH playback than to BCCH playback (P = 0.002). CACH approached the speaker closer to CACH playback than to BCCH playback (P = 0.046). CACH also spent more time closer to the speaker to CACH playback than to BCCH playback, however this value was not statistically significant (P = 0.238) (Figure 1). Trends suggest that CACH response to aberrant playback was intermediate for all three behavioral response categories (Figure 2).

Contact Zone responses – Contact zone individuals responded similarly to all four playback treatments in all three behavioral response categories (all P > 0.05). In addition, contact zone birds, on average, gave more vocalizations, approached closer, and spent more time close to the speaker than BCCH and CACH in their responses to the playback treatments (Figure 1).

Responses of BCCH and CACH to heterospecific song – Results of single factor ANOVAs showed that the responses of BCCH to CACH playback, and CACH to BCCH playback did not differ significantly in terms of total number of vocalizations (P = 0.24), mean closest approach to the speaker (P = 0.12), and mean amount of time spent within 5m of the speaker (P = 0.72).

Distance from contact line – For parental populations, the proximity to the contact zone did not appear to affect the responses for either species. No recorded behavioral responses to playback

were significantly different when comparing responses of populations greater than (far) and less than (near) 50 km from the closet point of the line of contact for either BCCH or CACH (Figure 3).

Use of multiple exemplars – We found no differences in the behavioral responses of conspecific individuals to the five playback exemplars for each species or dialect. BCCH behavioral responses to the five BCCH playback exemplars did not differ significantly for total vocalizations, closest approach, or time close to the speaker ($P = 0.11$, $P = 0.95$, $P = 0.69$, respectively). CACH behavioral responses to the five CACH playback exemplars also did not differ significantly for total vocalizations, closest approach, or time close to the speaker ($P = 0.36$, $P = 0.34$, $P = 0.18$, respectively).

Control trials – Chickadees were grouped into two categories; responding to any chickadee playback, and responding to CAWR playback. Results of single factor ANOVAs show that Chickadees responded more to any chickadee playback than to CAWR playback (all $P < 0.005$) (Figure 4).

DISCUSSION

Both BCCH and CACH responded more to conspecific song than to heterospecific songs. These parental individuals would presumably be most familiar with the local song from their conspecific neighbors. They should also respond more aggressively to their conspecific song for territorial defense, and as a way of familiarizing themselves with neighbors and their territories. This result was seen in a previous study with chickadees (Robbins et al. 1986).

Contact zone birds displayed similar behavioral responses to all playback treatments. Trends in the data also suggest that these contact zone birds were the most aggressive in their responses to playback. While this study focused on the two main aberrant dialects in Illinois,

seven others are considered common in the state, and numerous additional aberrant vocalizations have been documented (Enstrom and Bollinger, 2009). It may be necessary for contact zone individuals to recognize numerous song types. In an area in which numerous dialects occur, recognition and response may be imperative for territory establishment and defense, neighbor recognition, and responding to intruders. Additionally, as chickadee song is learned (Kroodsma et al. 1995), learning from parents and neighbors with a collective repertoire of multiple aberrant dialects may result in contact zone birds recognizing and responding aggressively to any song sharing acoustic similarity to a parent's song.

While responses of parental birds to conspecific songs and responses of parental birds to aberrant songs tend to be statistically indistinguishable, trends within the data suggest intermediate responses. This type of intermediate response was documented with responses to aberrant vocalizations from a contact zone of two closely-related species of African doves. They found that birds showed more response to conspecific vocalizations than to heterospecific playback, and found that response to hybrid vocalizations was intermediate (den Hartog et al. 2007). Another study with closely-related African *Streptopelia* doves suggested that responses to allopatric vocalizations would vary based on the acoustic similarity to conspecific or sympatric vocalizations (De Kort and Ten Cate 2001). They also concluded that in addition to vocalization structure varying with relatedness, individual perception of vocalizations can vary based on experience (De Kort and Ten Cate 2001). A study examining a hybridizing population of indigo and lazuli buntings (*Passerina cyanea, P. amoena*) presented birds with altered song playbacks (Baker 1991). Baker (1991) used a playback of indigo syllables with a lazuli temporal pattern, and a playback of lazuli syllables with an indigo temporal pattern. He found that responses of allopatric birds were determined by syllabic cues and not by the temporal pattern of the song

(Baker 1991). As these aberrant chickadee vocalizations may contain characteristics of both parental song types (Enstrom and Bollinger 2009), we would expect some type of response from, for example, a BCCH if an aberrant vocalization contained BCCH-like elements (e.g. slower song frequency, lower pitch interval, lower number of notes per song, etc.). It is possible that response from parental species to these aberrant vocalizations also varies based on the structure of the song being presented. The majority of the aberrant song types recorded in Illinois contain introductory phrases that are similar to typical BCCH song (Enstrom and Bollinger 2009). Perhaps most notably, the Greenville dialect starts with a two-note phrase that is similar in frequency to a typical BCCH song (Enstrom and Bollinger 2009). However, the phrase duration is shorter and more similar to a typical CACH song. In addition, these aberrant songs frequently contain high frequency, '"click"-like' elements that are also common components of CACH song. With aberrant vocalizations containing elements of both parental song types, a parental bird could be responding to a particular syllabic cue or phrase within the song which elicits a response that is less aggressive than conspecific playback, but more aggressive than heterospecific playback. Further investigation would be necessary to compare responses from partial songs, or from playbacks that have been manipulated to express different song characteristics and syllabic cues, to determine which syllabic cues elicit aggressive response.

We expected CACH birds to show a more aggressive response to heterospecific playback than BCCH birds due to previous research in Illinois that indicated CACH responded more aggressively to heterospecific playback than BCCH (Kershner and Bollinger 1999). However, our results showed that CACH and BCCH birds did not respond differently to heterospecific songs. Kershner and Bollinger (1999) noted that the CACH that responded most aggressively to vocalizations were concentrated in Fox Ridge State Park in Coles County, IL, that is

approximately 20 km from the contact line. This area is near the northernmost limit of CACH range in that area (Enstrom and Bollinger 2009). Due to a lack of habitat north of this park, it is possible that there is a bottlenecking of CACH individuals occurring in this area that have tried to expand northward. A higher concentration of birds in the area could lead them to be more responsive (and aggressive) to neighbors. One study of conspecific bluebirds (*Sialia sp.*) in the western United States showed that the most aggressive individuals were at the invasion front with less aggressive individuals away from the invasion front (Duckworth and Badyaev 2007). As this area is near the northernmost extent of CACH in the area, perhaps the most aggressive individuals are in this area and would show more response to playback than individuals farther from the contact zone. As our data were collected throughout the state, it is possible that the inclusion of more individuals from multiple areas leads to a more accurate picture of how birds throughout the state respond rather than individuals within a specific area.

We found no difference in the comparisons of behavioral responses from those individuals within 50 km of the contact line ('near' birds), and those farther than 50 km from the contact line ('far' birds). These results are consistent with Kershner and Bollinger (1999) who found no increase in aggression towards heterospecifics closer to the contact zone. This could be because of a lack of interaction between the two species. Other than the few, relatively small contact areas, latitudinal gaps appear to exist in which unfavorable habitat prevents the two species from interacting more closely (as in Grubb et al. 1994). With these gaps, it may not be necessary for a 'near' parental individual to respond to heterospecific chickadee vocalizations any more aggressively than a 'far' bird as territory defense would only be between conspecifics, regardless of distance from the contact line.

Horn et al. (1992) found that chickadees can match their song to playback tapes. This means that there could be bias towards the exemplar used in the playback treatment. This bias becomes important to note especially while examining behavioral responses of individuals in contact zones where bilingual individuals have been reported (Ward and Ward 1974, personal observation). For example, a bilingual contact zone individual responding to CACH playback with CACH song would have been labeled a CACH bird in our data analysis. We tried to eliminate as much area for this bias as possible by using multiple exemplars of playback treatments, and by following a specific order of those playback exemplars.

An interesting area would be to study the responses of contact zone individuals in Pennsylvania or Missouri (for example) to the most common Illinois aberrant dialects, and compare the behavioral responses from Illinois dialects to the aberrant dialects that are more common in those areas. Those comparisons could shed light on how localized these aberrant dialects are in relation to specific contact zone areas. Furthermore, those comparisons could show that contact zone individuals can recognize a vast repertoire of aberrant vocalizations, and not just vocalizations common in Illinois contact zones.

In conclusion, we observed that contact zone individuals responded similarly to all chickadee playback, most likely due to the presence of numerous aberrant dialects within the contact zones, and the necessity of responding aggressively to anything with chickadee-like song characteristics in the contact zone. Parental birds responded intermediately to aberrant song playback. Intermediate responses to these aberrant songs are probably due to specific syllabic cues within the songs that elicit aggressive response from parental individuals. We observed no difference in aggressive response to heterospecific song between 'near' and 'far' chickadees. This indicates a lack of heterospecific interaction between 'near' birds, and reinforces previous

research regarding gaps of favorable habitat between the two species' ranges. Future research may indicate which specific syllabic cues within songs elicit aggressive response. Additionally, a more detailed analysis of 'near' and 'far' birds may paint a more accurate picture of heterospecific interactions that occur closer to contact zones.

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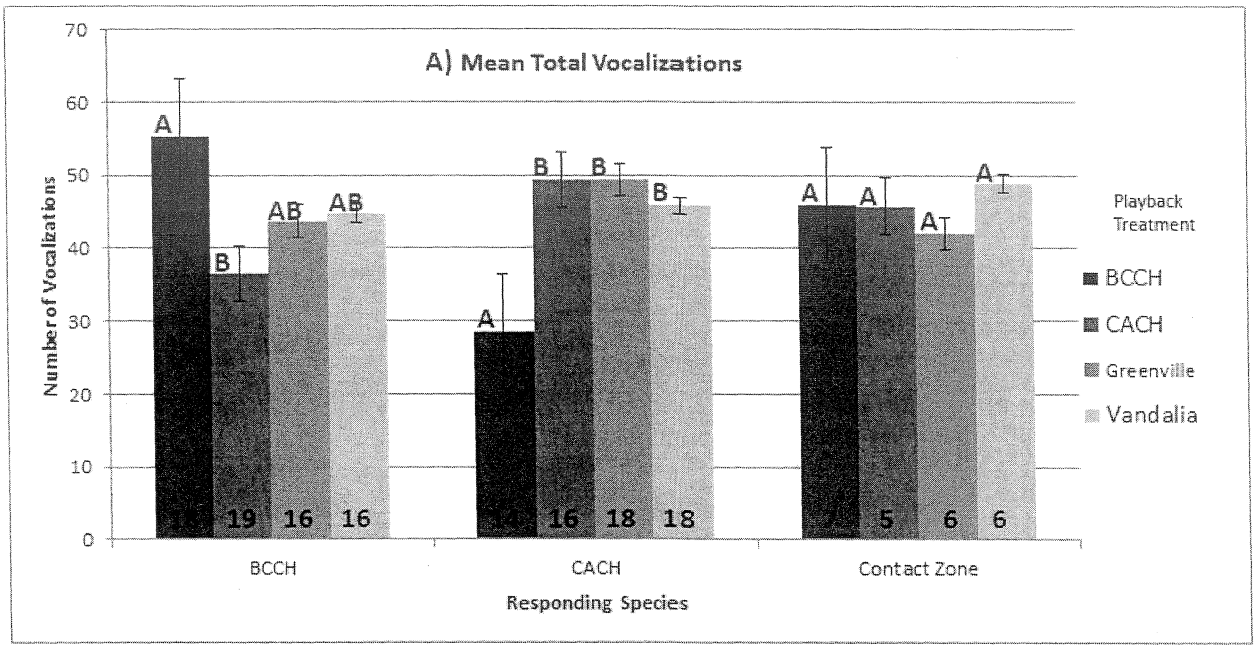
A) Mean Total Vocalizations
Number of Vocalizations
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50
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30
20
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A
B
AB
AB
A
B
B
B
A
A
A
A
19
16
16
16
18
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5
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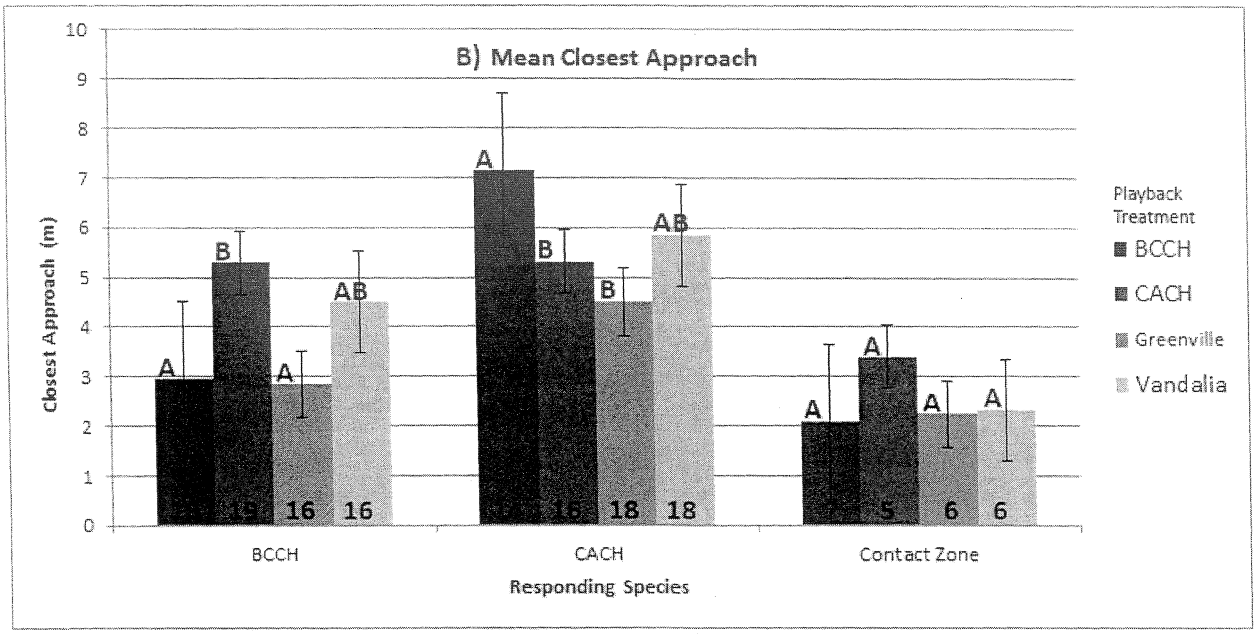
6
BCCH
CACH
Contact Zone
Responding Species
Playback Treatment
BCCH
CACH
Greenville
Vandalia


B) Mean Closest Approach
Closest Approach (m)
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AB
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AB
A
A
A
A
19
16
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Greenville
Vandalia

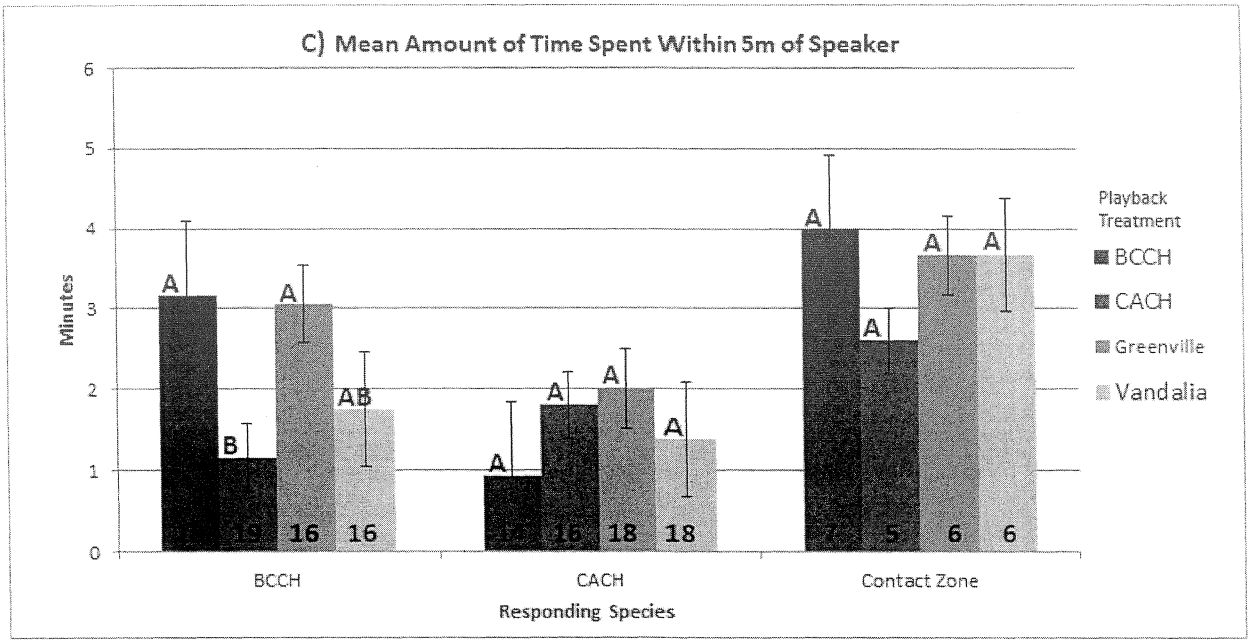
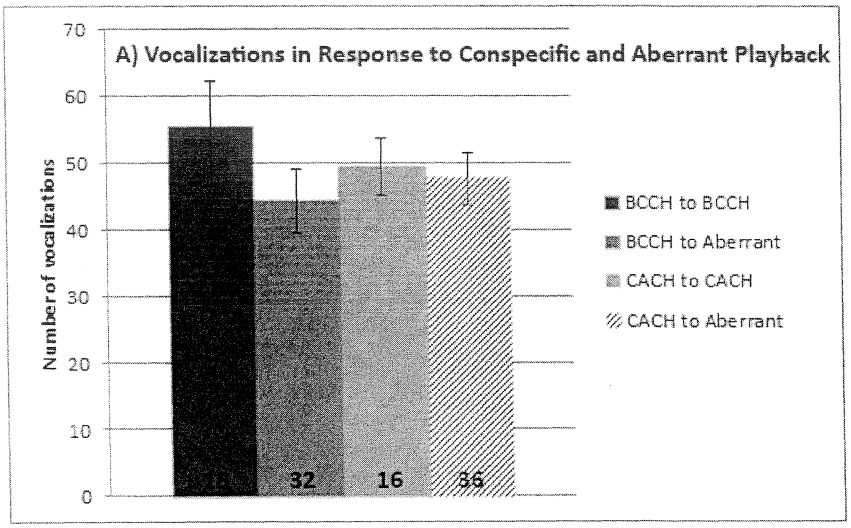
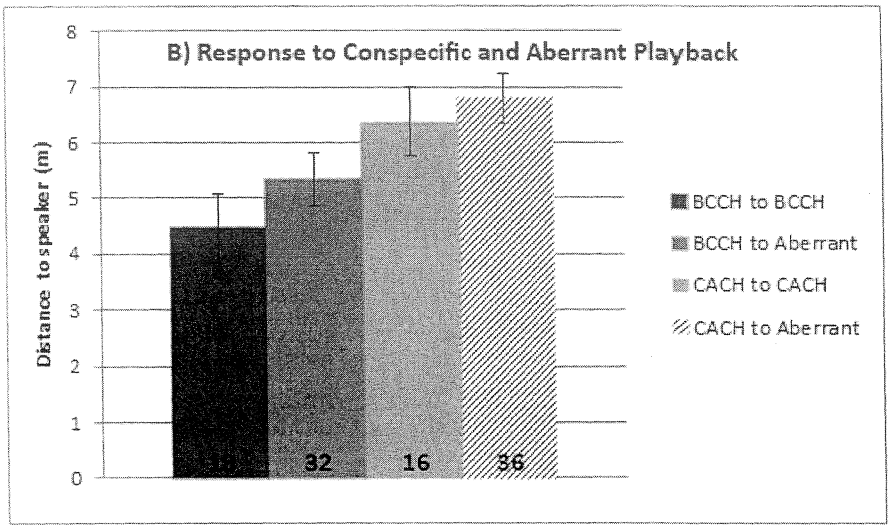


Figure 1. Comparisons of means for the three major behavioral response categories for each responding species type: (a) total number of vocalizations, (b) closest approach, (c) amount of time spent within 5 meters of the speaker. Bars with the same letter are not statistically different ($P > 0.05$). Sample sizes are shown at the bottom of columns.





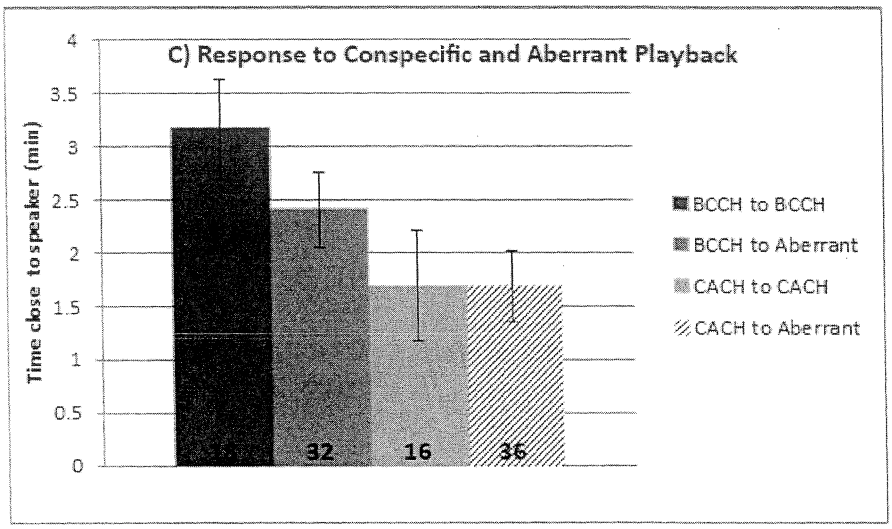


Figure 2. Comparisons of means for responses to conspecific playback and parental responses to aberrant playback for the three behavioral response categories; (a) total number of vocalizations, (b) closest approach, (c) amount of time spent within 5 meters of the speaker. While no comparisons are statistically different ($P > 0.05$), the trends within these data show less aggressive response from parental birds to aberrant vocalizations. Sample sizes are shown at the bottom of columns.

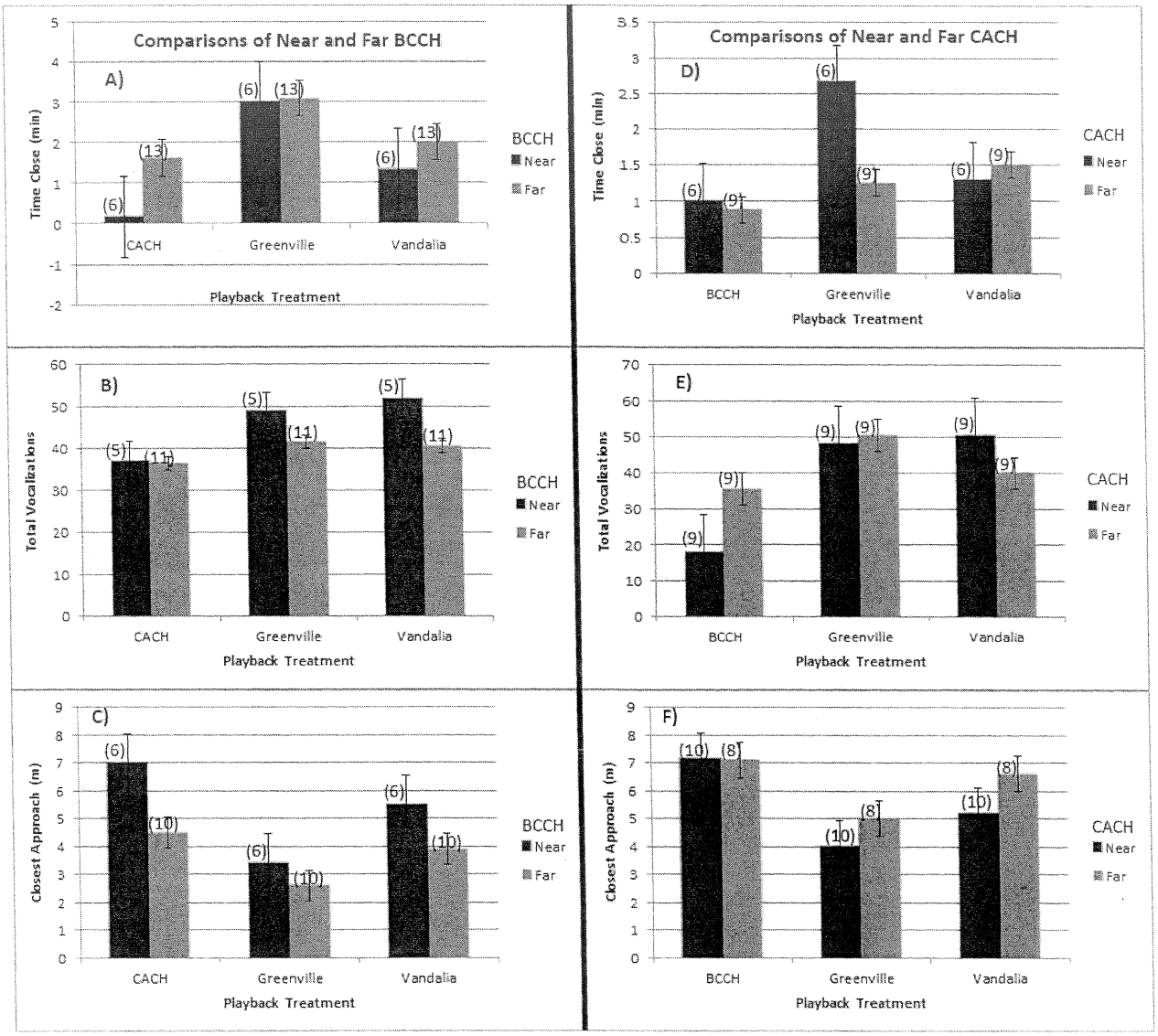


Figure 3. Comparisons of response categories of 'near' birds (recorded within 50 km of the contact line) and 'far' birds (recorded greater than 50 km from the contact line). A) BCCH response measured by mean amount of time (min) spent within 5 m of speaker. B) BCCH response measured by the total number of vocalizations given during the playback trial. C) BCCH response measured by the closest approach to the speaker. D) CACH response measured by mean amount of time (min) spent within 5 m of speaker. E) CACH response measured by the total number of vocalizations given during the playback trial. F) CACH response measured by the closest approach to the speaker. No comparisons were significantly different.

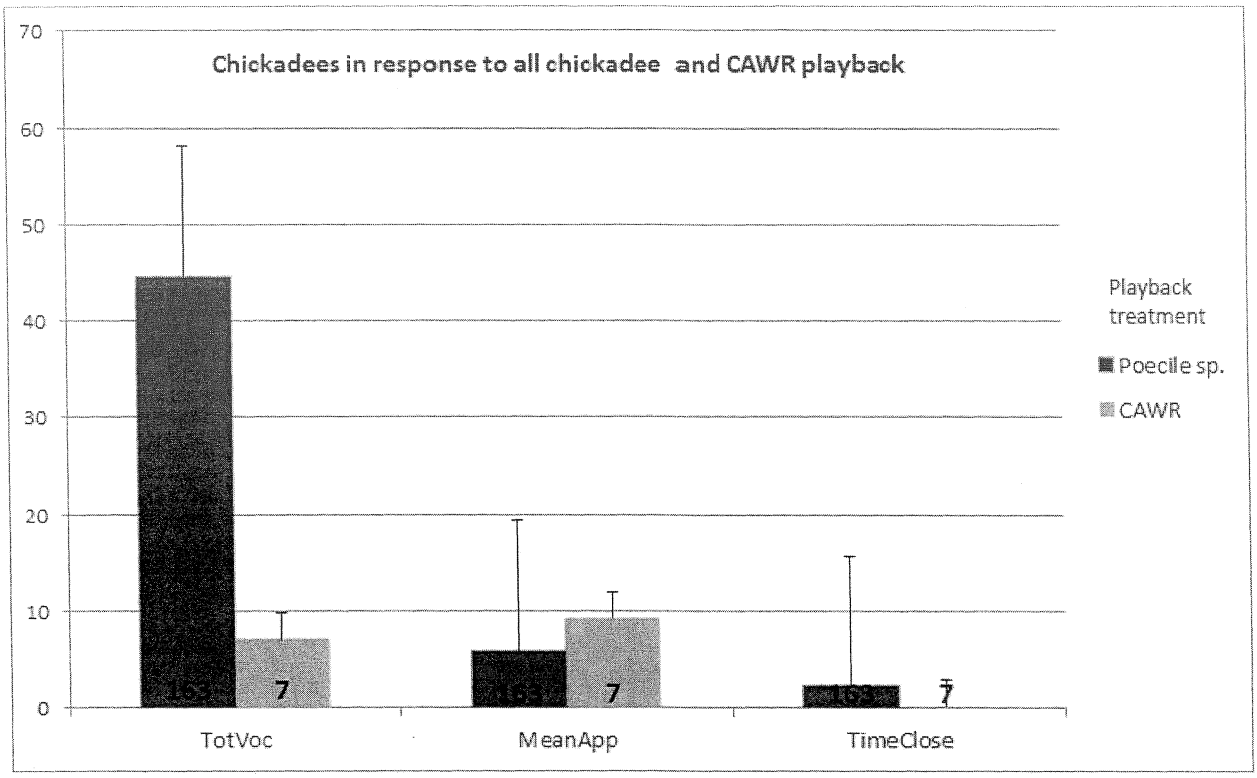


Figure 4. Behavioral responses of chickadees to any chickadee playback treatment compared to responses to CAWR playback. Chickadees responded more aggressively to any chickadee playback than to CAWR playback (all $P < 0.005$).

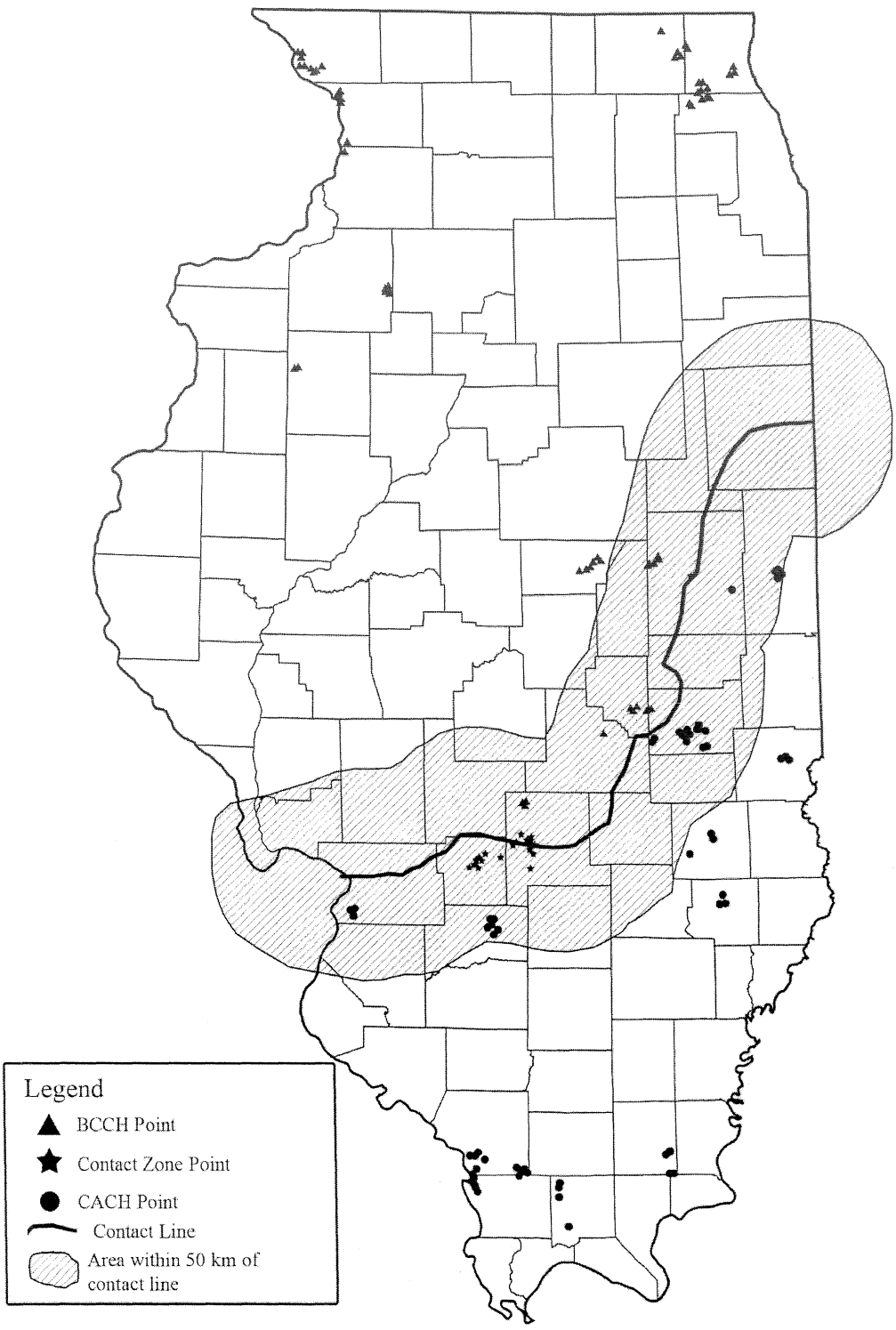


Figure 5. Map of Illinois showing the contact line moving from SW to NE across the middle of the state, locations of data collection, and area within 50 km of contact line.

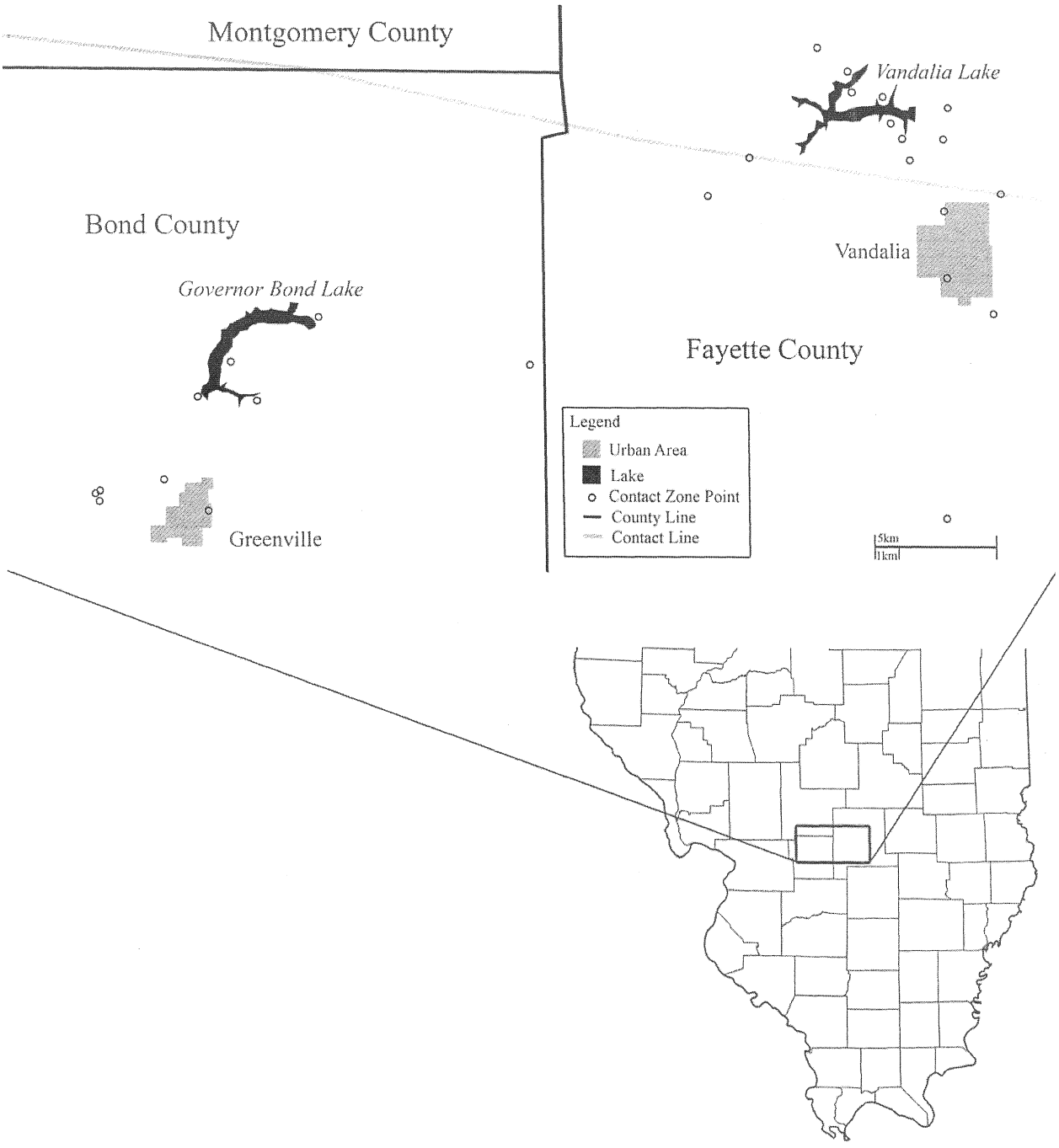


Figure 6. Map showing contact area around Bond and Fayette Counties (IL) with locations of contact zone chickadee data collection.

APPENDIX

Spectograms of song exemplars used in playback trials. Vertical axes are in kilohertz (kHz), horizontal axes are in seconds (s).

1. Black-capped chickadee song from 'Field Guide to Bird Songs: Eastern Region.'

   Elliott, L., D. W. Stokes, and L. Q. Stokes. 1997. Stokes field guide to bird songs: Eastern Region. New York: Time Warner Audio Books.

2. Black-capped chickadee song from 'Singing Life of Birds'.

   Kroodsma, D.E. 2005. The Singing Life of Birds: The Art and Science of Listening to Birdsong. Houghton Mifflin Company. New York, NY.

3. Black-capped chickadee song recorded by E. Glynn at Busey Woods in Urbana, Champaign County, February 2011.

4. Black-capped chickadee song recorded by E. Glynn at Busey Woods in Urbana, Champaign County, February 2011

5. Black-capped chickadee song recorded by E. Glynn in Coles County, February 2011

6. Carolina chickadee song from 'Field Guide to Bird Songs: Eastern Region.'

   Elliott, L., D. W. Stokes, and L. Q. Stokes. 1997. Stokes field guide to bird songs: Eastern Region. New York: Time Warner Audio Books.

7. Carolina chickadee song recorded by E. Glynn at Douglas Hart Nature Center, Mattoon, Coles County, February 2011

8. Carolina chickadee song from Cornell Lab of Ornithology, Macaulay Library of Natural Sounds.

ML 128911. Carolina Chickadee – *Poecile carolinensis*. Vyn, Gerrit. United States, Arkansas. 23 Mar 2005. Macaulay Library, www. macaulaylibrary.org. Cornell Lab of Ornithology.

9. Carolina chickadee song from Cornell Lab of Ornithology, Macaulay Library of Natural Sounds.

ML 129810. Carolina Chickadee – *Poecile carolinensis*. Little, Randolph S. United States, Arkansas. 23 Mar 2006. Macaulay Library, www. macaulaylibrary.org. Cornell Lab of Ornithology.

10. Carolina chickadee song from Cornell Lab of Ornithology, Macaulay Library of Natural Sounds.

ML 105210. Carolina Chickadee – *Poecile carolinensis*. Keller, Geoffrey A. United States, Texas. 1 May 1993. Macaulay Library, www. macaulaylibrary.org. Cornell Lab of Ornithology.

11. Greenville chickadee dialect recorded by P. Enstrom and S. Wayman in Bond County, April 2008.

12. Greenville chickadee dialect recorded by P. Enstrom and S. Wayman in Bond County, April 2008.

13. Greenville chickadee dialect recorded by P. Enstrom and S. Wayman in Bond County, April 2008.

14. Greenville chickadee dialect recorded by P. Enstrom and S. Wayman in Bond County, April 2008.

15. Greenville chickadee dialect recorded by P. Enstrom and S. Wayman in Bond County, March 2008.

16. Vandalia chickadee dialect recorded by P. Enstrom and S. Wayman in Fayette County, April 2008.

17. Vandalia chickadee dialect recorded by P. Enstrom and S. Wayman in Fayette County, April 2008.

18. Vandalia chickadee dialect recorded by P. Enstrom and S. Wayman in Fayette County, April 2008.

19. Vandalia chickadee dialect recorded by P. Enstrom and S. Wayman in Fayette County, April 2008.

20. Vandalia chickadee dialect recorded by P. Enstrom and S. Wayman in Fayette County, April 2008.

21. Carolina wren song from 'Field Guide to Bird Songs: Eastern Region.'

Elliott, L., D. W. Stokes, and L. Q. Stokes. 1997. Stokes field guide to bird songs: Eastern Region. New York: Time Warner Audio Books.

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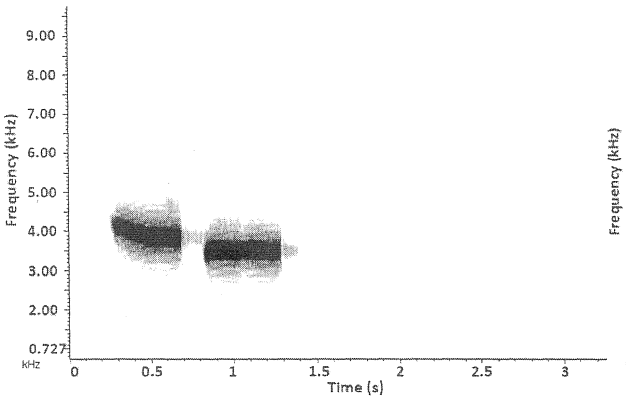
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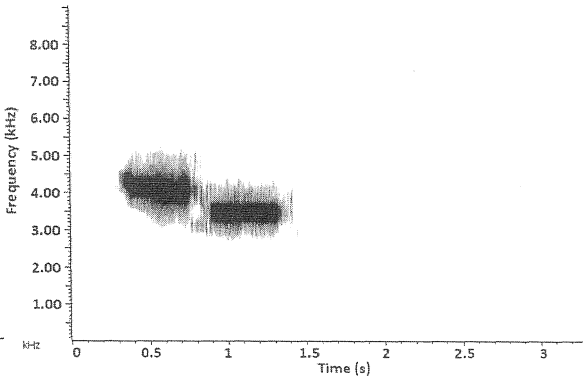
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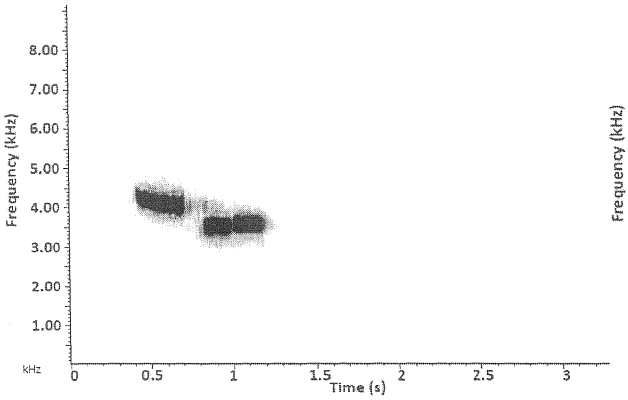
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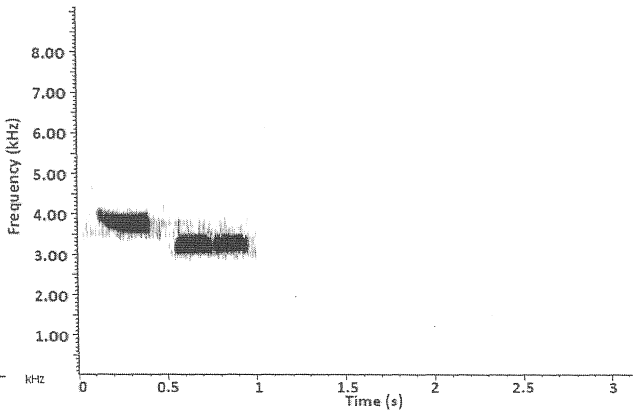
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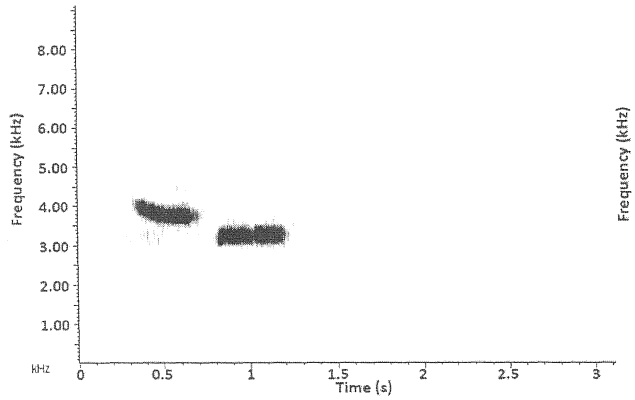
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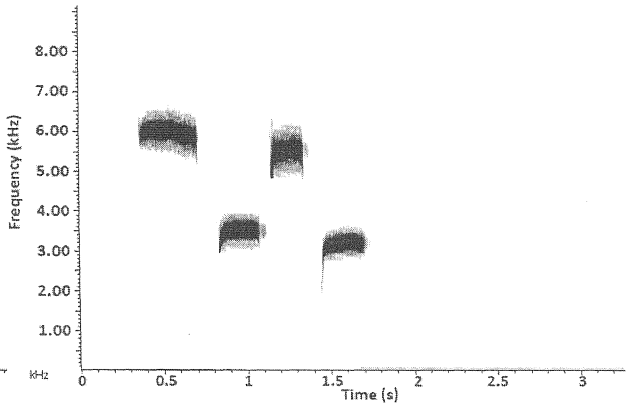
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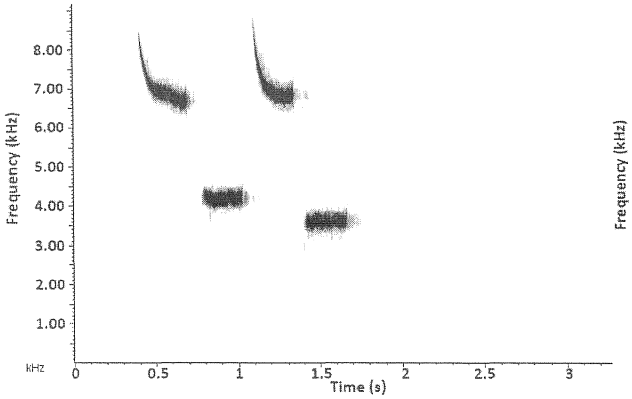
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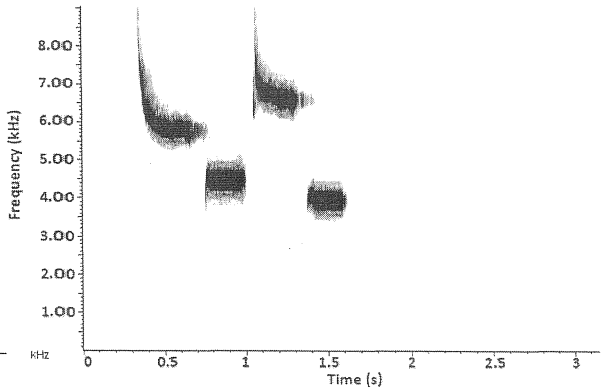
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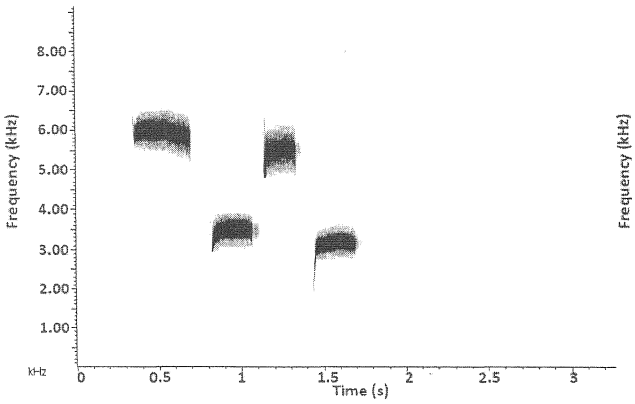
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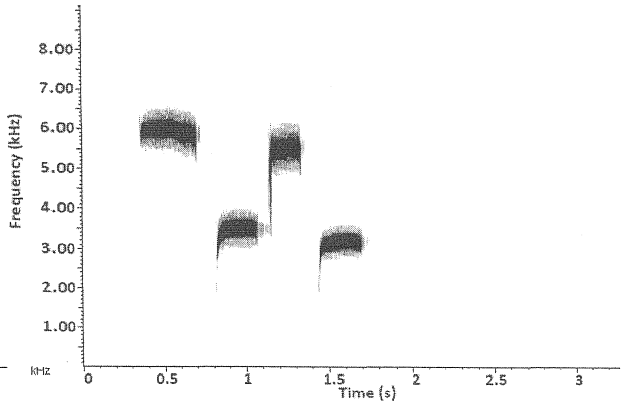
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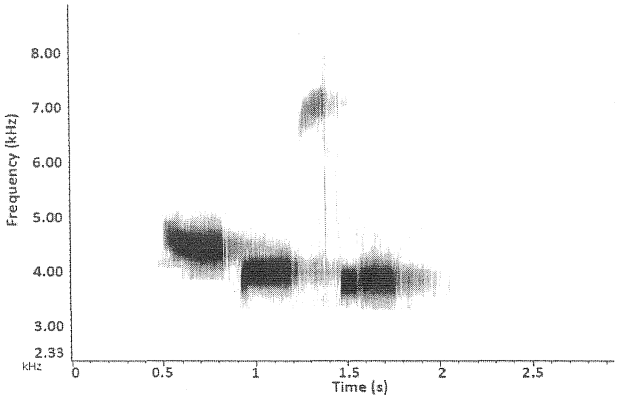
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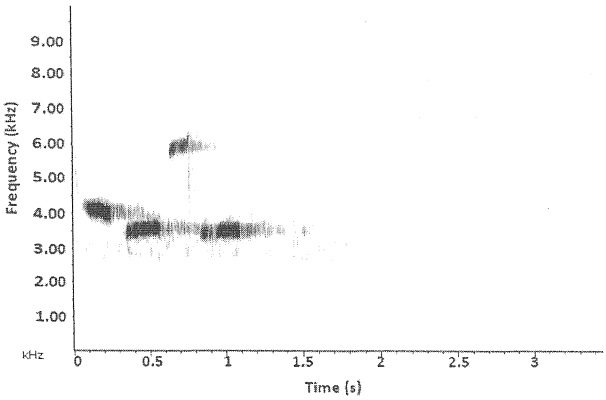
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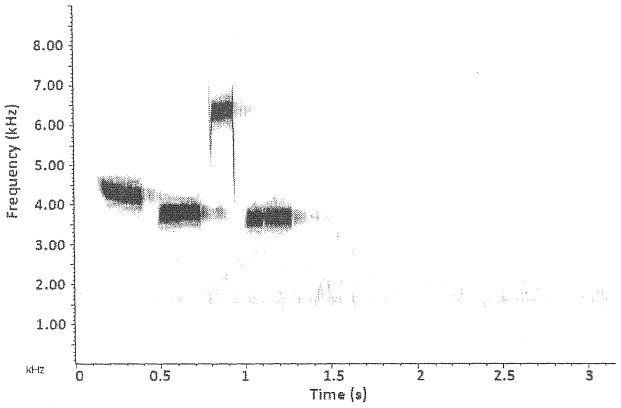

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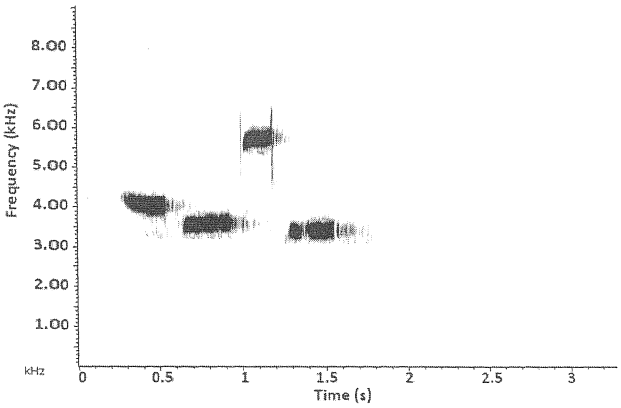

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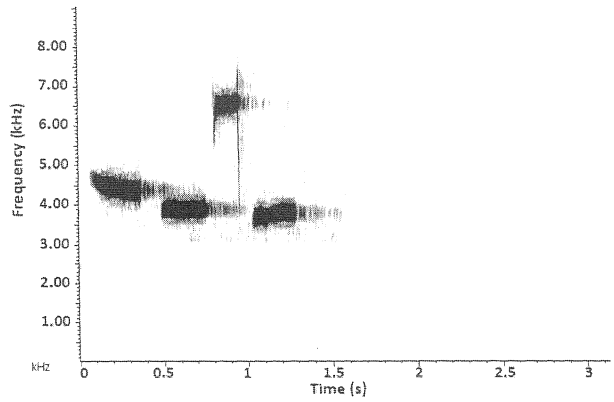

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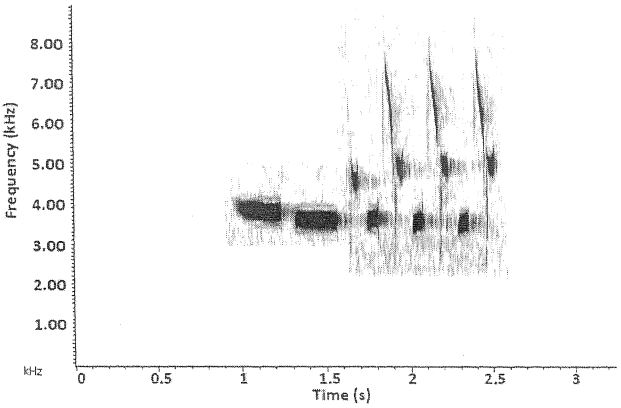

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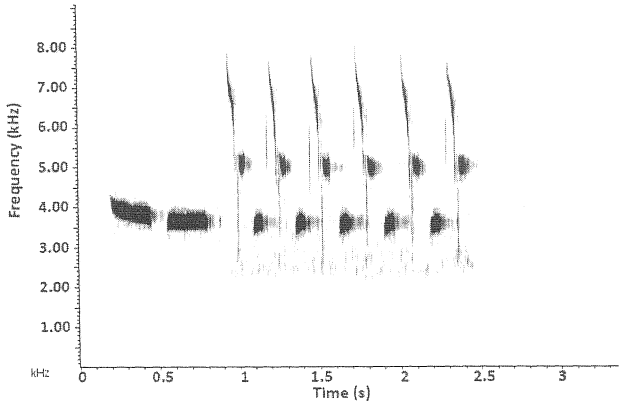

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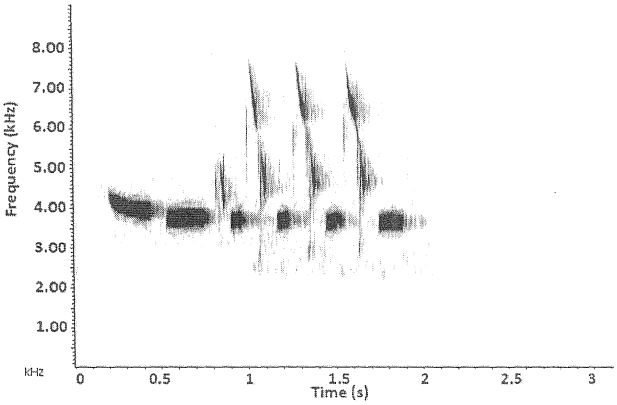

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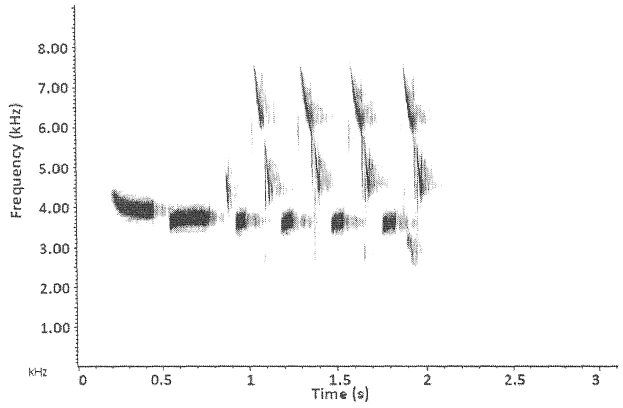
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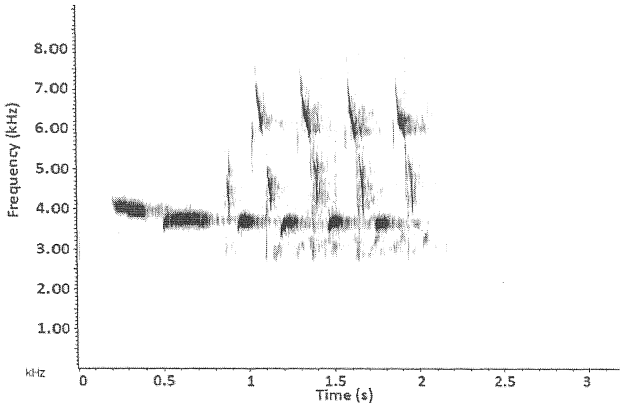
6.00
5.00
4.00
3.00
2.00
1.00
kHz
0
0.5
1
1.5
2
2.5
3
Time (s)

20.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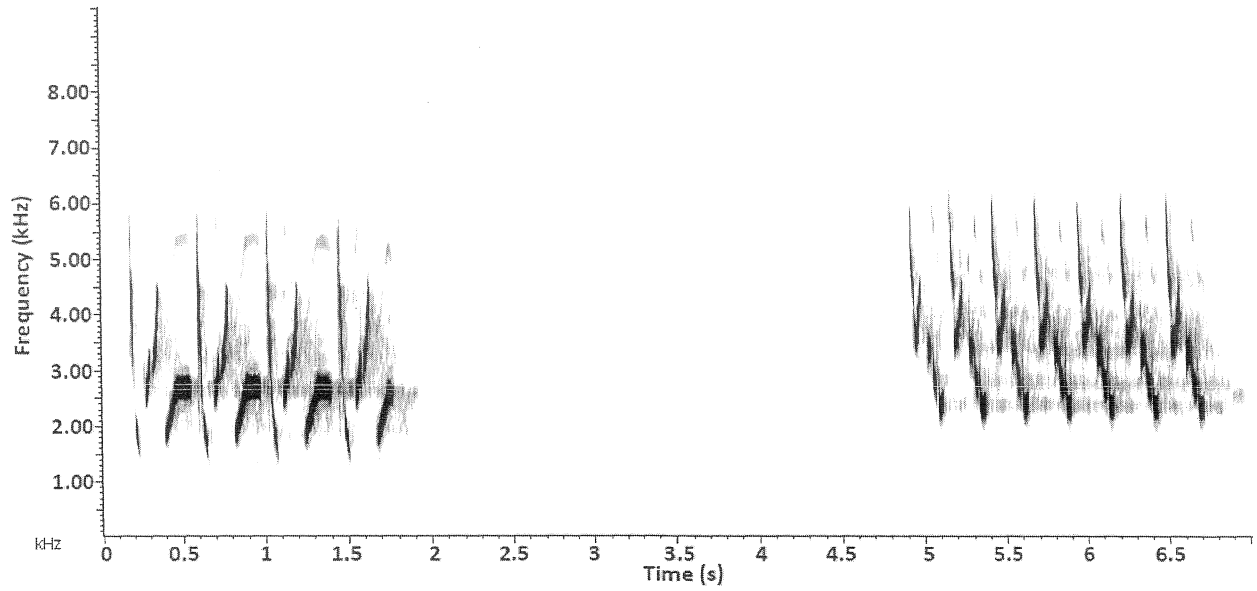
2
2.5
3
Time (s)

21.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kHz
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1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
6.5
Time (s)