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Habitat effects on chick-a-dee call complexity

Jacqueline Renee Lynch
Purdue University

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Is approved by the final examining committee:

Jeffrey Lucas

Kerry Rabenold

Esteban Fernandez-Juricic

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Approved by: Jeffrey Lucas 07/18/2014

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ABSTRACT

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Past studies on the communication systems of species in urban environments (such as Common Starlings (*Sturnus vulgaris*), nightingales (*Luscinia megarhynchos* Brehm), brown-headed cowbirds (*Molothrus ater*), Southern brown tree frogs (*Litoria ewingii*)) have shown multiple ways that species change vocal signaling behavior to adjust to urban habitats (e.g. alarm calls and singing). This study further investigates the changes in signaling in relation to the chick-a-dee call of the Carolina chickadee (*Poecile carolinensis*). A secondary goal of this study was to compare both the amount of information and rate of calling across seasons. Six different variants of chick-a-dee calls were used in playbacks at sites in three types of habitats: closed canopy, mixed and urban. Ad lib recordings were also conducted around the area. Playback trials and ad lib recordings overlapped both the breeding and the non-breeding season to facilitate observations of seasonal changes. The recordings were analyzed for seasonal and habitat differences in call rate, information encoded in call and notes, average call length, and probability of note transitions. Our results show that chick-a-dee rates differed significantly between treatments and seasons suggesting seasonality in the context of the calls. Across the habitat types, we found indications of increased vocal complexity in closed canopy flocks. Vocal response rates and distance of approach in these closed forest flocks differed significantly between playbacks compared to the other habitats. In urban habitats there was no difference between responses to the treatments suggesting less vocal complexity. Based on our results, habitat as well as season seems to create additional complexity in the chick-a-dee call system.

INTRODUCTION

1.1 Introduction

The uncontrolled expansion of urban areas, referred to as urban sprawl, has caused a decrease in species diversity and density (McKinney, 2006). Examples of decreases in species density due to urban sprawl have been shown in many species (dusky antbird (*Ceromacra tyrannina*), red-throated ant-tanager (*Habia* fuscicauda), cocoa woodcreeper (*Xiphorhynchus* susurrans) Withey, 2013; fox squirrels (*Sciurus niger*), Sheperd & Swihart, 1995). When examining territory boundaries of tawny owls (*Strix aluco)*, urbanization was the cause of decrease in density of territories, not defense, number of competitors or biomass. Tawny owls formed close adjacent territories in rural farms areas but increased nearest neighbor distance when in town (Galeotti, 1993). Alternatively, some studies have found that certain species flourish in urban areas. Urbanization facilitates the addition on nonnative species which increases diversity (McKinney, 2002). One mechanism proposed to better understand the changes in urban species population is the safe-habitat hypothesis. It hypothesizes that the number of natural predators decreases with the degree of urbanization leading to lower rates of nest predation and ultimately greater abundance of a species (Tomialojc, 1982). This hypothesis may not be the only explanation for population density changes though. Valcarcel and Fernandez (2007) tested this hypothesis by looking at perceived risk of predation by house finches in urban environments. House finches still perceived urban habitats as more dangerous than non-urban habitats despite the lower predator density. Other mechanisms such as increased food availability provided by humans, changes in vegetation complexity and reduction in climate extremes (Shochat et. al, 2006) have also been proposed to explain increases in population density in urban habitats.

Urbanization effects on species density have the potential to change the social structure of species that live in groups. The complexity of an individual's social group can also impact the vocal signals used in its interactions with others. The size and composition of animal groups is directly related to the complexity of their vocal system according to the social complexity hypothesis for communication (SCHC): as social complexity increases, so does vocal complexity (Freeberg, 2006). Larger groups require greater social complexity in order to meet the needs of managing groups. Social complexity refers to group size, density or diversity of member's roles, status or relationships. Vocal complexity can be characterized as information within signals and group member reactions to these signals (Krams et. al, 2012). For example, phylogenetic analysis of non-human primates' vocal repertoire showed an increase in repertoire size associated with increases in group size and time spent grooming- an important component of social interaction (McComb, 2005). Social bonding as a component of social complexity has been shown in avian species as well. When pairs of Carolina chickadees (*Poecile carolinensis*) perched more closely to one another, males increased the rate of chick-a-dee calls (Freeberg & Harvey, 2008). Group size is also used as an index of social complexity. Freeberg (2006) compared information encoded in the chick-a-dee calls of small and large flocks and found a greater degree of vocal complexity in larger flocks compared to smaller flocks. Studies have focused on changes in vocal communication caused by changes in group size and social relationships but there is a lack of knowledge about the effects that changes in density caused by urbanization have on vocal complexity. Our study aims to assess the degree of change in social and vocal complexity of a social species, the Carolina chickadee (*Poecile carolinensis*), in areas of varying degrees of urbanization.

We used Carolina chickadees for the study of habitat and seasonal effects on vocal communication for several reasons; 1) they live in multiple habitats (Blewett & Marxluff, 2005; Mostrom et al., 2002), 2) their flocks change throughout the year (Berner & Grubb, 1985; Ekman, 1989; Smith, 1991; Smith, 1972) and, 3) they display seasonal differences in vocal behavior (Clucas et al, 2004; Avey, 2007).

Carolina chickadees are cavity nesters and therefore prefer habitats with mature trees (Mostrom et. al., 2002). Typically, cavity nest sites are found in forests but cavity-nesters are successful at breeding and nesting in all types of habitats although their prevalence is lower in urban areas (Blewett & Marzluff, 2005). Since Carolina chickadees live in various habitats, this provided an easy way to compare directly the vocal system of one species in different habitats. Also, Carolina chickadees do not migrate which allowed for observation during both the breeding and non-breeding season (Smith, 1991; Smith 1972).

Chickadee flocks are dynamic: the species and total number of flock members change throughout the year. During the non-breeding season (fall and winter months), two or more pairs of chickadees can form a flock with heterospecifics such as the White-breasted nuthatch (*Sitta carolinensis*) and Tufted Titmouse (*Baeolophus bicolor*) (Berner and Grubb, 1985). During the breeding season, male chickadees begin to use the feebee feebay song to attract females and defend their territories causing the larger flock to break up male-female pairs (Ekman, 1989; Smith, 1991; Smith, 1972). The use of one type of vocalization over another type varies in each season as well. The syntax (order of notes) of the chick-a-dee call during the fall/winter months is more important than in the spring since chick-a-dee calls are used for social coordination. For example, studies that presented Carolina chickadees with atypical chick-a-dee calls elicited responses with different note types in the fall and winter but this difference was not observed in the spring (Clucas et al, 2004). Studies on seasonality have also been done with Black-capped chickadees (*Poecile atricapillus*). The highest rates of chick-a-dee calling were in the fall and winter (Avey, 2007). These seasonal changes in flock size and vocalizations add another layer of complexity for study in the social and vocal system of the Carolina chickadee.

1.2 Vocal Repertoire

Chickadees have three main vocalizations: gargle calls, feebee feebay songs, and chick-a-dee calls. The gargle is used year round in agonistic encounters which are often at territory boundaries (Ficken et al., 1978). It is a noisy call composed of a variety of elements (Ficken, 1981). The feebee feebay song is a four note whistled song used by males for territory defense and mate attraction (Smith, 1972). The chick-a-dee call is composed of a variety of note types and is used for social coordination (Smith, 1972). The chick-a-dee call was the focus of this study.

A combination of our own analysis and analyses from previous studies resulted in nineteen note types that were used to classify a total of 7819 notes collected. A description of each note type is included below. The final nomenclature is based on Freeberg & Lucas (2002) and Smith (1972). We used parameters of beginning, peak and end frequency, position of peaks and tails (sweeps leading up to and away from peak frequency). All frequencies and description of shape are summarized in Table 1.

1.2.1 Introductory notes

In previous works, introductory notes have been grouped into the category of A notes. In this study we distinguish six introductory note subtypes in our recordings. The first type of introductory note is a normal E (Freeberg & Lucas, 2012). It starts with a long ascending arm that peaks at 6-8 kHz. The peak is rounded and the descending tail is shorter that the ascending. The second type of introductory note is a Flat Tee. These have no ascending tail, are flat at the peak (8-10 kHz), and have a long descending tail. The Black-capped A is the third type of introductory note. This is the same note used by the Black-capped chickadee with the longer descending tail which is the opposite of the normal E note. The lisping tee comes from Smith's (1972) study on the chick-a-dee call. She describes it as a chevron with strongly emphasized (louder and longer) descending tail more gently sloped than the ascending tail. An E note was considered to be an E with an added element when it had additional frequency sweep below the original peak. The final type of introductory note is the tailed tee (Smith, 1972). It is similar in shape to the lisping tee but has small ascending tail.

1.2.2 B notes

We observed three B note subtypes: normal B, B with multiple elements and high B. They all share the same shape of a rounded chevron with tails of equal length. The B with multiple elements is distinguished by one or more added frequency sweeps above or below the main peak. The high B has a frequency in the range of 8-10 kHz compared to the normal B frequency range of 6-8 kHz.

1.2.3 C notes

C notes are a combination of multiple elements which makes a "noisy" structure. It has two or more stacked peak frequencies that are clearly visible at the center of the note. There is a general increase in frequency over the course of the note (Freeberg & Lucas, 2012).

1.2.4 D notes, Harsh D, Rapid D and Hybrid D

All D notes are comprised of two or three fundamental frequency bands with additional sidebands resulting from the interaction of signals from both sides of the syrinx (Nowicki, 1989). The normal D note is about 0.08-0.1 seconds in duration with clearly distinguishable fundamental frequencies. A harsh D is very noisy in appearance and the fundamentals are difficult to distinguish. A rapid D is less than half the length of a normal D note. Hybrid D notes are a concatenation of the preceding note (usually A or B) and the D note (Freeberg & Lucas, 2012).

1.2.5 Variable See

The variable see is a series of high frequency notes that usually end in a gargle call (Smith, 1972). Each note in the variable see has a rounded peak and little to no ascending and descending tails.

1.2.6 Normal tseet, Rounded tseet, and One-sided tseet

Tseet notes are sometimes used at the beginning of a chick-a-dee call or by itself as a contact call. A normal tseet has a chevron shape and has a peak frequency of 5-9 kHz. A rounded tseet has a rounded peak and nearly equal length tails. It is distinguished from a B note by its shorter duration. One-sided tseet notes only have the descending tail of the chevron.

1.2.7 Pause

Several calls were found to have a break in the normal rhythm of notes that was longer than the typical inter-note interval but shorter than the inter-call interval. This was categorized as a pause.

HYPOTHESIS AND PREDICTIONS

1.3 Hypothesis and predictions

Carolina chickadees use the chick-a-dee call in a variety of social contexts and arrangement of syntax may be used to convey different messages about the surrounding environment (Smith, 1972). If chick-a-dee call complexity depends on flock size, then vocal complexity will differ across habitats. Flock size was used as an index of social complexity in the different habitats. We predicted that the chick-a-dee call system in areas with large flock size will contain more information than areas with smaller densities of chickadees.

If social complexity is needed for organization of groups then flocks of different size should exhibit different amounts of information in their responses to call types eliciting social coordination. We predicted that call types containing E, C and D notes would have a significantly different meaning for areas with large flocks where vocalizations are used more frequently for social activity. In areas with small flock size, the responses were expected to be the same for each combination of notes. In the closed forest setting, the difference in the syntax is used to convey a larger number of different messages for coordination of flock activities. Specifically, presenting a string of E notes to forest chickadee flocks should elicit gargle and chick-a-dee calls because this call has similar properties to a variable-see call which is used when the bird is stressed (Smith, 1972). C notes are used in contexts with food such as leading birds to feeding sites (Freeberg & Lucas, 2002). Presenting chickadees with a string of C notes should cause them to come in to the speaker. Large numbers of D notes are used to coordinate mobbing of predators and convey the degree of predator threat (Soard, 2009). The chickadees were expected to give chick-a-dee calls with D notes and approach the speaker rapidly in response to the D notes.

We also predicted that the response to the chick-a-dee call will change by season across the habitats. If seasonality exists then the rate of chick-a-dee calls used in the fall/winter should be greater than in the spring for both playbacks and ad lib recordings since chickadees are part of a larger flock in the fall and will use the chick-a-dee call for coordination. If these larger flocks do not form in the fall/winter in more urbanized habitats, their call rates should not change throughout the year.

METHODS

1.4 Overview

A field study was conducted to examine the effects of habitat type on (1) flock size and (2) complexity of the chickadees' vocal communication system. For this study, flock size was measured as an index of social complexity. Recordings were done of chickadees in both urban and rural Lafayette areas using an ad libitum sampling design. Observations made during these recordings gave information about flock size (Figure 1). Analysis of these recordings in addition to previously conducted recordings allowed us to choose chickadee calls that elicited specific social behaviors such as mobbing. We also looked at the syntax of these calls to determine the best way to mimic naturally occurring calls in our playback study. We then created 6 exemplars each of 6 chick-a-dee calls with different syntax. We played these back in the chickadee habitats and calculated the (1) correlation between chick-a-dee rates, playback type, and season and (2) the ability of notes and calls to encode information (see statistical analysis section).

1.5 Sites

Data collection sites were chosen from in and around the greater Lafayette, IN area and were split into three main categories: urban, open canopy (mixed), and closed canopy (Table 2). These categories were determined based on relative characteristics of each location: measurement of percentage of tree cover, comparison of types of ground cover, light intensity, tree density and DBH (Table 3). Areas with greater than 80% tree cover compared to visible sky were classified as closed canopy. Areas that had a percentage cement cover (including buildings) greater than 50% were classified as urban. All areas intermediate values of tree cover (35-80%) but little to no cement cover were considered open canopy or a mix of urban and forested. Each category contained four individual sites. Tree density and DBH were used to assess the quality of the habitat for the chickadees. Sites were separated by at least 250 m to ensure that two playback sites were not in one territory (Mostrom, Curry & Lohr, 2002).

1.6 Ad Lib Recordings

Ad lib recordings were conducted at each location to observe chickadee behavior at various times of day throughout the entire site. Recordings were conducted during both the breeding and non-breeding season of the chickadee. In this way, seasonal changes in behavior and vocalizations were observed. A Sennheiser directional microphone ME66 and Marantz PMD670 were used for recording. Information about the date, time, temperature and area were recorded at each site. The chickadees were located at each site and recording began when any chickadee vocalizations were heard. The number of chickadees and heterospecifics, their behavior and the presence of predators were the main observations made. Since certain areas had attractive features such as feeders that draw birds to the area, distance between birds was estimated to ensure that the group being observed was a flock and not an aggregate. Chickadees typically keep 0.5 m to 1.5 m between individuals in a flock (Mostrom et. al., 2002).

1.7 Playbacks

Playback experiments were conducted at 12 sites split across the habitat gradient: 4 urban, 4 mixed, and 4 closed (Table 2). A radius of 30 m was marked out in 10 m increments around the microphone and speaker. A Sennheiser omnidirectional microphone ME62 and Marantz PMD670 were used for recording. The birds distance to the speaker was estimated using these markers. Each of the six treatments and a control were used at each site. The treatments were composed of various combinations of E, C, and D notes (6E, 6C, 6D, 3E 3D, 3C 3D and 2E 2C 2D) (Figure 2). These treatments were created using calls recorded at the Martell forest. Calls were chosen from these birds to eliminate the possibility of familiarity among test subjects. Freeberg and Lucas (2002) showed that chick-a-dee notes from Martell forest are spectrally different from those at the Ross reserve. These notes were cleaned in Cool Edit Pro 2.1 with a scientific filter to remove background noise and were normalized at 80% peak sound intensity.

A White-breasted nuthatch “quank” call with an inter-note interval of 0.05 seconds was used as the control. The pace of the call is slower than the “quank” call used for mobbing (Grubb & Pravosudov, 1993). The call served as a negative control because it is a neutral (non-mobbing) call from a heterospecific that should not elicit a response from Carolina chickadees (Ficken & Popp, 1996). It was used as a comparison for the response to the treatments in our analysis.

Each treatment and the control were played once at each site with at least one week in between playbacks. The playback experiment was divided into three time periods: the pre-playback, playback and post-playback. The pre-playback period was a ten minute recording time period prior to the playback to obtain a baseline of initial bird calls. Each playback was three minutes with a chick-a-dee (or “quank”) call every ten seconds. Each playback was immediately followed by a seven minutes post-playback period. The playback and post-playback period were repeated five times during a trial for a total of 50 minutes. The number of chickadees and other bird species that were seen and heard were counted to determine the density of individuals. We made observations every minute of number and type of calls, number of chickadees and distance from speaker.

1.8 Call Analyses

1.8.1 Spectral analysis

The syntax of each chick-a-dee call from all playback and ad lib recordings was examined using the spectral view in Cool Edit Pro 2.1. The scientific high pass band filter was used on sections of the recording to remove sounds below 2000 Hz. The amplitude was normalized when necessary to better visualize all parts of the note. Overall there were 19 categories used to label the syntax. The length of the call was measured from the beginning of the first note to the end of the last note excluding reverberation.

1.8.2 Information encoding capacity

The potential for information to be encoded was calculated using Shannon’s (Shannon & Weaver, 1949) equation for entropy following the methods in Freeberg and Lucas (2012). This equation calculated the encoding capacity for individual notes, calls, and note-to-note transitions within a call.

$$\mathbf{E} = \sum_{i=1}^{n} p_i \left(-\log_2 p_i\right)$$

Here p is the probability that the i^{th} chickadee note will occur if there are n note types. E is the ability of a note or notes to encode information. We calculated the total amount of encoded information in the system given the ordering constraints of the chick-a-dee call and the maximal potential encoded information. The total amount of encoded information for a system is the likelihood that certain elements (i.e. call types or notes) will be used when elements have an unequal chance of occurring. The maximal potential information is the total possible information in a system given that all elements in the system have an equal chance of occurring. To compare the data between sites the percent of encoded information was used. The percent of encoded information in a call, note, or transition between notes was calculated by dividing the actual amount of encoded information by the maximum potential encoded information.

The probability of a transition occurring from one particular note type to any of the other note types was also calculated. This was done by dividing the number of transitions between two notes by the total number of transitions for that site.

1.9 Statistical analysis

Averages of call rate, number of chickadees, total calls and calling time in response to the playbacks were calculated using Proc Means in SAS 9.3. The call rate is the total amount of calls heard divided by the total time of the trial. Call rate for individuals was calculated using the total number of calls for a site divided by the average number of chickadees at that site. The average number of chickadees at a site was calculated by dividing the total number of chickadees observed in each trial by the total number of trials.

The vocalization rates during the playbacks were analyzed with Generalized Linear Mixed Models using Proc GLIMMX in SAS (Version 9.3). The dependent variable was count data so a Poisson distribution was used. The vocalization rates were analyzed for differences both between treatments and habitat types. Each of the major types of vocalizations (feebee song, gargle and chick-a-dee) was used as a dependent variable in separate models to determine their rates in relation to treatment type, location and season.

RESULTS

1.10 Chickadee flock size

Flock size increased from urban to closed habitats. Density ranged from 1-2 chickadees in urban habitat, 1-3 chickadees in mixed habitats and 1-4 in closed habitats (Table 4). The composition of the mixed species flock varied depending on habitat type and season. Data from both the playbacks and ad lib recordings were used to assess the heterospecific flock composition. Number of chickadees observed during ad lib recordings were within the same ranges as those observed during playbacks. Our data show that while there is overlap in the flock size of chickadees across habitats, closed and mixed habitats had larger maximum flock size than urban habitats.

1.11 Information Encoding Capacity

Information encoding capacity was calculated separately for each habitat type for the playback data. The closed and mixed habitats had very similar percent of encoded information for total calls and individual notes. Sites at Horticulture Park showed a decrease in encoded information compared to the closed sites. One McCormick Woods site was much lower than any of the other sites and the other was much higher due to very few calls being heard. Urban sites had the lowest amount of encoded information and also had the fewest number of calls heard.

1.12 Total encoded information in calls

The amount of encoded information contained in the chick-a-dee call decreased overall from closed to urban habitats. Closed habitats and mixed habitats were relatively similar in the percent information (90.1% and 92.4% respectively). The percent information in urban habitats was 77.5% which is lower than both closed and mixed habitats. These differences in information content suggest that the need for a complex vocal system changes in relation to habitat.

The information encoding capacity from the ad lib recordings showed high amounts of encoded information in calls (84.4-100%) for the sites (Figure 3). The sample size of calls per site was smaller than those collected during playbacks.

1.13 Information in notes

The percent of information in the different notes types of the chick-a-dee call was compared across seasons and habitat type. Chick-a-dee call lengths ranged from 1 to 43 notes in our sample. The results show an overall decrease in the percent of information in notes from closed to urban habitats (closed 26-32%, mixed 15-27%, urban 13-15%) (Figure 5). Encoded information in notes for ad lib recordings show relatively lower percent information for urban sites as well (closed 26.2-31.2%, mixed 17.4-36.1%, urban 17.4-19.1%) (Figure 6).This suggests that the chick-a-dee calls used by individuals in urban habitats have a lower potential to encode information due to fewer note types.

1.14 Distribution of note types

The distribution of each type of chick-a-dee note was compared across habitat types (Table 5). D notes were most abundant in each of the habitats. In urban habitats the majority of the notes were normal D's, harsh D's and variable see notes. The most variable see notes were used in urban habitats. In mixed habitats the most abundant notes were the three different types of D notes. In closed habitats normal E, C, normal D and harsh D notes were the most abundant.

1.15 Note transitions

The amount of encoded information contained in the transition between two notes was calculated. The amount of encoded information contained in transitions increased from urban to closed habitats for note pairs (Figure 7). The greatest percent of information encoded in transitions was in closed habitats (closed= 44.5%, mixed= 36.4%, urban= 22.5%). The same trend was found in the percent encoded information for transitions between note pairs (closed= 44.4%, mixed= 36.4%, urban= 22.5%) and triplets (closed= 52.5%, mixed= 42.5%, urban= 29.0%).

1.16 Individual response rate

Chickadees responded with different calls and rates of calling to chick-a-dee calls of different syntax. The rates of chick-a-dee and feebee rates were significantly different between each treatment ($F_{1,253}$=13.31, p<0.0001) (Table 6) while gargles were not heard often enough in response to playbacks to be significant. The effect of gradient on vocalization rate was not seen but there was a significant effect of gradient and treatment type combined. The 6D and 3C3D treatments had the strongest response in closed habitats compared to the other treatments. Chickadees came all the way in to the speaker for 6D treatment in the closed habitat (Figure 8). Alternatively, urban chickadee flocks came within 25 meters of the speaker but did not chick-a-dee call (Figure 9) to the 6D playback. The 6E treatment received the next strongest rate of chick-a-dee response.

Chick-a-dee rates were significantly different across seasons (Table 7) and followed our prediction that chick-a-dee calls will be used more in the fall and winter months ($F_{1, 253}$=70.28, p<0.0001). This effect of playback type by season interaction term was also significantly different ($F_{6, 253}$=47.69, p<0.0001).

DISCUSSION

Our main goal of this study was to analyze the effects of different habitat types on the chick-a-dee call. In addition we attempted to further understand seasonal effects on vocal communication in chickadee. Previous studies have shown examples of the SCHC in various species including chickadees (Freeberg, 2006; McComb, 2005). Both the social structure and vocal system of the Carolina chickadee possess a great deal of complexity (Freeberg & Lucas, 2002, Freeberg & Harvey, 2008).

Our results show that season and habitat add additional aspects of complexity to be studied in the call system of the Carolina chickadee. We found that flock size is decreased and the amount of information in their call systems is less in urban habitats compared to flocks in mixed and closed forest habitats. The smaller flock sizes in urban areas could be explained by the fact that territories are more fragmented (Galeotti, 1993). Urban habitats could also be lower in quality if they have fewer mature trees to provide nesting sites. Smaller flock size could also be considered from the perspective of the safe-habitat hypothesis. It is possible that urban habitats are less safe than non-urban habitats for chickadees. One explanation is that the population densities of the chickadees' natural predators are not decreased in urban habitats. Some natural predators include eastern screech-owl, *Megascops asio*, American kestrel, *Falco sparverius*, sharp-shinned hawk, *Accipiter striatus*, Cooper's hawk, *Accipiter cooperii*, great horned owl, *Bubo virginianus*, and red-tailed hawk, *Buteo jamaicensis* (Ritchison & Cavanagh 1992; Curtis et al. 2006). American kestrel populations were found to have higher reproductive success in urban environments (Chace & Walsh, 2006). Further studies should measure aspects that may make urban habitats less safe such as nest predation and human disturbance to better understand the reasons for decreased flock size in urban habitats.

We assessed vocal complexity from the perspective of percent information in a call system and the responses of the receiver. Vocal systems are considered to be more complex if they contain more information. Our evidence for social complexity in the larger, closed forest and mixed habitats suggests that these chickadees also possess more vocal complexity. The rates of chick-a-dee calling were significantly different in response to each treatment type. This demonstrates that different note types used in the chick-a-dee call convey different messages in large flocks that rely heavily on social communication. Previous studies on Carolina chickadees explored the variety of notes and note combinations which means there is potential for the chick-a-dee call system to convey a wide range of messages (Lucas & Freeberg, 2007; Freeberg & Lucas, 2012). The larger amount of encoded information and variety of notes in our data used in closed forest habitats also shows that they have the potential for a more complex vocal system. Less note repetition and more uncertainty cause more variation in the chick-a-dee call which could be used to convey more messages.

A greater understanding about the messages being conveyed can be gained by looking at the response to each treatment type. In closed forests, the strongest response was to the 6D or mobbing call treatment. Previous studies on the D notes in chick-a-dee calls found that there is useful information contained in these notes and this information is important to chickadees as well as their flock mates the red-breasted nuthatch (*Sitta canadensis*) (Templeton, 2005, Templeton & Greene 2007). Our prediction was that there would be more responses (calling and approaching speaker) for the 6D treatment based on these previous findings. For these treatments chickadees called at a higher rate and came all the way in to the speaker. The strong response to the mobbing call in closed forest habitats and not in the other habitats also suggests that social coordination is more important to chickadees in these habitats. However, other individuals may understand the mobbing call but not respond if the flock is too small to mob a predator. Additional studies with banded birds to determine territory size of urban flocks would be needed to further understand urban chickadees' response to mobbing calls.

Clucas et al (2004) found patterns in vocalization rates of chickadees across seasons. We further explored this by conducting playbacks in both the breeding and non-breeding season. Our analysis of vocalization rates across seasons show that the rates do change based on the time of the year. Higher response rates to playbacks in the fall/winter months indicate that the chick-a-dee call is more important in the non-breeding season. The non-breeding season is a time when chick-a-dee flocks are larger, containing multiple pairs as well as heterospecifics, and social coordination is necessary.

Overall, the combination of our data shows that there is a difference in the way that the chick-a-dee call is used in different habitats and seasons. Future studies to further explore the complexity of the chick-a-dee call should increase the number of site where playbacks are done to get a better idea of how fine the differences are between habitats. Using banded birds would also be useful to compare the territory ranges of flocks in each habitat.

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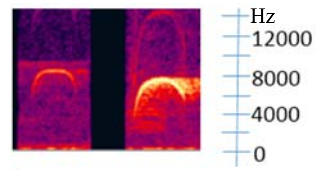
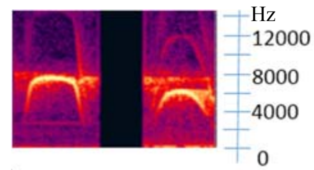
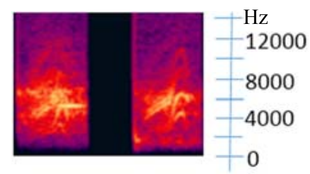
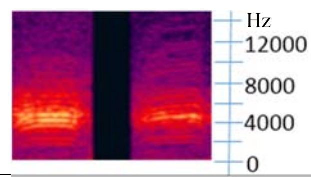
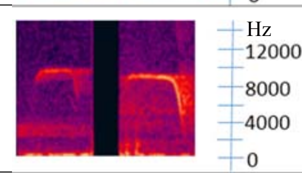
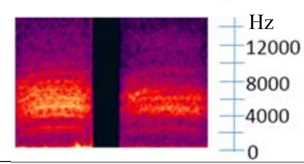
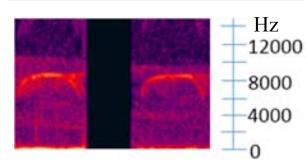
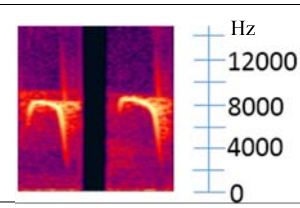
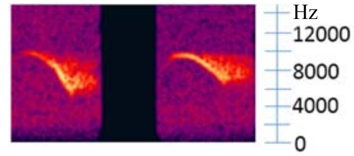
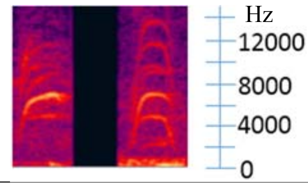
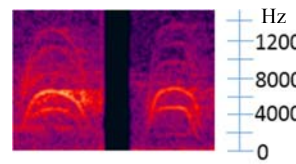
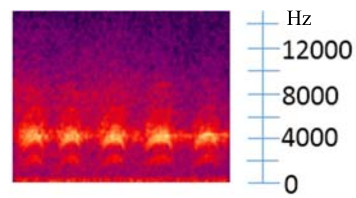
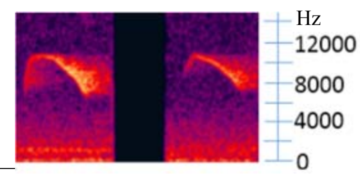
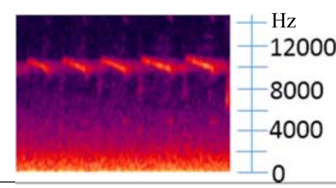
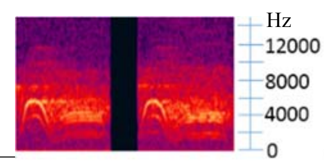
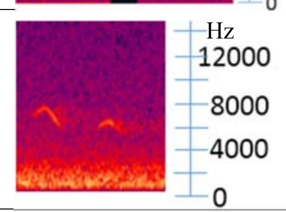
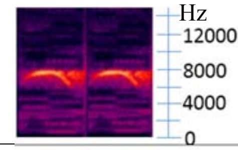
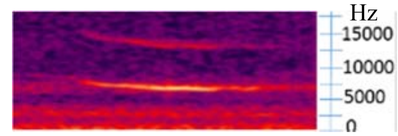
TABLES AND FIGURES

Table 1 Chick-a-dee note classifications

Note name	Shape	Range of peak frequency	
Normal E	Rounded chevron with long ascending arm short descending arm	7-8kHz	
Normal B	Rounded chevron, ascending and descending arms or the same length	6-8 kHz	
Normal C	Narrow chevron with pointed peaks occurring with 3-4 resonance harmonics	6-8 kHz	
Normal D	Occur as series, broad, flat bands of closely stacked harmonics	4-6 kHz	
Flat tee	Flat broad FM with a long descending tail, no ascending tail	8-10 kHz	
Harsh D	Similar to normal dee with additional ‘noise’ that makes the frequency band undistinguishable	5-7 kHz	
High B	Same shape as normal B with equal length tails at a higher frequency	8-10 kHz	
Black-capped A	Chevron with nearly flat peak, short ascending tail and long descending	7-9 kHz	

Lisping Tee	Chevrons with strongly emphasized (louder and longer) descending tail more gently sloped than the ascending tail	9-11 kHz	
E with added element	A normal E note with an single or multiple additional frequencies below the original peak	6-8 kHz	
B with added elements	A normal B not with single or multiple frequecies	5-7 kHz	
Rapid D	Broad stacked frequency bands with a duration of 0.05 s or less, usually curved upward	3-5 kHz	
Tailed Tee	Chevron with longer, more sloped descending tail	10-12 kHz	
Variable See	Series of rapid chevron shaped notes	8 kHz or greater	
Hybrid Dee	Typically composed of a C or B note and a normal Dee with no internote interval	4-6 kHz	
Tseet	A chevron typically given singly or as an introductory note	6-8 kHz	

Rounded Tseet	A chevron with a rounded peak given singly or as an introductory note	8-9 kHz	
One-sided Tseet	A chevron with no ascending tail, often a very steep descending sometimes inverted tail, given singly or as an introductory note	5-9 kHz	
Pause	A space inserted into a call that is longer than the typical internote interval	N/A	

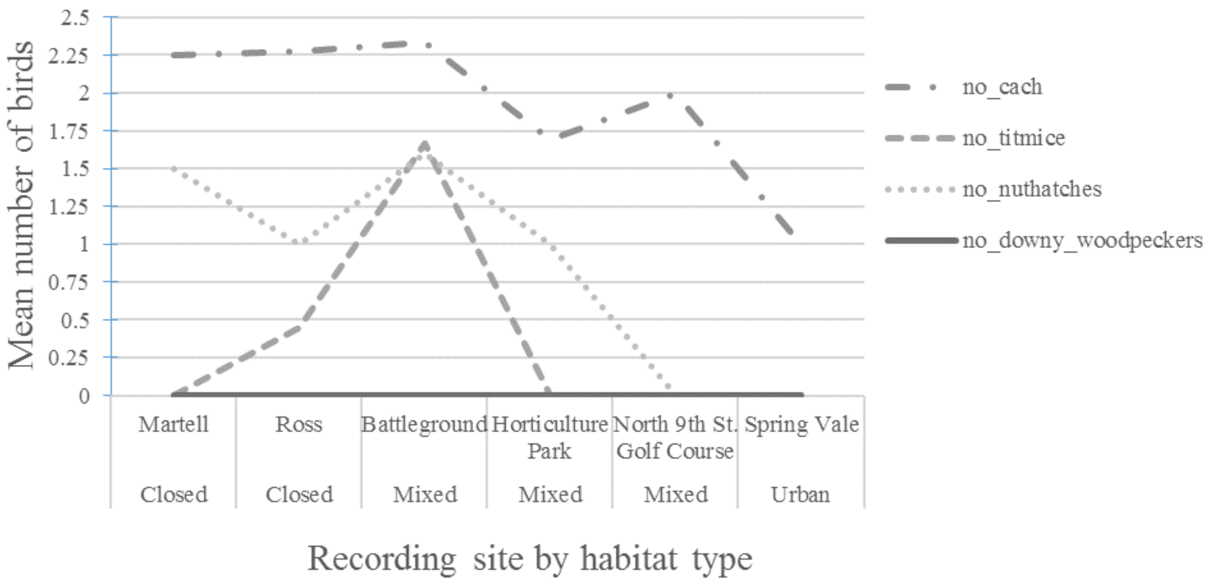


Figure 1 Mean flock size of individuals for ad lib recording sites.

The mean number of species that make up the mixed species flock of the chickadee. Means are the total birds observed divided by the number of recordings. There were no Downy Woodpeckers seen during the recordings. All number of birds decreased in open habitats. The largest flocks of chickadees were seen in closed habitats.

Table 2 Playback sites divided by habitat type

Closed Canopy Sites	Mixed Sites	Urban Sites
Ross Reserve (1)	Horticulture Park (1)	Spring Vale Cemetery
Ross Reserve (2)	Horticulture Park (2)	House on 12th St.
Hoffman Property (1)	McCormick Woods (1)	Campus (1)
Hoffman Property (2)	McCormick Woods (2)	Campus (2)

Table 3 Measurements of light intensity, cover and GPS coordinates of playback sites.

Study area	Hort 1	Spring Vale	Hort 2	Campus 1	Campus 2	Hoffman 2	Hoffman 1	McCormick 1	McCormick 2	Ross 1	Ross 2	12th St.
Light intensity **(lux)**	28500	99000	90800	5790	173	43.8	56.7	15900	6780	45.6	52.3	8950
Tree cover (%)	40	20	35	60	10	90	95	70	75	80	90	20
Shrub cover (%)	0	0	5	0	40	70	30	40	30	10	40	10
Grass cover (%)	98	60	45	70	1	15	0	10	0	5	0	50
Cement cover (%)	2	40	0	5	25	0	0	0	0	0	0	50
Bare earth cover (%)	0	0	15	25	34	15	3	60	70	60	60	0
Gps North Latitude	40° 25 0.057	40° 25 0.095	40° 25 0.646	40° 25 0.578	40° 25 0.296	40° 30 0.35	40° 30 0.545	40° 26 12.8	40° 26 16.8	40° 24 38.056	40° 24 35.032	40° 24 25.763
Gps West Longitude	86° 56 0.049	86° 51 0.639	86° 56 0.125	86° 55 0.224	86° 54 0.843	86° 46 0.447	86° 46 0.487	86° 55 53.55	86° 55 59.6	87° 3 49.532	87° 3 59.471	86° 52 58.397
Gps Elevation **(ft)**	609	560	636	662	578	588	798	209	210	179	198	205
Gps Accuracy **(ft)**	20	14	24	27	12	28	72	16	17	24	20	18

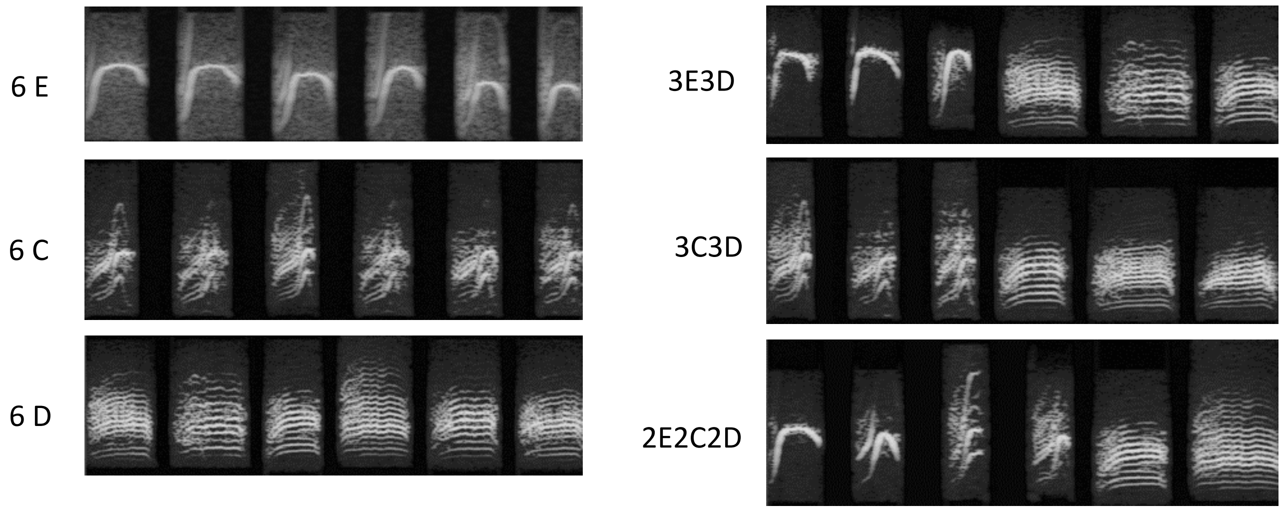


Figure 2 Sonogram of example playback treatments

Table 4 Flock size for each treatment at each playback site

Total number of chickadees observed during each playback treatment for each place is listed. Average flock size is the total number of chickadees from all trials divided by the number of trials.

	Treatment Name							
Playback site	2E2C2D	3C3D	3E3D	6C	6D	6E	Quank	Average flock size
12th St.	0	1	2	0	0	1	0	0.57
Campus 1	0	2	0	0	0	1	0	0.42
Campus 2	0	0	0	0	0	0	0	0
Hoffman 1	3	3	3	3	2	2	2	2.57
Hoffman 2	2	2	2	1	0	1	3	1.57
Hort 1	2	1	2	0	2	2	0	1.28
Hort 2	0	2	1	2	1	1	1	1.14
McCormick 1	1	2	2	2	1	0	0	1.14
McCormick 2	0	0	2	0	0	0	0	0.28
Ross 1	0	1	1	2	0	1	2	1
Ross 2	3	2	2	2	4	2	1	2.28
Spring Vale	1	0	2	1	1	0	0	0.71

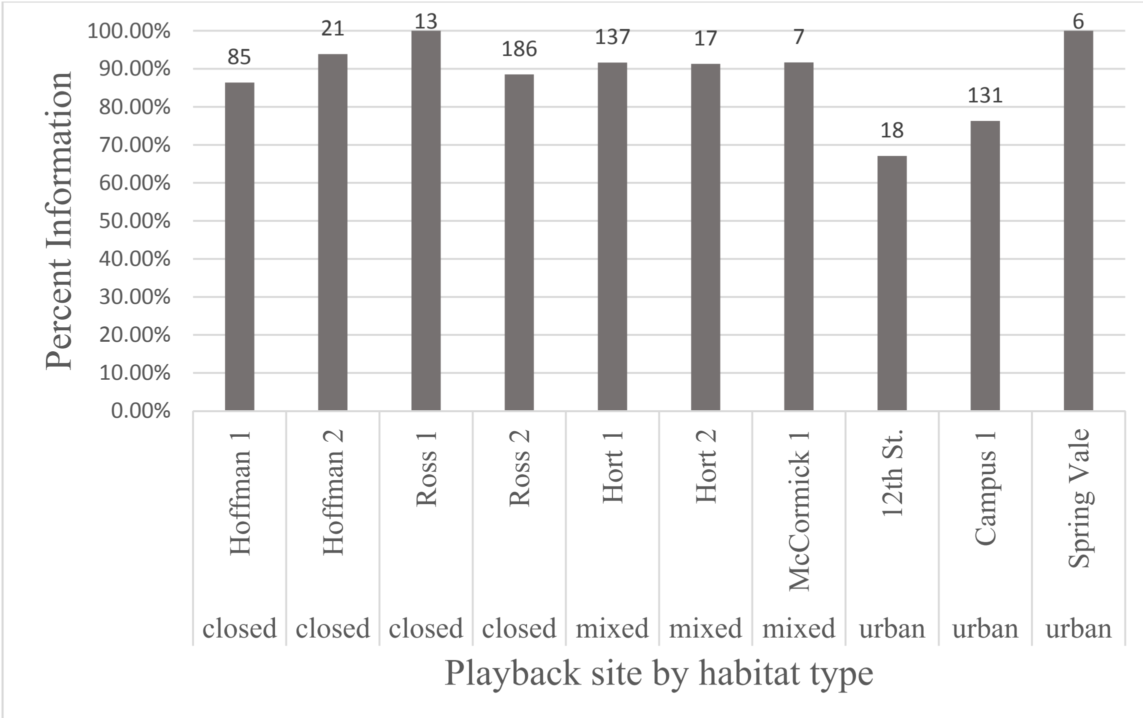


Figure 3 Percentage of information in chick-a-dee call type for each playback location

Sample size is listed above each bar. Percent information is the entropy in the system taken as a percent of the peak information. McCormick 2 and Campus 2 did not have any calls recorded during trials and were not included in this analysis. Percent information in the whole call is relatively similar across playback sites. Ross 1 and Spring Vale have the highest percent information which could be explained by the small sample size of calls recorded during those playbacks.

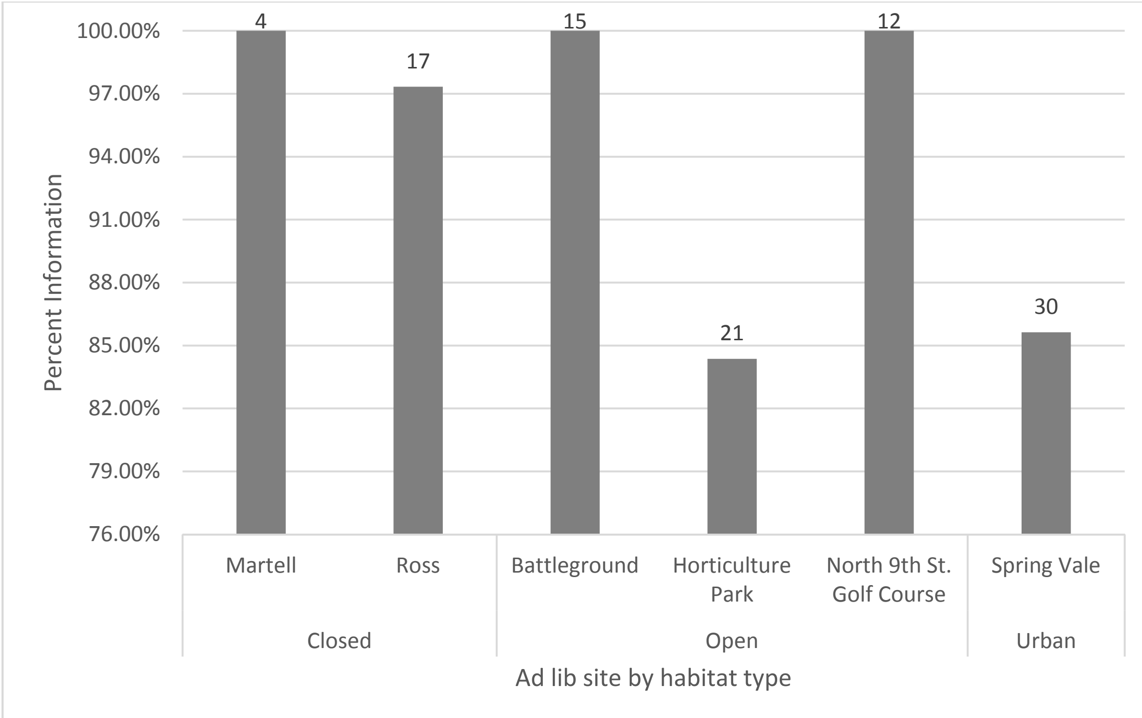


Figure 4 Percentage of information in chick-a-dee call type for each ad lib sites

Sample size is listed above each bar. Percent information is the entropy in the system taken as a percent of the peak information. Percent information in the whole call is relatively similar in closed and open sites compared to the urban site. Sample size for calls collected was under 50 for each site.

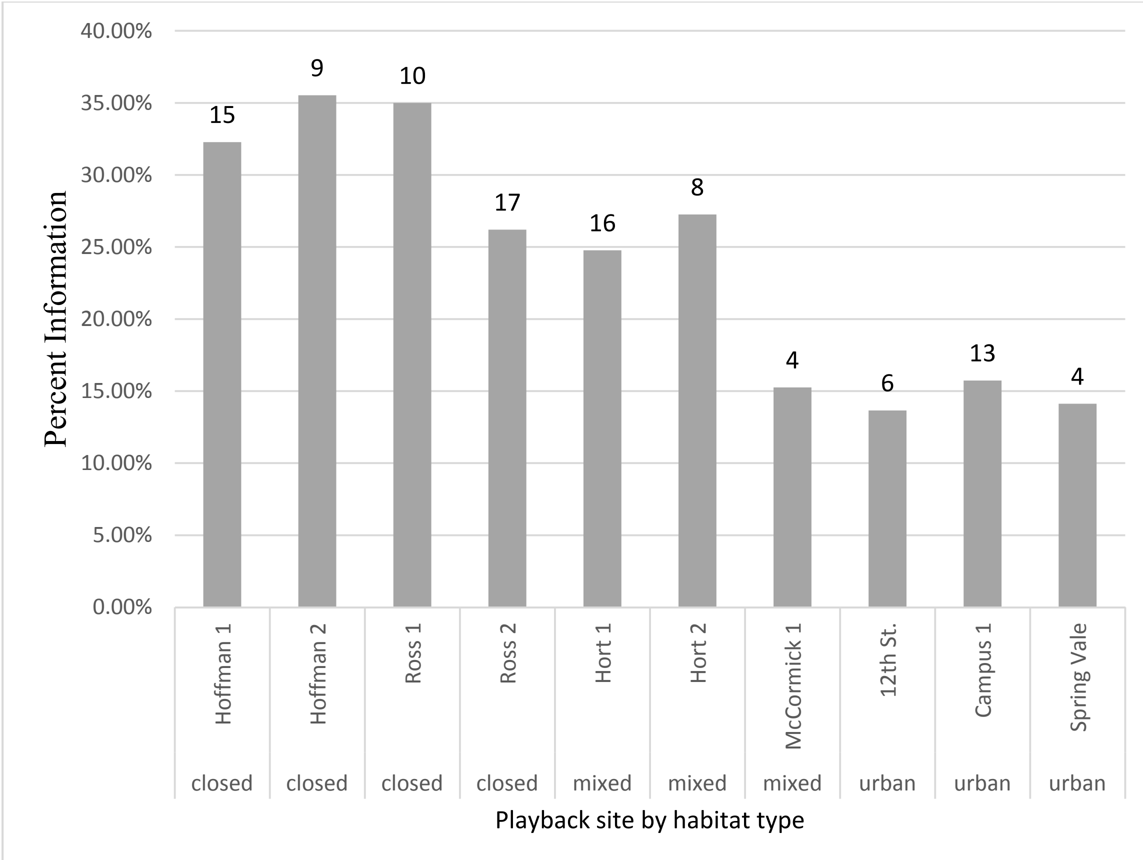


Figure 5 Percentage information in individual chick-a-dee notes for each playback site Sample size is listed above each bar. McCormick 2 and Campus 2 did not have any calls recorded during trials and were not included in this analysis. Percent information in notes for closed habitats it relatively higher than mixed and urban habitats. Percent information in all mixed habitats except McCormick 1 is relatively higher than all urban habitats.

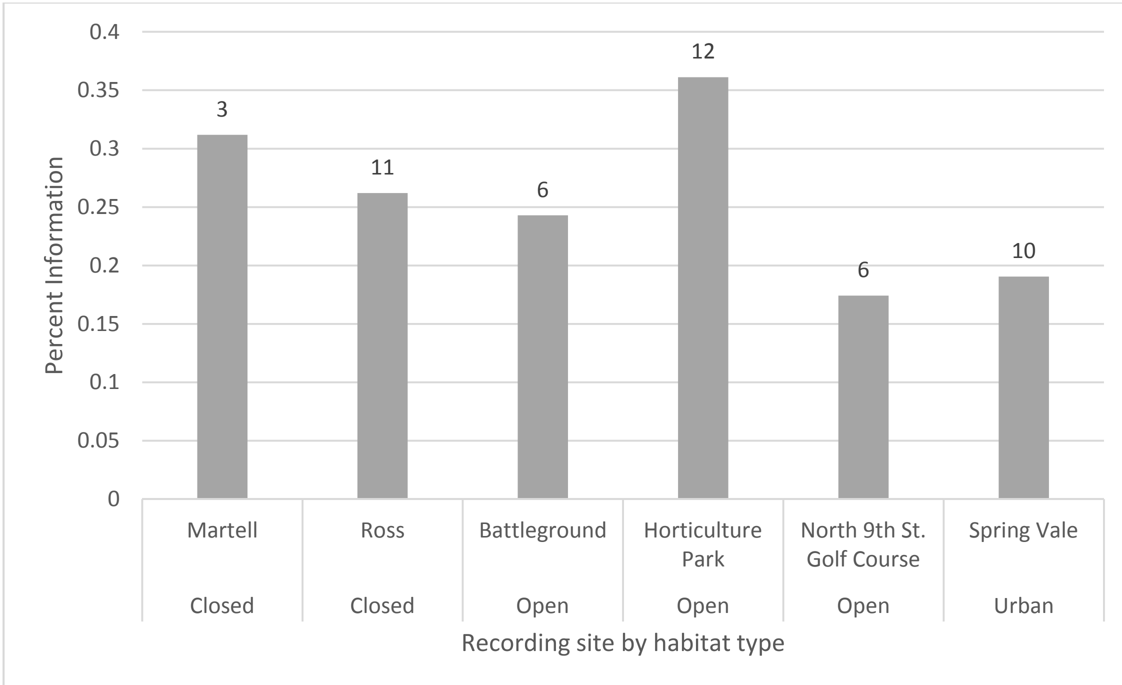


Figure 6 Percent information calculated for notes in the chick-a-dee call at ad lib recording locations.
Sample size is listed above each bar. Sample size is listed above each bar. Percent information encoded in notes is relatively lower in urban locations.

Table 5 Distribution of notes in each habitat type (percent)
Distribution of notes within each habitat type. N is the sample size of each note within each habitat. Distribution for each note calculated as a percent of the total number of that specific note across all habitats.

Note type	**Closed**	N	**Mixed**	N	**Urban**	N
B	0.0139	40	0.004	8	0.000	0
C	0.149	427	0.070	131	0.029	90
D	0.169	485	0.422	790	0.163	504
Normal E	0.227	653	0.070	132	0.022	68
Flat tee	0.032	91	0.010	20	0.001	4
Harsh D	0.220	633	0.143	267	0.236	730
High B	0.008	22	0.003	5	0.002	6
Black-capped A	0.001	3	0.015	28	0.006	20
Lisping tee	0.012	35	0.002	4	0.004	12
E with added elements	0.046	133	0.013	24	0.012	38
B with added elements	0.006	17	0.000	0	0.000	0
Pause	0.003	10	0.003	6	0.003	9
Rapid D	0.044	127	0.162	303	0.000	0
Tailed tee	0.032	92	0.018	33	0.011	34
Rounded tseet	0.002	7	0.000	0	0.000	0
Variable see	0.030	85	0.057	107	0.507	1565
One-sided tseet	0.0007	2	0.000	0	0.000	0
Hybrid D	0.003	10	0.006	11	0.000	0
Tseet	0.0003	1	0.000	0	0.003	8

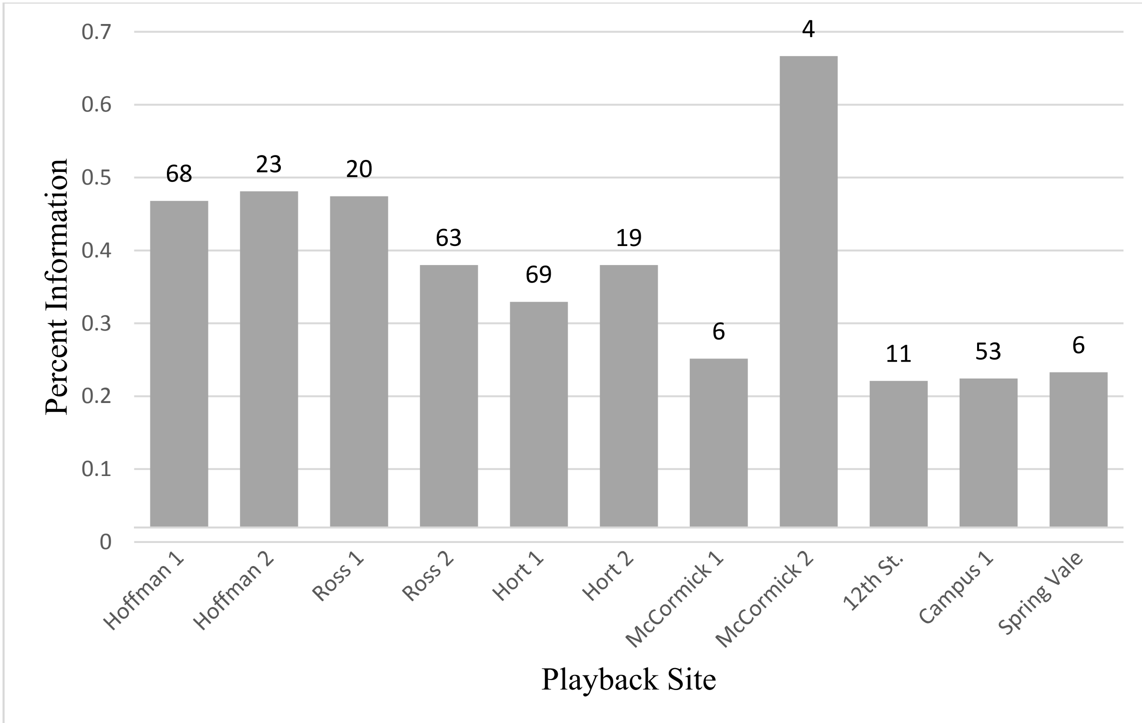


Figure 7 Percent information of transitions between pairs of note types

Table 6 F and p values for vocalization rates

Chick-a-dee and feebee rates per trial and per individual. F and p values calculated using a GLIMMIX model in SAS 9.3. Gradient, treatment name, gradient*treatment name, month and month*treatment were included in all models but only the models that converged are included.

	F	d.f.	P
Chick-a-dee rate (per trial)_			
Gradient	5.14	1, 253	0.0242
Treatment	55.69	6, 253	**<0.0001**
Gradient*Treatment	13.31	6, 253	**<0.0001**
Month	70.28	1, 253	**<0.0001**
Month*Treatment	47.69	6, 253	**<0.0001**
Feebee rate			
Gradient	0.13	1, 255	0.7233
Treatment	39.91	6, 255	**<0.0001**
Gradient*Treatment	36.27	6, 255	**<0.0001**
Total CAD per trial			
Gradient	5.56	2, 61	**0.006**
Treatment	76.25	6, 61	**<0.0001**
Main effects			
Treatment	10.49	7, 270	**<0.0001**
Chick-a-dee rate (per individual)			
Gradient	6.36	1, 540	**0.0119**
Treatment	28.77	6, 540	**<0.0001**
Gradient*Treatment	17.49	6, 540	**<0.0001**

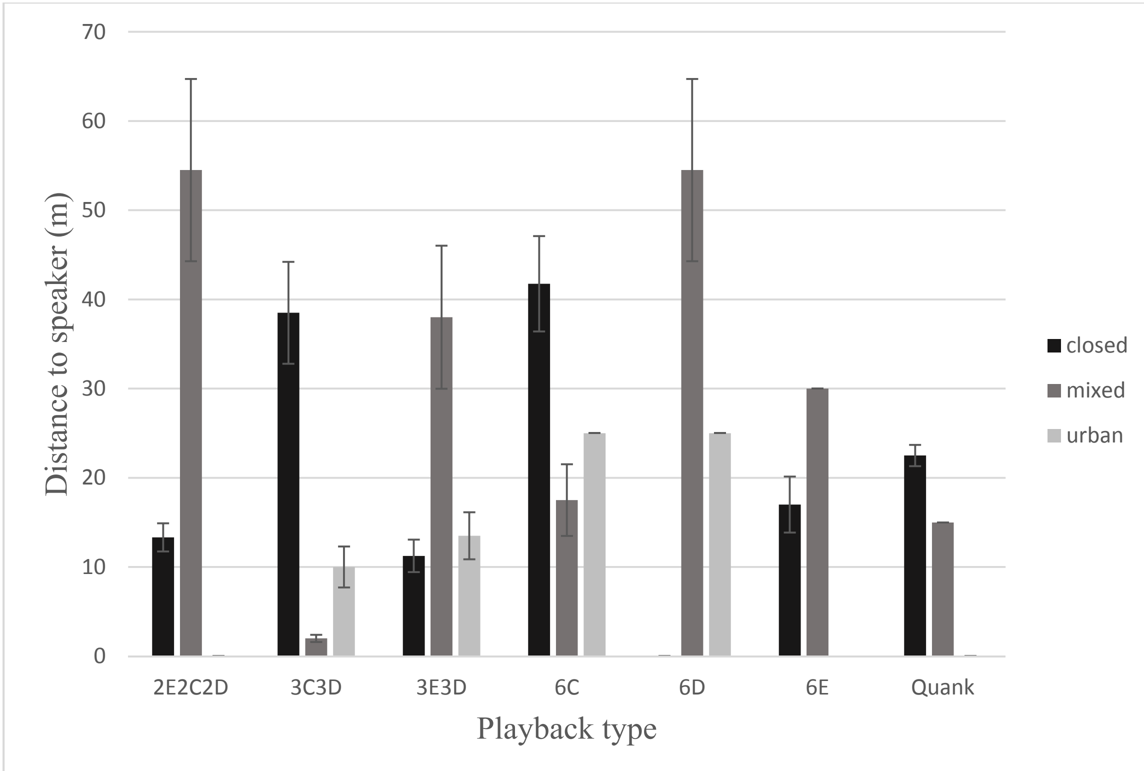


Figure 8 Closest approach of individuals to playback speaker
Average closest distance that the chickadee approached the speaker for each playback treatment. Chickadees came all the way into the speaker to the 6D treatment in closed habitats. There were no chickadees seen in the urban habitats for 2E2C2D, 6E and Quank treatments.

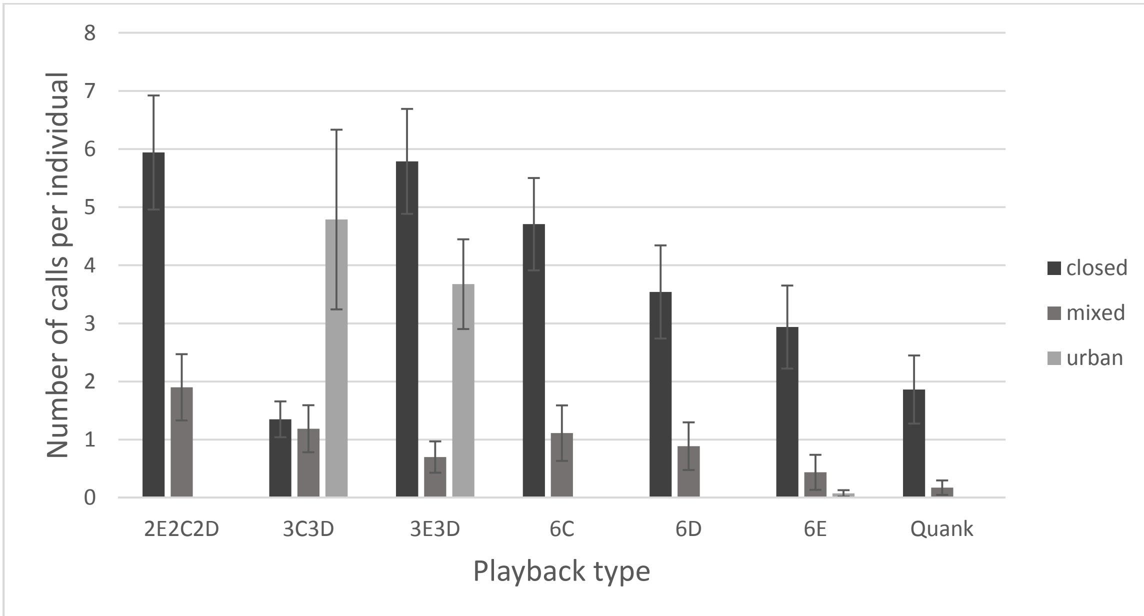


Figure 9 Mean chick-a-dee call rates for individuals in each trial
Call rates calculated from # chick-a-dee calls/# total chickadees. Treatments listed for each gradient. Closed habitat flocks have more variation in the number of responses per individual than mixed and urban habitats.

Table 7 : F and p values for call rates across seasons

Chick-a-dee and feebee rates per trial and per individual. F and p values calculated using a GLIMMIX model in SAS 9.3. Gradient, treatment name, gradient*treatment name, month and month*treatment were included in all models but only the models that converged are included.

	F	d.f.	P
Chick-a-dee rate			
Month	70.28	1, 253	**<.0001**
Month*Treatment	47.69	6, 253	**<.0001**
Feebee rate			
Month	0.16	1, 258	0.6919
Month*Treatment	66.69	1, 258	**<.0001**
Percent information			
Spring	12.4	2, 3	**0.0355**
Winter	0.85	1, 2	0.4545