

University of Alberta

Bioacoustic Analyses of the *Chick-a-dee* Call of the Mexican Chickadee
(*Poecile sclateri*) and the Boreal Chickadee (*Poecile hudsonica*).

by

Michele Kathryn Moscicki

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Examining Committee

Christopher Sturdy, Psychology

Marcia Spetch, Psychology

Doug Grant, Psychology

Colleen Cassady St. Clair, Biology

Abstract

To understand the communicative functions of any vocalization it is important to first classify, describe, and measure the elements of that vocalization. Mexican (*Poecile sclateri*) and boreal (*P. hudsonica*) chickadees both produce a name-sake *chick-a-dee* call. Here, the note types present in samples of Mexican and boreal *chick-a-dee* calls are identified and described. Frequency and temporal measures of each note type are analyzed and show that frequency measures may be useful for note-type and individual discrimination. Call syntax is also analyzed and shows that both Mexican and boreal chickadees produce the notes within their *chick-a-dee* calls in a fixed order with the potential for any note type to be repeated or omitted within the sequence. This work provides a foundation for future studies aimed at understanding the communicative significance of this call within these species, as well as for comparative work on the *chick-a-dee* call among all chickadee species.

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List of Abbreviations and Nomenclature

AD	Ascending Duration
<i>Aegithalos caudatus</i>	Long-tailed Tit
ANOVA	Analysis of Variance
<i>Aptenodytes forsteri</i>	Emperor Penguin
<i>Arctocephalus tropicalis</i>	Fur Seal
<i>Athene noctua</i>	Little Owl
<i>Basileuterus leucoblepharus</i>	White-browed Warbler
<i>Cardinalis cardinalis</i>	Northern Cardinal
CV _b	Coefficient of Variation Between
CV _w	Coefficient of Variation Within
DD	Descending Duration
<i>Dendrocygna viduata</i>	White-faced Whistling Duck
D _h	D-hybrid
EF	End Frequency
FM _{asc}	Ascending Frequency Modulation
F _{max}	Frequency at Maximum Amplitude
FM _{desc}	Descending Frequency Modulation
f ₀	Fundamental Frequency
<i>Formica xerophila</i>	Ant
GFD	Greatest Frequency Difference
kHz	Kilohertz
<i>Lonchura striata domestica</i>	Bengalese Finch

<i>Melospiza georgiana</i>	Swamp Sparrow
<i>Melospiza melodia</i>	Song Sparrow
ms	Milliseconds
NPF	Note Peak Frequency
<i>Pan paniscus</i>	Bonobo
<i>Parus caeruleus</i>	Blue Tit
<i>Parus major</i>	Great Tit
PF	Peak Frequency
PIC	Potential for Individual Coding
<i>Poecile atricapillus</i>	Black-capped Chickadee
<i>Poecile carolinensis</i>	Carolina Chickadee
<i>Poecile gambeli</i>	Mountain Chickadee
<i>Poecile hudsonica</i>	Boreal Chickadee
<i>Poecile rufescens</i>	Chestnut-backed Chickadee
<i>Poecile sclateri</i>	Mexican Chickadee
<i>Poecile cincta</i>	Grey-headed Chickadee
PNTC	Potential for Note-Type Coding
<i>Rana catesbeiana</i>	American Bullfrog
SD	Standard Deviation
<i>Sericornis frontalis</i>	White-browed Scrubwrens
<i>Serinus canaria</i>	Common Canary
SF	Start Frequency
<i>Sturnus vulgaris</i>	European Starling

Taeniopygia guttata

Zebra Finch

TD

Total Duration

Toxostoma rufum

Brown Thrasher

Zonotrichia albicollis

White-throated Sparrow

Zonotrichia leucophrys

White-crowned Sparrow

1. INTRODUCTION

1.1 Songbird Vocal Communication

Communication is an important, and yet often overlooked, component of survival for many animal species. Although there are a variety of communication systems, vocal communication is one of the most well studied means of communication in animals (see Hauser and Konishi 1999). Diverse aspects of animal vocal communication have been studied, from the call types produced by bonobos (*Pan paniscus*) when presented with different food types (Clay and Zuberbuehler 2009), to the vocal risk factors and training needs of telemarketers (Hazlett et al. 2009), to the songs of various songbird species (see Catchpole and Slater 1995 for a review).

Songbird vocal communication is one of the most well studied forms of animal communication (see Konishi et al. 1989 and Hauser 1997 for reviews). One reason for this is that songbirds are one of only a few animal groups that learn their vocalizations; other groups with this ability include parrots, hummingbirds, bats, cetaceans, elephants, and humans (see Tyack 2008 for a review). Songbirds learn their vocalizations in a manner analogous to the way humans learn to speak, namely, from a tutor in distinct stages, and thus we can use songbirds as a model for human language learning (Doupe and Kuhl 1999). Perhaps songbirds are one of the most well studied non-human vocal learners because there are many different species to choose from, songbirds are abundant in many areas, and they are relatively easy to record. Regardless of why songbirds are chosen, songbird vocal communication is considered to be well studied because these studies have focused on the four perspectives initially outlined by Tinbergen (1963) that

are necessary to explore to fully understand a trait. Tinbergen (1963) suggested all traits should be studied mechanistically, ontogenetically, functionally, and phylogenetically.

The following are examples of how songbird vocal communication has been studied from each of the four perspectives outlined by Tinbergen (1963). In addition, the roll of bioacoustics, the study of sound production and reception in animals, is linked to each perspective in the context of how this technique has been used to study songbird vocal communication or how it may be used in the future to enhance studies from each perspective. Bioacoustic analyses are at the foundation of work aimed at understanding songbird vocal communication.

1.2 Mechanistic Studies of Songbird Vocal Communication

Tinbergen's (1963) first perspective, mechanistic, has been studied with respect to songbird vocal communication by investigating the songbird vocal apparatus, the syrinx (e.g., Goller and Larsen 1997; Fee et al. 1998; Jensen et al. 2007). Over the last two decades a great deal has been learned about how birds produce vocalizations. Goller and Suthers (1996) measured the airflow through the syrinx, air sac pressure beneath the syrinx, and the activity of syringeal muscles via electromyograms (EMGs) to determine how the syrinx is used to produce various sounds in brown thrashers (*Toxostoma rufum*). Studies of the syrinx also revealed that some birds are able to produce two acoustically unrelated sounds that can seem as two distinct birds to a casual observer (e.g., Suthers 1997).

Studies have also gone beyond the syrinx to understand the mechanisms of songbird vocal production and how the components of this production are used. For example, a study of bill morphology in Bengalese finches (*Lonchura striata domestica*)

has revealed that birds with larger bills tend to produce shorter call bouts (Soma et al. 2008). In addition, Suthers and Zollinger (2004) have shown that songbird mimics that have been tutored with songs of heterospecifics use the same motor patterns as the tutor species when producing vocalizations, thus showing that the mechanisms used affect the vocalizations produced.

In order to know that some birds produce two acoustically unrelated songs a bioacoustic analysis must be performed, such as that conducted by Suthers (1997) on the songs of Northern cardinals (*Cardinalis cardinalis*). As well, to state that birds with larger bills produce shorter call bouts some cursory measurements of call length must be taken. Thus, bioacoustic analyses pervade the mechanistic study of songbird vocal communication. However, this area would benefit from even more thorough bioacoustic analyses of vocalizations to pinpoint precise changes in songs and calls that occur as a result of specific changes in the mechanisms of vocal production.

1.3 Ontogenetic Studies of Songbird Vocal Communication

Because songbirds learn their vocalizations in a manner analogous to humans, a great deal of research has focused on examining the ontogeny of birdsong, the second of Tinbergen's (1963) four perspectives. Some of this research has been aimed at understanding how birds learn to produce vocalizations by examining neural pathways associated with song learning and production. These studies have revealed that there are certain neurons that selectively attend to a bird's own song in order to compare that song to an internal representation of a tutor song and provide the feedback necessary to refine that song until it closely matches the representation of the tutor song (Poirier et al. 2009). It was also recently discovered that in zebra finches (*Taeniopygia guttata*) the production

of subsong does not require the high vocal center of the brain, an area required for vocal production in adult birds, but does require the lateral magnocellular nucleus of the nidopallium (LMAN), a brain area involved in learning (Aronov et al. 2008).

Some ontogenetic studies also investigate how a species will learn a vocalization when tutored with various vocalizations that may differ from the species norm. For example, Shackleton and Ratcliffe (1993) tutored black-capped chickadees (*Poecile atricapillus*) with various versions of the species typical two note tonal *fee bee* song: a high frequency, low frequency, and one note only version. They found that these birds would still sing over a wide range of frequencies regardless of the frequency of the tutor song. In addition, studies are currently being undertaken to determine the vocal effects of raising black-capped chickadees with mountain chickadee (*P. gambeli*) vocal tutors (Guillette et al. In prep).

Guillette et al. (In prep) will use bioacoustic analyses to compare the calls produced by the mountain-chickadee tutored black-capped chickadees to the calls produced by black-capped chickadees raised with conspecific vocal tutors. While this is interesting, bioacoustic analyses are not only used to examine vocalizations produced during experimental conditions. This type of analysis is also useful for studying the vocalizations of species during normal development to determine how songs and calls change over time. In these ways, bioacoustic analyses are an integral component of evaluating the ontogeny of songbird vocal production and communication.

1.4 Functional Studies of Songbird Vocal Communication

The third of Tinbergen's (1963) four perspectives is functional; a great deal of research has been focused on understanding the various functions of songbird vocal

communication. Songbird vocalizations are generally divided into two types: songs and calls. This distinction is often made based on the function of the vocalization (see Spector 1994 for a review). Songs are given primarily by males and are used for such purposes as mate attraction and territory defense (Armstrong 1963). The function of mate attraction has been ascribed to songs by analyzing female choice. For example, female canaries (*Serinus canaria*) have been shown to prefer songs with louder amplitude (Pasteau et al. 2009), female white-throated sparrows (*Zonotrichia albicollis*) give more copulation solicitation displays to longer songs (Wasserman and Cigliano 1991), and female song sparrows (*Melospiza melodia*) prefer males with a larger song repertoire (Searcy 1984).

The second general function of song, territory defense, has been examined using methods such as song matching and playback. Krebs et al. (1981) found that great tits (*Parus major*) responded to playback of songs from their own repertoire by matching the song type being played. Great tits were also found to match the songs of blue tits (*P. caeruleus*) in the wild (Gorissen et al. 2006). In addition, song sparrows were found to engage in song matching and matched songs of strangers more frequently than those of neighbours even though the neighbour songs were generally more similar to the focal bird's own repertoire (Stoddard et al. 1992). This may indicate that the birds did not need to defend a territory against a neighbour because the neighbour is no threat to the territory, an idea proposed as the 'dear enemy' effect by Fisher (1954).

The second type of songbird vocalization is the call; this vocalization is more ubiquitous than song and is generally given by both males and females year round (Smith 1991). Calls serve a variety of functions including flock identification (Nowicki 1989), contact between mates (McLaren 1976), recruiting flock mates to a food source (Mahurin

and Freeberg 2009), mobbing (Templeton et al. 2005), and may even contain information about species (Charrier and Sturdy 2005) and individual identity (e.g., Charrier et al. 2004). The function of calls has been studied in the field using playback experiments such as that conducted by Leavesley and Magrath (2005) using alarm calls recorded from white-browed scrubwrens (*Sericornis frontalis*). Alarm calls were recorded from these birds when an aerial predator was close, indicating more danger and producing calls with more elements, and when the same predator was farther away. The playback results show that the calls with more elements produced more urgent responses from listening birds, including immediately fleeing for cover. Thus, the authors have shown that the structure of the call in this species is closely tied to its function and the message being conveyed.

In addition to field playback studies, call function has also been studied more naturally in the field and more rigorously in the laboratory. For example, McLaren (1976) observed the context in which certain vocalizations were given when attempting to determine the function of a variety of boreal chickadee (*Poecile hudsonica*) calls. In the laboratory, techniques such as operant discrimination tasks have been employed to study the function of calls. Bloomfield and Sturdy (2008) showed that black-capped chickadees and mountain chickadees are capable of discriminating each species' calls into open-ended categories, thus suggesting that calls may contain information important for species identification, or at least discrimination.

In order to study any aspect of function it is first important to know about the vocalization in question. For example, one must first know what the elements are in the songs of canaries, white throated sparrows, or song sparrows in order to know what changes in them will elicit the most favourable responses from females. This knowledge

is gained by conducting bioacoustic and syntactical analyses on the songs of these species. Examples such as these emphasize the crucial role bioacoustic analyses play in studies examining the functions of songbird vocal communication.

1.5 Phylogenetic Studies of Songbird Vocal Communication

The last of Tinbergen's four perspectives, phylogenetic, is perhaps the least well studied with regards to songbird vocal communication. The phylogenetic perspective involves first understanding the evolutionary history of the species in question in order to examine the structure of the trait in light of ancestral features (Tinbergen 1963). There has been some work aimed at unraveling the evolutionary history of various species of songbirds. Of special note is the work by Gill et al. (1993, 2005) examining the genetic relationships of songbirds in the family *Paridae* and in particular the genus *Poecile*, the North American chickadees. Gill et al. (2005) have determined, through genetic analyses, that there are two subgroups of chickadees, the black-headed and the brown-headed chickadees. The black-headed subgroup consists of the black-capped, mountain, and Carolina (*Poecile carolinensis*) chickadees while the brown headed subgroup consists of the boreal, chestnut-backed (*P. rufescens*), grey-headed (*P. cincta*), and Mexican (*P. sclateri*) chickadees. However, some relationships, such as the relationship of Mexican chickadees to the rest of the chickadee species, are still somewhat ambiguous. This phylogenetic work satisfies the last of Tinbergen's (1963) four perspectives that should be studied to gain a full understanding of a communication system and is a foundation for further studies examining songbird vocal communication from an evolutionary or species comparison perspective.

In order to examine the phylogeny of songbird vocal communication, it makes sense to perform comparative studies and determine the similarities and differences in vocalizations across species to better understand how the present form of the vocalization for each species emerged. Tinbergen (1963) has suggested that it is best to conduct comparative studies in closely related species as this is the best method for drawing conclusions about common descent, though in recent decades the benefits of studying species in more distantly related phylogenetic groups for comparative purposes have also been discussed (e.g., Harvey and Pagel 1991). The genus *Poecile* is an excellent candidate for comparative studies because there are seven closely related species in this group (Gill et al. 2005). In addition, the chickadee species in this genus are abundant in North America and cover a vast range, making them easily accessible for study. Some chickadees produce a tonal, whistled, two note *fee bee* song and all species produce the name-sake *chick-a-dee* call. The fact that all seven species produce this call type is yet another reason why this genus makes a sound choice for comparative vocal studies.

1.6 Bioacoustic Analysis

Bioacoustic analyses play an integral role in attempting to understand songbird communication from a phylogenetic perspective as one of the first steps in studying any type of vocalization should be to identify and describe the elements of that vocalization. For comparative studies such as those that would satisfy the phylogenetic study of songbird vocal communication, the vocalizations of each species should first be studied independently. Bioacoustic work focused on this aspect of vocal analysis has been completed on the *chick-a-dee* calls of four of the seven species of chickadees, black-capped (Charrier et al. 2004), mountain (Bloomfield et al. 2004), Carolina (Bloomfield et

al. 2005), and chestnut-backed chickadees (Hoeschele et al. In press). These works have used similar methodology to facilitate comparisons among species. The analyses included identifying and describing the note types present in the *chick-a-dee* call of each species, measuring various spectral and temporal features of each note type to determine if any of these features would be useful in note-type or individual discrimination, and analyzing the syntax of the *chick-a-dee* call to determine the rules that govern the order of note-type production within the call. These analyses give a comprehensive description of the *chick-a-dee* call of each species studied in this manner to date and serve as an excellent basis for comparative studies.

The present work will focus on similar bioacoustic analyses for two of the remaining three species of chickadee that have not yet been studied in this manner, the Mexican chickadee and the boreal chickadee. These species are the last two easily accessible chickadee species to be studied bioacoustically using these methods as the seventh chickadee species, the grey-headed chickadee, has a limited northern range that makes obtaining vocalizations for study difficult (Hailman and Haftorn 1995). The studies in this work use methodology similar to that used in previous bioacoustic studies of other chickadee species. The present work seeks to identify and describe note types, measure frequency and duration features of each note type for each species, and conduct analyses to determine which features, if any, may be best used for discriminating among note types in each species and for discriminating among individuals in boreal chickadees. Finally, the syntax of the *chick-a-dee* call of each species is examined in depth to determine the order in which note types are generally produced in the call. These studies will serve to add information about these less well studied species to the growing body of

knowledge about *chick-a-dee* call structure. With this information, comparative studies on the *chick-a-dee* call can be conducted on a set of closely related species which may provide insights into the evolution of this particular vocalization, and, by incorporating the four perspectives proposed by Tinbergen (1963) to understand a trait, perhaps contribute to the understanding of songbird vocal communication in general.

1.7 Literature Cited

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2. NOTE TYPES AND CODING IN PARID VOCALIZATIONS: THE *CHICK-A-DEE* CALL OF THE MEXICAN CHICKADEE (*POECILE SCLATERI*)

2.1. Introduction

The use of oscine songbirds as a model for human language learning (Doupe and Kuhl 1999), and vocal communication in general (see Slater 2003 for a review), has become increasingly popular over the last few decades. One songbird group that has received a great deal of attention in this line of research is the genus *Poecile*, the North American chickadees. All members of this genus produce a *chick-a-dee* call that is learned in at least one species (Hughes et al. 1998). There is reason to believe that the *chick-a-dee* call contains useful and important species-relevant information, therefore it has been the subject of much research (for reviews see Lucas and Freeberg 2007 and Sturdy et al. 2007).

The *chick-a-dee* call is a common chickadee vocalization, is given by both males and females year round, and contains many discrete units (notes), thus allowing for many potential note combinations and encoded messages (e.g., Ficken et al. 1994). Syntactic evidence from black-capped chickadees shows that these birds possess “open” call systems (Hailman et al. 1985, 1987), meaning that one can find an increasing number of call types within increasing call sample sizes. Finally, the *chick-a-dee* call is given in a variety of contexts, such as mobbing (Templeton et al. 2005), contact (Smith 1991), flock identification (Nowicki 1989), and food location (Freeberg and Lucas 2002) to name but a few. Taken together, this evidence suggests that the *chick-a-dee* call is a vocalization that has the potential to convey a variety of messages.

Previous work on chickadee calls has shown that different calls, and in fact different note types within those calls, are used in different contexts. Black-capped chickadees in close proximity to a predator produce calls with more B notes while calls with more A notes are produced when farther from the same predator (Baker and Becker 2002). D notes in this species may be important for flock identification (Nowicki 1989) and predator mobbing (Templeton et al. 2005). Carolina chickadee D notes may play a role in recruiting flock-mates to a food source (Mahurin and Freeberg 2009) while C notes are used with increased frequency in the presence of a food source (Freeberg and Lucas 2002) as well as when the bird is in flight (Freeberg 2008). In contrast, Mexican chickadees appear to use A notes during flight and movement, C notes in reaction to a disturbing stimulus, and D notes when perched (Ficken et al. 1994). It appears then that closely related *Poecile* species use the note types in their *chick-a-dee* calls for a variety of different functions. Uncovering commonalities and differences in call and call note usage within the genus may be best accomplished using a comparative approach.

Tinbergen (1963) stated that comparative studies are best carried out in members of closely related species as this is the most effective way to draw conclusions about homology, or common descent. There are seven species of *Poecile* with varying degrees of relatedness (Gill et al. 2005) making them an excellent choice for Tinbergen's (1963) ideal comparative work. Kroodsma and Byers (1991) have noted that the first step when comparing behaviour across species is to describe how that behaviour appears within each species in question. To date, detailed bioacoustic analyses have been performed on the *chick-a-dee* calls of four of the seven *Poecile* species (Charrier et al. 2004; Bloomfield et al. 2004; Bloomfield et al. 2005; Hoeschele et al. In press). Previous work

on the calls of Mexican chickadees (Dixon and Martin 1979; Ficken 1990; Ficken et al. 1994) did not provide an in-depth analysis of the many individual note features present in these calls, such as frequency and duration measurements, which are necessary for future detailed comparative work.

The present work will focus on the *chick-a-dee* call of the Mexican chickadee and has five goals: i) to identify the note types present in a sample of Mexican chickadee calls in a manner analogous to previous bioacoustic studies of other chickadee species; ii) to perform a detailed analysis of various frequency and duration measurements for each of the note types identified; iii) to provide a syntactical analysis of Mexican chickadee calls in a manner analogous to that provided for chestnut-backed chickadees (Hoeschele et al. In press) for ease of species comparisons; iv) to provide a comprehensive description of the Mexican chickadee call to serve as a foundation for future laboratory and field work designed to examine the perceptual and discriminatory capabilities of this species; and v) to serve as a base for future in-depth comparative work among all the *Poecile* species by employing methodology similar to previous bioacoustic studies of the *chick-a-dee* call of this genus.

2.2. Materials, Methods, and Results

2.3. Study I – Call Note Classification

In this study, we sorted individual call notes of Mexican chickadee calls into categories based on visual similarity of spectrograms. The goal of this study was to provide reliable descriptions of the various note types found within the Mexican *chick-a-dee* call. Following note-type identification and classification, we were able to measure and summarize various acoustic features for each note type (Study II) as well as

determine the syntactical rules governing the placement of each note type within a call (Study III).

2.4. Methods

a. Recordings. For our analyses, we obtained multiple recordings of Mexican chickadee calls from three sources, with each recording containing a variable number of *chick-a-dee* calls: 278 calls in 10 recordings from the Macaulay Library of Natural Sounds at the Cornell Laboratory of Ornithology; 218 calls in 7 recordings provided by the Borror Laboratory of Bioacoustics at Ohio State University; and 167 calls in 5 field recordings made by Millicent Ficken. In total, we obtained 663 *chick-a-dee* calls composed of a total of 1,999 individual notes. See Table 2-1 for a complete list of the recordings used for analysis, as well as details about those recordings, such as equipment used, location, year, and time of day. All recordings were sampled at a rate of 44.1 kHz.

We used a subsample of the recordings described above for analysis in Study I and Study II (below) because it was not feasible to conduct the analyses on all 1,999 individual notes. The subsample was chosen by first selecting the recordings from each of the sources listed above that contained at least 10 Mexican chickadee *chick-a-dee* calls. We then randomly chose 10 recordings from this pool to include in the analysis, resulting in 5 recordings from the Macaulay Library, 3 recordings from the Borror Laboratory, and 2 recordings from Millicent Ficken. 10 calls were then randomly selected from each of these recordings to include in the analyses. This sampling procedure resulted in 100 Mexican chickadee *chick-a-dee* calls, 10 from each of 10 different recordings, composed of a total of 320 individual notes.

b. Sound spectrograms and note classification. Following procedures similar to those of previous bioacoustic studies completed by our lab (Charrier et al. 2004; Bloomfield et al. 2004; Bloomfield et al. 2005), and to standardize analyses, individual notes were cut from calls and saved as sound files of 300 ms (non D-type notes) or 500 ms (D-type notes) by adding trailing silence to each sound file using SIGNAL 5.10.25 Sound Analysis Software (Engineering Design, Berkeley CA). Both D- and non D-type notes were saved as spectrogram images with a cut-off amplitude of -35dB relative to the peak amplitude of the note in a 512 point Hanning window to achieve both adequate frequency and time resolution. Each note spectrogram was given a unique, random, four digit code and was printed, 15 spectrograms per page, on 8.5" x 11" glossy photo paper. Individual note spectrograms were cut out to form note 'cards' and thus produce a 'deck' of note spectrogram cards for sorting.

In a preliminary analysis, the first author sorted the 'deck' of Mexican *chick-a-dee* note spectrogram cards into an open number of categories based on visually similarity. Four note-type categories were determined in this process (see Fig. 2-1). To provide the two additional sorters with accurate information as to the note types determined in this preliminary analysis, a written description of each of the categories was prepared (see Note descriptions below). In addition, an exemplar of each category was provided; exemplars were selected from calls that had not been included in the current study. The descriptions, spectrogram card exemplars, and deck of note spectrogram cards were given to two additional sorters to sort; all three sorters had previous experience sorting call notes of other chickadee species. Once all three sorters had sorted the entire deck of note cards into note-type categories, the percent agreement

among sorters was calculated to determine the reliability of the note-type categories and a meeting was held to resolve any disagreements in note sorting.

2.5. Results

a. Call-note classification. Four note-type categories (see Fig. 2-1) were identified by sorting the 320 Mexican chickadee note cards. The percent agreement among the three sorters was 98.73% (4 note disagreements) before a meeting was held to revise the note-type category criteria. The criteria for D_h note types was refined to ensure that D_h note types with a short terminal D note-type portion were not misclassified as A note types. This clarification resolved the 4 disagreements and percent agreement among sorters reached 100%.

b. Note-type descriptions. We based the nomenclature for our four note-type categories on note names previously described by Ficken (1990), as well as on similar note types appearing in calls of closely related chickadee species (e.g., black-capped chickadees; Charrier et al. 2004).

A Notes: A notes are tonal, as with the A notes of other chickadee species, and generally occur between 6-8 kHz. However, these notes contain oscillating periods of ascending and descending frequency modulation throughout; this is different from the A notes of all other chickadee species studied to date. There is a very slight decrease in frequency from note start (about 8 kHz) to note end (about 6 kHz; see Fig. 2-1). These notes are typically between 150-300 ms in duration.

C Notes: C notes cover a wider frequency range than A notes (typically about 6 kHz between 2-8 kHz). These notes have ‘stacks’ of relatively parallel frequency bands. The main frequency band begins at a low frequency (around 4 kHz) and increases,

generally linearly, to a peak frequency (around 5 kHz) and either ends at this peak frequency or decreases very slightly in frequency before note termination (see Fig. 2-1). All other frequency bands follow this general pattern of relatively linear frequency increase to a peak where they either terminate or decrease in frequency slightly before termination. C notes typically range from 40-60 ms in duration.

D Notes: D notes appear like a band of noise with a roughly distinguishable harmonic-like structure. These notes are much longer in duration than both A and C notes and range from 350-500 ms. D notes typically cover a frequency range of about 5 kHz from 3-8 kHz, although this can be quite variable. There is little to no frequency modulation throughout the D note (i.e., the frequency remains constant throughout the note; see Fig. 2-1).

D hybrid (D_h) Notes: D_h notes are a combination of an A note-type portion and a D note-type portion. The A note-type portion has an oscillating ascending and descending frequency modulation (between about 6-8 kHz) similar to an A note and typically spans a duration of between 100-150 ms. This portion terminates with a rapid decrease in the frequency of the tonal band over a short duration (see Fig. 2-1). The D note-type portion of the D_h note is continuous with the tonal frequency band and appears as a band of ‘noise’ between about 3-6 kHz. This band of sound decreases in bandwidth over a roughly 50 ms duration and terminates with a more narrow frequency band (between about 3-5 kHz) for a duration between 100-200 ms. The entire note spans a duration of 300-500 ms.

2.6. Study II – Quantitative Note-Type Analysis

In Study II, we measured various frequency and temporal characteristics of notes in the four note-type categories identified and described in Study I. The goal of this study was to compare the variability of frequency and temporal characteristics across the various note types to determine if the measured note features can potentially be used to discriminate among note types.

2.7. Methods

a. Note measurements. The same subsample of 320 Mexican chickadee notes described in Study I was used in the present study. SIGNAL 5.10.25 Sound Analysis Software (Engineering Design, Berkley CA) was used to make all note measurements following similar procedures used to analyze the notes of other chickadee species' *chick-a-dee* calls (e.g., Charrier et al. 2004; Bloomfield et al. 2004; Bloomfield et al. 2005; Hoeschele et al. In press). Frequency measurements were taken on spectrograms with a Hanning window size of 1,024 points with a precision of 43 Hz. Temporal measurements were taken on spectrograms with a Hanning window size of 256 points with a precision of 5.8 ms.

We gathered different frequency and duration measurements on each note type depending on the characteristics of the note type. For A, C, and the A note-type portion of D_h notes we analyzed the following frequency measurements on the frequency band with the highest amplitude (i.e., the darkest band in the spectrogram): start frequency (SF), peak frequency (the highest frequency of the loudest frequency band; PF), and end frequency (EF; see Fig. 2-2A). Temporal measurements on these note types consisted of ascending duration (AD) and descending duration (DD). We calculated total duration (TD) on all note types (A, C, D, and D_h ; see Fig. 2-2B).

Since A notes and the A note-type portion of D_h notes have many oscillations of ascending and descending frequency modulation, the AD and DD temporal measurements were taken on the oscillation with the greatest frequency range (GFR; see Fig. 2-2B). We defined one frequency oscillation as one cycle of ascending frequency, peak frequency, and descending frequency (see Fig. 2-2B). We calculated the slope of the ascending (FM_{asc}) and descending (FM_{desc}) frequency modulations for A, C, and the A note-type portion of D_h notes. Note that, for A and the A note-type portion of D_h notes separate SF, PF, and EF measurements were taken on the oscillation with the greatest frequency range and these measurements were used in the calculation of FM_{asc} and FM_{desc} . Frequency modulation is calculated as follows: $FM_{asc} = PF - SF / AD$ and $FM_{desc} = PF - EF / DD$.

For all note types, we generated a spectrum (with a window size of 4,096 for C notes and 16,384 for A, D, and D_h notes) that encompassed the entire note and had a smoothing width of 88.2 Hz. This spectrum was used to calculate the frequency at maximum amplitude (i.e., the loudest frequency; F_{max} ; see Fig. 2-2C) for all note types. We also used this spectrum to calculate the fundamental frequency (i.e., the lowest frequency within 35dB of the peak amplitude of the note; f_0) and the note peak frequency (i.e., highest visible frequency; NPF) for C notes, D notes, and the D note-type portion of D_h notes (see Fig. 2-2D).

b. Statistical analyses. In order to determine whether certain features of a note can be used to classify that note into a certain note-type category, we examined the variation of the measured note features within each note type and across all note types. Following the methodology of Charrier and colleagues (2004) we calculated a measure of potential

for note-type coding (PNTC) which indicates whether a certain feature could be used to discriminate among note types. PNTC is calculated separately for each note feature by dividing the coefficient of variation between note types (CV_b) for that note feature by the mean coefficient of variation within note types (mean CV_w) for that note feature. The idea behind this measure is that if the variation of a note feature is greater across note types than within a note type then the PNTC value will be > 1 and that feature may be useful for note-type coding. Alternatively, if variation for a feature is greater within note types than across note types then PNTC will be < 1 and that feature is likely less useful for note-type coding.

The coefficient of variation between note types is calculated as follows: $CV_b = (SD/\bar{x}) \times 100$, where SD is the standard deviation and \bar{x} is the mean of the note feature measure calculated across all note types. The mean coefficient of variation within note types is calculated using the same formula, $CV_w = (SD/\bar{x}) \times 100$; however, now SD is the standard deviation and \bar{x} is the mean of the note feature measure within one note type. This calculation is done separately for each note type and the mean of those values is taken to obtain the mean CV_w . PNTC equals the ratio $CV_b/\text{mean } CV_w$. PNTC is used as a measure of the effect size of the difference between note types.

In addition to PNTC calculations, we used SPSS version 15.0.0 (SPSS Inc. 2006) to perform univariate analyses of variance (ANOVAs) in order to assess whether there were significant differences among note types on the note features we measured. Because we conducted multiple comparisons we used Bonferroni corrections to control type I error. We measured 9 note features for A notes, 11 note features for C and D_h notes, and 5 note features for D notes; thus, our α levels were set at $\alpha = 0.05/9 = 0.0056$ for A notes,

$\alpha = 0.05/11 = 0.0045$ for C and D_h notes, and $\alpha = 0.05/5 = 0.01$ for D notes. We used the Games-Howell post-hoc test for samples where equal variance is not assumed.

Bonferroni corrections were used for all post-hoc tests depending on the number of comparisons used. Because some note features were not measured for all note types, the Bonferroni corrections were either $\alpha = 0.05/3 = 0.017$ (for SF, PF, EF, DD, FM_{asc}, FM_{desc}, F_o, and NPF) or $\alpha = 0.05/4 = 0.0125$ (for AD, TD, and F_{max}).

2.8 Results

All 320 notes from Study I were used in the analysis for Study II. We measured a total of 85 A notes, 134 C notes, 56 D notes, and 45 Dh notes.

a. Note-type acoustic features. Table 2-2 shows a summary of the PNTC and ANOVA results for all note features measured for each note type. The PNTC results show that all note features measured, except for note peak frequency (NPF), have PNTC values > 1 and thus could potentially be used to determine note type. Peak frequency (PF) has the highest PNTC value, 6.26, and seems the most likely feature to use for note-type discrimination. Descending duration (DD), both frequency modulation measures (FM_{asc} and FM_{desc}), as well as all measurements taken on power spectra (F_{max}, F_o, and NPF) appear to be less useful for determining note type as their PNTC values are much closer to 1 than any of the frequency measures (SF, PF, EF), ascending duration (AD), or total duration (TD). All of the latter note features have PNTC values greater than 2.

All note types differed significantly on every note feature measured ($F_s \geq 21.023$, all $ps \leq 0.001$; see Table 2-2). The results of the Games-Howell post-hoc test show that a few note types were not significantly different on a subset of the note features measured. Bear in mind that all post hoc α levels have been Bonferroni corrected to either 0.017 or

0.0125 based on the number of note types that were measured for a specific feature (see Statistical analyses above). See Table 2-2 for a list of which features did not differ significantly in post-hoc tests. All other features differed across note types (mean differences ≥ 8.3 , $ps \leq 0.015$; see Table 2-2 for F values).

2.9. Study III – Syntactical Analysis

In Study III, we expanded our subsample of Mexican chickadee calls to examine the order in which the notes occur within the call. The goal of this study was to uncover and describe any syntactical rules that may be governing the order of note production within Mexican chickadee *chick-a-dee* calls.

2.10. Methods

a. Recordings and sound spectrograms. The entire sample of Mexican chickadee *chick-a-dee* calls described in Study I was considered for analysis in this study; this comprised a total of 663 calls composed of 1,999 notes (see Table 2-1 for a description of recordings). Spectrograms of whole calls were visually assessed for quality of recordings and calls with excess noise, multiple birds calling simultaneously, or calls that were too faint to adequately classify note types were removed from the analyses. The final analyses were conducted on the following sample: 235 calls from the Macaulay Library of Natural Sounds at the Cornell Laboratory of Ornithology, 209 calls from the Borror Laboratory of Bioacoustics at Ohio State University, and 99 calls from field recordings made by Millicent Ficken. These calls were composed of a total of 1,360 notes. Since it was not feasible to make 1,360 separate note cards, each whole call was saved to a separate sound file using Syrinx v.2.6h (Burt 2006) software. Spectrograms of individual calls were then made using SIGNAL 5.10.25 Sound Analysis Software (Engineering

Design, Berkeley CA). Spectrograms were 1,800 ms in duration with a 512 point Hanning window. The cut-off amplitude for all spectrograms was set to -40 dB relative to the peak amplitude of the call and each individual whole call spectrogram was saved as an image file. Call spectrograms were printed, four spectrograms per page, on 8.5" × 11" white paper, given a unique file name, and compiled into a binder for syntax determination.

b. Call syntax determination. The same sorters from Study I determined call syntax in the whole call spectrograms by sorting notes into note-type categories using the category descriptions and exemplars described in study I. All note sorters were blind to the classifications of the other sorters. The note classification procedure was slightly different between this study and study I (seeing notes in the context of the whole call in the former and seeing notes in an isolated context in the latter). We compared the classification of notes used in study I to the classification of those same notes using the methodology of this study; this was done to ensure that the different note classification methods would not lead to different results. Percent agreement among the three sorters was determined and a meeting was held to discuss any discrepancies in note classifications.

c. Probability calculations. Once note types were determined for all 1,360 notes in the sample, the number of different call syntax types produced in the sample, and the number of times they occurred, was determined. To examine the syntactical rules of the Mexican chickadee *chick-a-dee* call, conditional transition probabilities for all syntax types were calculated. This measure involved calculating the probability that a certain note type would occur given that a certain note type had directly preceded it; for example,

the probability was calculated that a D note would occur given that an A note was produced directly before it in the call. In order to calculate this measure, the number of transitions from the note type of interest to the second note type of interest was counted (e.g., the number of transitions from an A note to a D note) and this was divided by the total number of transitions from the preceding note type (A notes in this example). This was done for all note type combinations as well as the probability that the note was the last note in the call (i.e., that it was followed by no note type).

We also calculated note position probabilities. We calculated the probability that a certain note type occurred in a certain position within the call (e.g., the probability of an A note occurring as the 1st note in the call), or, vice versa, that a certain position in the call contained a certain note type (e.g., the probability of the 1st note in a call being an A note). To calculate the first part of this measure, the total number of the note type of interest (in this example, A notes) in the position of interest (in this example, the 1st note in the call) was summed and divided by the total number of times that note position occurred. The 1st note position would occur in all calls; however, if a call was only 3 notes long then the 4th note position onwards would not occur in that call. To calculate the second part of this measure, instead of dividing the number of A notes that were in the 1st position in the call by the number of 1st positions in the call, the number of A notes in the 1st position in the call were divided by the total number of A notes in all calls.

2.11. Results

Note-type percent agreement among sorters for all 1,360 notes was initially 92.06% (108 note disagreements). No disagreements came from notes that had been used previously in study I or II and the classification from study III matched the classification

given to each note in study I. This suggests that seeing the note in the context of the whole call did not affect the ability of experienced sorters to classify the note type. After meeting to resolve note-type sorting discrepancies we further refined the description of D_h notes to ensure that A and D notes in close temporal proximity were not misclassified as D_h notes (see Note descriptions above). This refinement brought the percent agreement among all note sorters to 98.68% (18 note disagreements). The primary sorter made the final note-type decision on these last 18 notes.

In the literature, the number of call types in a sample has been defined in one of two ways: call types are either reported with repetitions of the same note type indicating a different call type (i.e., ACCD is a different call type than AACCCDD, henceforth referred to as expanded syntax types), or disregarding repetitions of same note types and lumping repetitious calls into one call type (i.e., ACCD and AACCCDD are the same call type, namely, A, C, D, henceforth referred to as condensed syntax types). Previous work by Ficken (1990) examining Mexican chickadee calls and work by Hoeschele et al. (In press) on the brown-headed chestnut-backed chickadee use the first convention for call type reporting. Charrier et al. (2004) and Bloomfield et al. (2004, 2005) use the second method of lumping call types when analyzing the syntax of birds of the black-headed chickadee subgroup. We have reported our findings using both methods so that our work may be comparable to all previous works mentioned above. In total, we identified 33 different expanded syntax types and 11 condensed syntax types in our sample of Mexican *chick-a-dee* calls (see Table 2-3A and 2-3B for a detailed list of call types reported in each manner described above).

All calls in our sample, except one, follow a pattern of note production; notes are produced in the order $A \rightarrow C \rightarrow D_h \rightarrow D$ within a call. Some note types may be omitted or repeated within certain calls, but this rule remains true for all calls, except call D_hACCC . This one call comprises 0.18% of our sample.

Table 2-4 shows note-type transitions along with conditional transition probabilities. We found that C notes are most often followed by other C notes (19.72% of all transitions), D notes are most often the final note in a call (19.35% of all transitions), and A notes are most often followed by D notes (10.60% of all transitions). When we look at conditional transition probabilities we see that A notes can be followed by all other note types as well as be the final note in a call. C notes are more rigid in that 99.46% of the time they are either followed by another C note or are the final note in the call. This pattern holds true for D_h and D notes as well, with 98.55% and 100% respectively either being followed by another of the same note type or being the final note in a call.

Relative to other chickadee species the *chick-a-dee* call of the Mexican chickadee is short (Charrier et al. 2004; Bloomfield et al. 2004; Bloomfield et al. 2005). Only 34.81% of calls in this sample are 3 notes or longer. When examining the note position probabilities we discovered that when A notes are present they are usually the first note in the call (70.39%); this is also true for D_h notes (71.50%). When C notes are present they are most often the second note in a call (27.12%); this is also true of D notes (63.75%; see Table 2-5). This distribution of note types further reflects the brevity of Mexican chickadee *chick-a-dee* calls.

2.12 Discussion

There is a growing body of evidence suggesting that different notes within a call convey different meanings or are at least used in different contexts (e.g., Mahurin and Freeberg 2009; Freeberg and Lucas 2002). It follows that it would be advantageous for birds to be able to identify individual note types to understand the message being conveyed. Based on previous field research, the composition of any given *chick-a-dee* call appears to depend on the context in which that call was given (e.g., Ficken et al. 1994). In our sample of Mexican chickadee notes, we observed many, but not all, of the note types seen in other species' calls. For instance, Mexican chickadees produced an A note type that was acoustically distinct from A notes used by other chickadee species. However, we did not detect another, albeit rare, note type previously documented in Mexican chickadee calls, the B note (Ficken 1990). There are at least two possible explanations for this omission. One possibility is that our recordings did not occur in contexts in which Mexican chickadees use B notes, the other is that B notes are rare or absent in the calls of all members of the brown-headed chickadee clade.

Although our sample contained a large number of calls and many of each of the four note types reported here, we did not find Ficken's (1990) exceedingly rare 'B' note type (only 3 in 6,918 notes). In species from the black-headed clade, B notes are not nearly so scarce. In fact, in mountain and Carolina chickadees there are variations of B notes (i.e., A/B, mountain chickadee, Bloomfield et al. 2004; B₁, B₂, B₃, Carolina chickadee, Bloomfield et al. 2005). The same cannot be said for samples of boreal and chestnut-backed chickadee calls (Moscicki et al. In prep; Hoeschele et al. In press) where this note type is either absent or rare. The paucity of 'B' note types found in the *chick-a-dee* calls of the brown-headed species studied to date may be due to the context of the

recordings. It remains to be determined in what context calls rich in 'B' notes in these species would occur.

Of the four note types that were identified in our sample of Mexican chickadee calls, all human sorters were able to categorize notes with a high degree of accuracy; however, these note-type categories ultimately need to be verified by the Mexican chickadees themselves. In an operant experiment, black-capped chickadees were faster at learning between note-type discriminations than within note-type discriminations (Sturdy et al. 2000). Also, Sturdy et al. (1999) showed that zebra finches (*Taeniopygia guttata*) were faster at learning a true note-type category operant discrimination task than a pseudo-category discrimination task. Methods such as these, using Mexican chickadees, can be used to determine the validity of the note-type categories described in this study.

Beyond simply sorting notes into types and determining whether Mexican chickadees can do likewise, it would be fruitful to understand the mechanisms underlying such discriminations. In order to test which features could be important for note-type classification it is imperative to first describe the acoustic features of each note type and to identify acoustic features putatively important for note identification. Our analyses showed that all note features differed among all note types, indicating that there are potentially many features a bird could use when attempting to classify a note. That there are many cues potentially useful for note type classification embedded within each note type would increase signal redundancy and reduce the probability a signal would be lost or misinterpreted due to the noisy environment in which the signal is generally used (i.e., dense foliage, other singing birds, wind through branches; Wiley and Richards 1982).

Previous work from our lab has examined the mechanisms of note-type perception in black-capped chickadee call notes (Charrier et al. 2005, Nickerson et al. 2006, 2007) using both birds performing operant discriminations and artificial neural network models (ANNs). Collectively, this research has revealed a prominent role of pitch in note type classification, although this is not universal (see Nickerson et al. 2007). Our results presented here provide the foundation to use similar operant and ANN studies to uncover the role of the various acoustic features in Mexican *chick-a-dee* call note-type discrimination.

Not only does pitch appear to play a prominent role in the PNTC values of *chick-a-dee* call notes of black capped chickadees (as described above), but this is a common theme among many chickadee species (Charrier et al. 2004, Bloomfield et al. 2004; Bloomfield et al. 2005). A predominance of pitch was also observed in our study. In fact, the PNTC values for each of the frequency parameters measured in Mexican chickadees is far above those measured in the *chick-a-dee* call notes of all other chickadee species quantified to date. Future research will be needed to uncover the genesis and possible functional role driving this difference.

In addition to individual note analyses, we examined the syntax of Mexican chickadee calls in two ways: an expanded syntax version where calls with repetitions of note types were considered different syntax types and a reduced version where calls with repetitions of note types were not considered different syntax types. Hailman et al. (1987) proposed that repetitions of note types within calls may serve to convey the level of motivation or urgency of the signaler. In this way, reporting call types using the reduced methodology may give a more accurate picture of the repertoire of the Mexican

chickadee *chick-a-dee* call. Conversely, call types tallied using the more expanded methodology may treat calls that encode the same message as distinct when in fact they are simply qualified as to the importance of that message. Whether repeated note types convey a sense of motivation or urgency in Mexican chickadees has yet to be determined; therefore we report both methods here.

Call syntax appears to encode information about locomotion, alarm, and food along with information about species identification. Prior research has shown that black-capped chickadees use syntax information for species identification in the field (Charrier and Sturdy 2005). Having a fixed set of syntactical rules within a species may be important for efficient message production and perception. Our sample of Mexican chickadee calls followed a fixed rule of note-type production, in common with other chickadee species studied to date. All calls in our present sample, except for one, follow this rule. In our sample A notes can be followed by any other note type, C notes are most often followed by other C notes, and D and D_h notes are most often the last notes in a call. C notes are most often followed by other C notes in other chickadee species as well (Charrier et al. 2004; Bloomfield et al. 2004; Bloomfield et al. 2005).

Producing C notes in isolation from other note types may be due to vocal constraints; A notes and D_h notes have much higher start frequencies than C notes. It could potentially be difficult for birds to produce a note with a high start frequency followed immediately by a note with a much lower start frequency, and again followed by a note with a higher start frequency. In line with this reasoning, it has been shown in several songbird species that producing vocalizations with high trill rates (rapidly alternating between high and low frequency) is difficult and costly (Nowicki et al. 1992).

Thus, constraints on vocal production may contribute to the syntax of Mexican chickadee calls.

In addition to vocal constraints being a possible contributor to the syntax of Mexican chickadee calls, learning may also play a role as the *chick-a-dee* call is a learned vocalization, at least in black-capped chickadees (Hughes et al. 1998). There is a growing body of evidence that syntax learning affects other aspects of a vocalization as well. For example, white crowned sparrows (*Zonotrichia leucophrys*) tutored with the correct phonology (i.e., structure) of learned species typical song notes, but not tutored with syntax information, produced songs deficient in both syntax and phonology (Plamondon et al. 2008). Further, sparrows tutored with individual song phrases were unable to arrange the phrases into species typical syntax unless they were tutored with at least two of the phrases overlapping (Plamondon 2008). Determining the role of syntax during vocal development in all species of *Poecile* is an area ripe for future investigation.

Taken together, our studies provide a rigorous, detailed, comprehensive description of the Mexican chickadee *chick-a-dee* call. We have described and identified the note types present in this call, quantitatively measured features of those note types, and examined syntax rules in this call. Studies such as this provide a necessary foundation for future field and laboratory experiments aimed at understanding the messages encoded in this call as well as the mechanism the birds may be using to decode those messages. Also, because this work has followed similar methodology to bioacoustic studies of other chickadee species' *chick-a-dee* calls it provides a necessary foundation for future in-depth comparative studies that may examine the similarities and differences

among the *chick-a-dee* calls of the *Poecile* genus, and, through that work, shed light on the evolution of this genus' name-sake *chick-a-dee* call.¹

¹ A version of this chapter has been submitted for publication.

2.13 Tables

Table 2-1. Sampling information for recordings of Mexican chickadee (*Poecile sclateri*) chick-a-dee calls.

Total Sample					
Recording Dates	Time of Day	Source	Location	Recording Equipment	Number of Recordings
8 July 1957 - 14 July 1996	0545 - 0735	Macauley Library of Natural Sounds	Portal, Arizona	Nagra III recorder and American D33 microphone; Marantz PMD-700 recorder and Sennheiser ME-20 microphone	10
27 June 1964 - 9 May 1996	0630 - 1710	Borror Laboratory	Portal, Arizona	No Information	7
6 October 1985 - 31 April 1992	0800 - 1400	Millicent Ficken	Portal, Arizona	Sony Walkman Professional cassette tape recorder and i) Electrovoice Soundspot microphone (1985) ii) Nakamichi CM-100 cardioid microphone (1986)	5
Subsample Used for Studies I and II					
Recording Dates	Time of Day	Source	Location	Recording Equipment	Number of Recordings
27 May 1977 - 14 July 1996	0545 - 0718	Macauley Library of Natural Sounds	Portal, Arizona	Nagra III recorder and American D33 microphone; Marantz PMD-700 recorder and Sennheiser ME-20 microphone	5
11 April 1981 - 9 May 1996	0840 - 1710	Borror Laboratory	Portal, Arizona	No Information	3
6 October 1985 - 17 May 1986	0800 - 1200	Millicent Ficken	Portal, Arizona	Sony Walkman Professional cassette tape recorder and i) Electrovoice Soundspot microphone (1985) ii) Nakamichi CM-100 cardioid microphone (1986)	2

Table 2-2. Potential for note-type coding (PNTC) for the 11 features measured on Mexican chickadee note types (A, C, D_h, and D)

Note: SF, start frequency; PF, peak frequency; EF, end frequency; AD, ascending duration; DD, descending duration; TD, total duration; FM_{asc}, ascending frequency modulation; FM_{desc}, descending frequency modulation; F_{max}, frequency at maximum amplitude; f₀, fundamental frequency; NPF, note peak frequency. See text for measurement descriptions.

*Signifies notes were significantly different. See text for adjusted *p* values.

**Signifies significant differences, except those indicated, among all note pairs in Games-Howell post-hoc tests.

	SF	PF	EF	AD	DD	TD	FM _{asc}	FM _{desc}	F _{max}	f ₀	NPF
CV_b	57.9	43.3	35.8	89.0	59.0	82.6	95.5	103.4	23.6	32.3	36.9
Mean CV_w	11.5	6.9	13.6	31.1	38.6	26.1	62.7	56.4	15.3	26.6	39.3
PNTC	5.0	6.3	2.6	2.9	1.5	3.2	1.5	1.8	1.5	1.2	0.9
F	1630.1*	4180.2*	1145.9*	262.2*	2573.7*	416.9*	35.4*	545.7*	112.2*	21.0*	32.7*
Games-Howell test	**	** except between A and Dh notes where <i>p</i> = .03	** except between C and Dh notes where <i>p</i> = .09	** except between A and Dh notes where <i>p</i> = .96	** except between A and Dh notes where <i>p</i> = .35	** except between D and Dh notes where <i>p</i> = .10	**	**	** except between A and C notes where <i>p</i> = .03	**	** except between A and Dh notes where <i>p</i> = .54

Table 2-3. Syntax types observed in our sample of Mexican chickadee *chick-a-dee* calls.

A) Expanded syntax types. Calls with repeated note types are considered different syntax types (i.e., AAD is a different syntax type than AAAD). B) Condensed syntax types.

Calls with repeated note types are considered the same syntax type (i.e., AAD is the same as AAAD and is denoted as syntax type A, D).

A.			B.		
Syntax	Number of Calls	Percentage of Sample	Syntax	Number of Calls	Percentage of Sample
A	17	3.13%	A	89	16.39%
AA	61	11.23%	A, D	144	26.52%
AAA	10	1.84%	A, C, Dh	1	0.18%
AAAA	1	0.18%	A, C	34	6.26%
AAAD	9	1.66%	A, Dh	40	7.37%
AAADD	2	0.37%	A, Dh, D	16	2.95%
AACCDh	1	0.18%	C	70	12.89%
AAD	21	3.87%	C, D	1	0.18%
AADD	3	0.55%	Dh	47	8.66%
AC	2	0.37%	Dh, A, C	1	0.18%
ACC	32	5.89%	Dh, D	100	18.42%
AD	89	16.39%			
ADD	20	3.68%			
ADh	40	7.37%			
ADhD	14	2.58%			
ADhDD	1	0.18%			
ADhDDD	1	0.18%			
C	1	0.18%			
CC	18	3.31%			
CCC	12	2.21%			
CCCC	10	1.84%			
CCCCC	5	0.92%			
CCCCCC	11	2.03%			
CCCCCCC	7	1.29%			
CCCCCCCC	6	1.10%			
CCCCCCDD	1	0.18%			
Dh	45	8.29%			
DhACCC	1	0.18%			
DhD	77	14.18%			
DhDD	19	3.50%			
DhDDD	3	0.55%			
DhDDDD	1	0.18%			
DhDh	2	0.37%			

Table 2-4. Transitions from one note type to another in our sample of *chick-a-dee* calls from Mexican chickadees. A) Total number of transitions from each note type to each other note type. B) Conditional transition probabilities (i.e., the probability that one note type will occur given that a certain note type has occurred just previously).

A.			B.		
Transitions	Number	Percentage of Sample	Conditional Transitions	Conditional Percentage	
A->A	132	9.71%	Given A first	A->A	28.76%
A->C	36	2.65%	Total of 459 transitions from A	A->C	7.84%
A->D	144	10.60%		A->D	31.37%
A->D _h	56	4.12%		A->D _h	12.20%
A-> no note	91	6.70%		A-> no note	19.83%
C->A	0	0.00%	Given C first	C->A	0.00%
C->C	268	19.72%	Total of 373 transitions from C	C->C	71.85%
C->D	1	0.07%		C->D	0.27%
C->D _h	1	0.07%		C->D _h	0.27%
C-> no note	103	7.58%	C-> no note	27.61%	
D->A	0	0.00%	Given D first	D->A	0.00%
D->C	0	0.00%	Total of 320 transitions from D	D->C	0.00%
D->D	57	4.19%		D->D	17.81%
D->D _h	0	0.00%		D->D _h	0.00%
D-> no note	263	19.35%	D-> no note	82.19%	
D _h ->A	1	0.07%	Given D_h first	D _h ->A	0.48%
D _h ->C	0	0.00%	Total of 207 transitions from D _h	D _h ->C	0.00%
D _h ->D	116	8.54%		D _h ->D	56.04%
D _h ->D _h	2	0.15%		D _h ->D _h	0.97%
D _h -> no note	88	6.48%		D _h -> no note	42.51%

Table 2-5. Note position probabilities. A) The probability of note types in each position in the call in our sample of Mexican chickadee *chick-a-dee* calls (i.e., the probability that the 1st note in a call will be an A note). B) The probability of the position of each note type within our Mexican chickadee *chick-a-dee* call sample (i.e., the probability that an A note will be the 1st note in a call).

A.

	Note 1	Note 2	Note 3	Note 4	Note 5	Note 6	Note 7	Note 8
Total Notes	540	477	188	63	38	30	17	6
Prob. A	59.44%	22.85%	11.70%	1.59%	7.89%	0.00%	0.00%	0.00%
Prob. C	12.78%	20.75%	44.15%	66.67%	76.32%	70.00%	94.12%	100.00%
Prob. D	0.37%	44.23%	44.15%	31.75%	13.16%	30.00%	5.88%	0.00%
Prob. D_h	27.41%	12.16%	0.00%	0.00%	2.63%	0.00%	0.00%	0.00%
Prob. of Position	100.00%	88.33%	34.81%	11.67%	7.04%	5.56%	3.15%	1.11%

B.

	Prob. Note 1	Prob. Note 2	Prob. Note 3	Prob. Note 4	Prob. Note 5	Prob. Note 6	Prob. Note 7	Prob. Note 8
A	70.39%	23.90%	4.82%	0.22%	0.66%	0.00%	0.00%	0.00%
C	18.90%	27.12%	22.74%	11.51%	7.95%	5.75%	4.38%	1.64%
D	0.60%	63.75%	25.08%	6.04%	1.51%	2.72%	0.30%	0.00%
D_h	71.50%	28.02%	0.00%	0.00%	0.48%	0.00%	0.00%	0.00%

2.14 Figures

Figure 2-1. Sound spectrograms (Hanning window = 512 points) showing exemplars of each of the four note types identified in our sample of Mexican chickadee *chick-a-dee* calls.

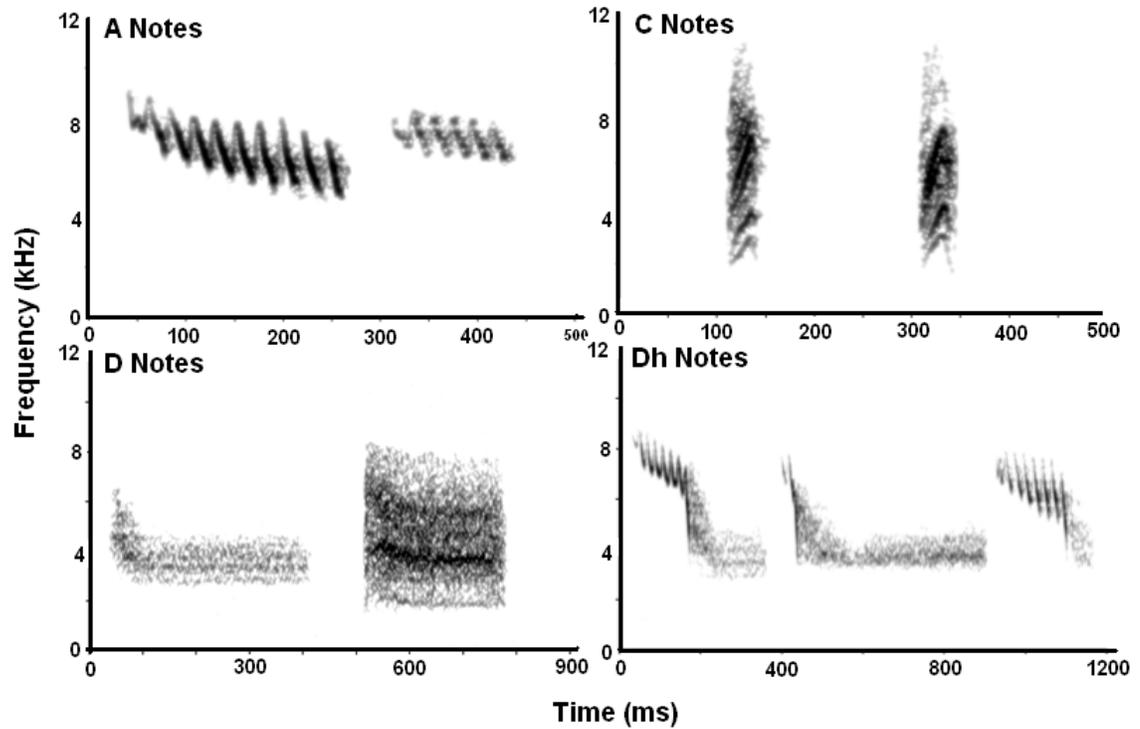
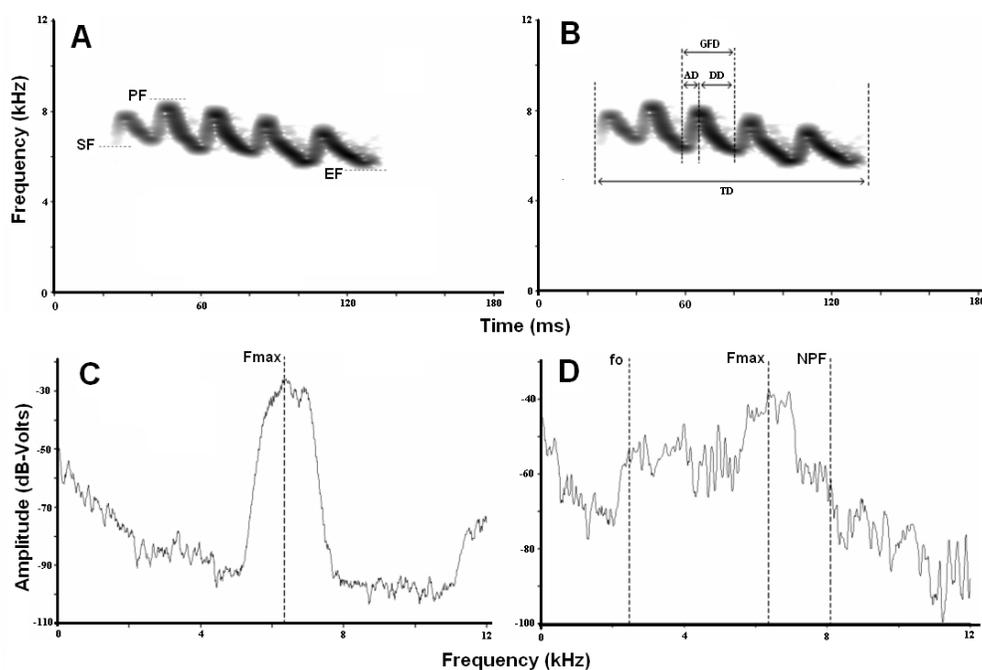


Figure 2-2. : Sound spectrograms (Hanning window = 512 points) and spectra illustrating measurements of note-type features. Panels A, B, and C feature a representative A note as an example while panel D features a representative C note. A) Spectrogram showing frequency measurements used on A, C, and the tonal portion of D_h notes. SF = start frequency; PF = peak frequency; EF = end frequency. B) Spectrogram showing duration measurements as well as the oscillation of A notes with the greatest frequency difference (GFD) between start/end frequency and peak frequency. Vertical lines indicate the boundaries of duration measurements and the greatest frequency difference oscillation. AD = ascending duration; DD = descending duration; TD = total duration. C) Spectrum (window size = 16,384 points) showing the frequency at maximum amplitude (F_{\max} ; indicated by the vertical line). D) Spectrum (window size = 4,096 points) indicating the lowest visible frequency above -35dB relative to note peak amplitude (f_0 ; indicated by the vertical line), F_{\max} , and the highest frequency above -35dB from note peak amplitude (NPF; indicated by the vertical line).



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3. NOTE TYPES AND CODING IN PARID VOCALIZATIONS: THE *CHICK-A-DEE* CALL OF THE BOREAL CHICKADEE (*POECILE HUDSONICA*)

3.1. Introduction

One commonly studied group of songbirds is the North American chickadees (genus *Poecile*). This genus consists of seven species (Gill et al. 2005) whose ranges, collectively, cover most of North America. Chickadees are abundant and most species are easily accessible (Sibley 2000). Their abundance, combined with their ability to learn vocalizations, and the existence of many closely related species, make chickadees an ideal group to use for studies of vocal communication and cross-species comparisons.

Tinbergen (1963) suggested that comparative studies are most advantageous when carried out with closely related species and provide an excellent method for drawing inferences about common descent. Gill et al. (2005) examined the genetic relationships among the seven *Poecile* species and classified them into two subgroups, black- and brown-headed chickadees. All chickadees produce a name-sake *chick-a-dee* call; in contrast, the black-headed chickadees produce a whistled *fee bee* song that the brown-headed chickadees lack (Hailman 1989; Bent 1946). These similarities and differences in vocalizations among closely related groups are interesting topics for cross-species comparisons that may shed light on the evolution of these vocalizations.

Significant research has been aimed at understanding the *chick-a-dee* call shared by the two chickadee subgroups. Putative uses of this call include conveying information about flock identity (Nowicki 1983), food location (Freeberg and Lucas 2002), predators (Hurd 1996; Templeton et al. 2005), motivation and urgency (Baker and Becker 2002), species identification (Bloomfield and Study 2008), and perhaps individual identity (e.g.,

see PIC analyses in Charrier et al. 2004). Individual notes within the *chick-a-dee* call have also been shown to convey information, though this information seems to differ across species. For example, black-capped chickadees (*Poecile atricapillus*) appear to use D notes for mobbing (Templeton et al. 2005) and flock identification (Nowicki 1983), Carolina chickadees (*P. carolinensis*) seem to use this note for recruitment to a food source (Mahurin and Freeberg 2009), and Mexican chickadees (*P. sclateri*) give more D notes when perched (Ficken et al. 1994). These functional differences in the use of the same note type among species provide further support for interest in the *Poecile* genus for vocal studies of cross-species comparisons.

Kroodsma and Byers' (1991) suggestion of fully describing behaviour within a species as a critical first step in our understanding can be applied to the cross-species comparisons of vocal behaviour in *Poecile*. To date, extensive bioacoustic studies have been conducted on the *chick-a-dee* calls of five of the seven species in this group (Charrier et al. 2004; Bloomfield et al. 2004; Bloomfield et al. 2005; Hoeschele et al. In press; Moscicki et al. In prep). The two remaining species are the grey-headed chickadee (*P. cincta*) and the boreal chickadee (*P. hudsonica*). Here we focus our analyses on the *chick-a-dee* call of the boreal chickadee.

Previous work on boreal chickadee calls had a broad focus and examined the vocal repertoire of the boreal chickadee in various contexts (McLaren 1976). Here we provide a detailed examination of the *chick-a-dee* call of the boreal chickadee using methodology similar to that used to investigate the *chick-a-dee* calls of other *Poecile* species. Our goals with this work are i) to provide an in-depth acoustic description of the note types within the boreal chickadee *chick-a-dee* call; ii) to examine the syntax of this

vocalization; iii) to provide a foundation for future studies of boreal chickadee call production and perception, and iv) to lay the groundwork for future comparative studies examining the *chick-a-dee* vocalization of all members of the genus *Poecile*.

3.2. Materials, Methods, and Results

3.3. Study I – Call Note Classification

We classified individual call notes of boreal *chick-a-dee* calls into categories based on visual similarity of spectrograms. Our goal with this study was to provide reliable descriptions and spectrographic examples of the note types found in the *chick-a-dee* calls of boreal chickadees.

3.4. Methods

a. Subjects. We used boreal chickadee recordings from the field (see recordings) as well as from birds housed in our laboratory. Seven adult (> 1 year of age) male (n = 1) and female (n = 6) boreal chickadees were captured between January 2004 and March 2004 at several locations in central and southern Alberta, Canada. Sex identification was conducted by DNA analysis (Griffiths et al. 1998). Birds were housed at the University of Alberta (Edmonton, Alberta) in individual Jupiter Parakeet cages (0.3 m wide × 0.4 m high × 0.4 m deep; Rolf C. Hagen Inc., Montreal QC, Canada) which allowed visual and auditory communication but not physical contact between birds. Birds had free access to food (Mazuri Small Bird Maintenance Diet; Mazuri, St. Louis, MO), water, and grit mixture (Rolf C. Hagen Inc., Montreal QC, Canada). Liquid vitamin (Hagen Vitamin Supplement Conditioner for Birds; Rolf C. Hagen Inc., Montreal QC, Canada) was added to the water 3 times per week. Hard boiled eggs and greens were provided once per week, 1 mealworm was provided 3 times per week, and birds received 3-5 sunflower seeds

daily. Birds were maintained on a light-dark cycle typical for the season in Edmonton, Alberta. The temperature was maintained at approximately 20°C.

b. Recordings. Boreal chickadees from our lab were individually recorded from June 2004 to July 2004 between 0900 and 1700 h by placing their home cage in a large (1.83 m wide × 1.83 m high × 1.83 m deep) sound attenuating chamber (Industrial Acoustics Corporation, Bronx, NY). On occasion, a mirror was attached to the inside of the bird's cage to induce vocalizations. Birds were recorded using a C 1000 S condenser microphone (frequency response: 50-20,000 Hz; AKG Acoustics, Vienna, Austria) connected to a Marantz PMD 670 digital recorder (frequency response: 10-20,000 Hz; Eindhoven, Netherlands). Twenty calls were randomly chosen from each of the seven birds for analysis in Studies I and II (see below).

We also obtained 28 samples (i.e., continuous recording sessions) of boreal chickadee calls from the Macaulay Library of Natural Sounds at the Cornell Laboratory of Ornithology. These recordings contained multiple *chick-a-dee* calls from multiple boreal chickadees.

In total, 140 calls composed of 494 individual call notes were obtained from birds recorded in our laboratory and 445 calls containing 1,231 individual call notes were obtained from the Macaulay Library. All calls were included in analyses. Table 3-1 contains a complete list of the recordings used for analysis and details about those recordings, including equipment used, location, year, and time of day.

c. Sound spectrograms and note classification. All individual call notes were cut from whole call recordings. These notes were saved as sound files with durations of 300 ms (non D-type notes) or 500 ms (D-type notes) by adding trailing silence to each sound

file using SIGNAL 5.10.25 Sound Analysis Software (Engineering Design, Berkeley CA). Each note was saved as a spectrographic image (Hanning window = 512 points, cut-off amplitude = -35dB relative to note peak amplitude) and labeled with a unique four digit code. Note spectrograms were printed, 15 spectrograms per page, on 8.5" x 11" glossy photo paper and cut to form individual note 'cards' of approximately 2" x 1.5".

In a preliminary analysis, the first author sorted the note cards into an open number of categories based on visual similarity of spectrograms; this process yielded five distinct note-type categories (see Fig. 3-1). A written description of the visual features of each category was prepared (see Note descriptions below). To augment the written descriptions, three spectrographic exemplars were randomly chosen from within each category and were reprinted with the word 'Exemplar' instead of the four digit identification number. The written descriptions, spectrogram card exemplars, and deck of spectrogram note cards were given to two additional sorters for sorting. All sorters had experience classifying notes from a variety of chickadee species using this methodology. Percent agreement among note-type classifications was calculated to determine the reliability of the note-type categories. A meeting was held to resolve note-type classification disagreements among sorters.

3.5. Results

a. Call note classification. We identified five boreal *chick-a-dee* call note-type categories: A, B, C, D, and Dh (see Fig. 3-1). The three note sorters achieved 93.80% agreement (107 note-type disagreements) before meeting to revise note-type category descriptions. The description for B note types was refined to ensure that these note types were not misclassified as A note types. This refinement involved a more detailed

description of the brief and highly frequency modulated terminal portion of B note types that is not present in A note types. This clarification, as well as discussion among sorters, resolved the 107 note-type disagreements and percent agreement among sorters reached 100%. We ultimately identified 563 A notes, 164 B notes, 70 C notes, 670 D notes, and 258 D_h notes.

b. Note-type descriptions. We use nomenclature similar to that used to describe the note types of black-capped *chick-a-dee* calls (Hailman et al. 1985).

A Notes: These notes are tonal (i.e., few or no additional frequency bands or modulation) and begin and end at a high frequency (ca. 6-8 kHz; see Fig. 3-1). Often the main (i.e., highest amplitude) frequency band is accompanied by an upper and lower frequency band. There may be a slight increase or decrease in frequency in the first or last few milliseconds of the note and an overall gradual decrease in frequency as the note progresses. These notes are typically around 150 ms in duration.

B Notes: B notes appear to be in transition from an A note to a D-hybrid (D_h) note (see below). B notes begin at a high frequency (similar to A notes). There is a brief portion of ascending frequency modulation at the beginning of the note after which the frequency remains relatively unmodulated for the remaining first half of the note. At approximately the mid-point of the note there is a rapid decrease in frequency. Harmonic-like bands may be present above and below the main frequency band. The final portion of the note is brief (ca. 50 ms) and highly frequency-modulated (see Fig. 3-1). Some parts of this terminal portion (i.e., one band or more) begin higher in frequency than the highest frequency of the initial, relatively unmodulated portion of the note (ca. 10 kHz or higher) and end at approximately the same frequency as the end of the first portion of the note.

These notes may appear as truncated (shorter) versions of D_h notes; however, the second portion of B notes does not have obvious stacked frequency bands like those that occur in D_h notes.

C Notes: These notes begin at a relatively low frequency (ca. 2 kHz) and remain at this frequency for approximately half the duration of the note before a rapid portion of ascending frequency modulation. Once this note reaches peak frequency (ca. 6 kHz), the frequency either remains constant or there is a portion of rapid decreasing frequency modulation. The note terminates at a frequency higher than the start frequency.

Harmonic-like structures are present throughout the note (see Fig. 3-1).

D Notes: This note type consists mainly of stacked frequency bands (see Fig. 3-1). These frequency bands have little to no frequency modulation and generally have a bandwidth of about 8 kHz. D notes are longer in duration than the other note types and typically range between 250 and 500 ms.

D-hybrid (D_h) Notes: D-hybrid notes, like B notes, have two distinct portions. The first portion of the note has a main (i.e., highest amplitude) tonal frequency band with one or more harmonic-like bands above or below this band. The main band begins at a relatively low frequency (ca. 4 kHz), undergoes a period of rapid ascending frequency modulation, reaches a frequency peak of approximately 6 kHz, then undergoes a period of decreasing frequency modulation to a frequency approximately equal to the start frequency (see Fig. 3-1). This main frequency band forms the lowest band of the second portion of the note. Occasionally this lowest frequency band is not visible and thus it is not obvious that the tonal portion is continuous. The second portion of the note consists of stacked frequency bands (similar to a D note). The top of these stacked bands begins at

a frequency equal to, or higher than, the peak frequency band of the tonal portion of the note. The bandwidth of the main portion of this section of the note is generally about 7 kHz. The second portion of this note type can range widely in duration from 25 ms to 250 ms while the total D_h note can range in duration from 200 ms to 500 ms.

3.6. Study II – Quantitative Note-Type Analysis

With the note-type information gained from Study I, we were able to conduct Study II in which we measured and calculated a variety of frequency and temporal characteristics for each of the five note types. The purpose of this study was to compare the variability in frequency and temporal characteristics within and between the five note types, as well as within and between individual birds, to determine if certain note features could be used to discriminate among note types or individuals.

3.7. Methods

a. Chick-a-dee call sample selection. For this study, we chose to use recordings for analysis that contained at least 20 distinct boreal chickadee *chick-a-dee* calls. Six samples from the Macaulay Library met our criteria; these samples yielded 137 calls composed of 335 individual notes. Each of the seven boreal chickadees recorded in our laboratory produced recordings with at least 20 *chick-a-dee* calls and therefore calls from these birds were also included in the analysis. Twenty calls were randomly sampled from each of the seven laboratory birds resulting in 140 calls containing 494 individual call notes. These were the same 494 call notes used in Study I. In total, for analysis in Study II we used 277 boreal *chick-a-dee* calls composed of 829 individual call notes consisting of 306 A notes, 37 B notes, 26 C notes, 318 D notes, and 142 D_h notes.

b. Note measurements. SIGNAL 4.0 Sound Analysis Software (Engineering Design, Berkley CA) was used to measure the calls from birds recorded in our laboratory; SIGNAL 5.10.25 Sound Analysis Software (Engineering Design, Berkley CA) was used to measure the calls from the Macaulay Library samples, obtained at a later date than our initial, in-house recordings. Both versions of SIGNAL employ the same algorithms for sound measurement. All recordings from both samples were made at a sampling rate of 44.1 kHz.

We used different window settings for frequency (Hanning window = 1,024 points, precision = 43 Hz) and duration measurements (Hanning window = 256 points, precision = 5.8 ms). All measurements were conducted on spectrograms with a cut-off amplitude of -35dB relative to note peak amplitude.

For A, B, C, and the initial A note-like portion of D_h notes, we conducted three different frequency measurements: start frequency (SF), peak frequency (PF), and end frequency (EF; see Fig. 3-2A). All measurements were obtained from the frequency band with the highest amplitude (i.e., the darkest band in the spectrogram). We also took duration measurements of ascending duration (AD), descending duration (DD), and total duration (TD) on these note types. We used the above measurements to calculate the slope of the ascending ($FM_{asc} = PF - SF / AD$) and descending ($FM_{desc} = PF - EF / DD$) frequency modulations (FM) for each of these note types. Because D notes and the terminal D note-like portion of D_h notes do not contain frequency modulation like the other note types we only measured total duration (TD) on these note types. Note that total duration was measured on the entire D_h note.

We generated a spectrum for all note types (average window size for A and B notes = 8,192 points, C notes = 4,096 points, D and D_h notes = 16,384 points; smoothing width of 88.2 Hz) to measure the loudest frequency (i.e., frequency at maximum amplitude; F_{\max}) on all note types. For C, D, and the terminal portion of D_h note types we used this spectrum to measure the highest and lowest frequencies above the cut-off amplitude of -35dB relative to note peak amplitude (i.e., note peak frequency, NPF and fundamental frequency, f_0 , respectively; see Fig. 3-2C).

c. Statistical analyses. Following the methods of Charrier et al. (2004) we calculated potential for note-type coding (PNTC) values for each note type. This analysis compares the variability for a single measured note feature (e.g., SF) across note types to variation for that feature within a note type. The rationale is that if there is greater variation between note types than within a note type for the feature in question that feature may be useful for note-type differentiation.

PNTC is calculated separately for each note feature with the formula $CV_b/\text{mean } CV_w$. CV_b is the coefficient of variation between note types and is calculated as follows: $CV_b = (SD/\bar{x}) \times 100$, where SD is the standard deviation and \bar{x} is the mean of the note feature measure calculated across all note types. Mean CV_w , the mean coefficient of variation within note types, is calculated using the same formula, $CV_w = (SD/\bar{x}) \times 100$; however, now SD is the standard deviation and \bar{x} is the mean of the note feature measure within one note type. This calculation is done separately for each note type (A, B, C, D, and D_h) and the mean of those values is taken to obtain the mean CV_w . A PNTC value greater than 1 indicates there is greater between note-type variation than the average within note-type variation; thus, that particular note feature may be used by birds to

discriminate among note-type categories. A PNTC value closer to 1 indicates there is about equal variability between note types as the average variability within note types and the feature in question may be less useful to birds for note-type discrimination.

Because we had a sample of boreal *chick-a-dee* calls in which the individual producing the call was known (the calls recorded in our laboratory) we were able to calculate potential for individual coding (PIC) values. This type of analysis has been used with several different species (e.g., emperor penguins (*Aptenodytes forsteri*), Robisson et al. 1993; fur seals (*Arctocephalus tropicalis*), Charrier et al. 2002, and black-capped chickadees, Charrier et al. 2004). PIC is similar to PNTC but is applied to individuals rather than note types; thus, PIC is calculated separately for each note feature within each note type within an individual (i.e., a separate PIC value for SF of A notes for bird one and SF of B notes for bird one). PIC is also calculated as $CV_b / \text{mean } CV_w$; however, CV_b is now the coefficient of variation between individuals and is calculated as follows: $CV_b = 100 * (SD / \bar{x})$, where SD and \bar{x} are the overall standard deviation and mean for each note type for each feature. Mean CV_w is now the mean coefficient of variation within individuals using the formula for small samples: $CV_w = [(SD / \bar{x}) * (1 + 1/(4n))] * 100$, where SD and \bar{x} are the standard deviation and average of the individual means per feature per note type, and n is the number of exemplars per individual. A PIC value greater than 1 indicates more inter- than intra-individual variability on the particular feature and note type and thus may indicate a useful feature for individual discrimination. A PIC value less than 1 indicates less variability between individuals than the average variability within an individual, therefore indicating the feature of the note type in question may not be useful in discriminating among individuals.

Although we calculated PNTC and PIC as measures of effect size for the difference between note types and individuals we also wanted to assess whether there were significant differences between the note types and individuals, thus, we used SPSS version 15.0.0 (SPSS Inc. 2006) to perform univariate analyses of variance (ANOVAs). We used the Games-Howell post-hoc test for samples where equal variance is not assumed. Bonferroni corrections were used for all tests depending on the number of comparisons made (number of note types compared for each feature). Because some note features were not measured on all note types, the Bonferroni corrections were either $\alpha = 0.05/5 = 0.01$ (for TD and F_{\max}), $\alpha = 0.05/4 = 0.0125$ (for SF, PF, EF, AD, DD, FM_{asc} , and FM_{desc}), and $\alpha = 0.05/3 = 0.017$ (for NPF and f_0).

3.8. Results

a. Note-type acoustic features. Table 3-2 shows a summary of the PNTC and ANOVA results for all note features measured on each note type. The PNTC results indicate that all note features measured, except descending duration (DD), have PNTC values >1 and thus could potentially be used for note-type coding. Total duration (TD) has the highest PNTC value of 2.19 and therefore may be the most useful feature for discriminating among note types in boreal chickadee *chick-a-dee* calls.

All note types differed significantly on every note feature measured (all $F_s \geq 4.409$, all $p_s \leq 0.004$; see Table 3-2). Games-Howell post-hoc tests show that some note types did not differ significantly from other note types on a subset of the note features measured. Recall that all post hoc α levels have been Bonferroni corrected to either $\alpha = 0.01$, 0.0125 , or 0.017 (see Statistical analyses above). See Table 3-2 for a list of all note

types that did not differ significantly in post-hoc tests. The remainder of note types differed from all other note types on all features (mean differences ≥ 9.4 , $ps \leq 0.007$).

b. Individual coding in acoustic features. Among the potential for individual coding (PIC) values for each measure, SF, PF, and EF are among the highest for all note types and thus these features appear to be more variable among birds than within an individual bird; this is especially true of PF in B notes with a PIC of 3.0, the highest PIC value obtained in this sample (see Tables 3-3 and 3-4). AD, DD, and their frequency modulation slopes (FM_{asc} and FM_{desc}) are among the lower PIC values for all note types, between 1.0 and 1.5, and therefore may be less variable among birds than within individual birds and would be less useful for individual discrimination. This indicates that the frequency measures, namely SF, PF, and EF, may be the best features to use to discriminate among individual boreal chickadees based on *chick-a-dee* vocalizations.

In the PIC analyses described next, it is important to keep in mind that significant Bonferroni corrected p values will be $p \leq 0.006$ for A, B, and C notes (9 features measured), $p \leq 0.005$ for D_h notes (11 features measured), and $p \leq 0.013$ for D notes (4 features measured). The ANOVAs revealed significant differences between individuals on several features for each note type (see Tables 3-3 and 3-4). Among the more common note types, A, D_h , and D, all measures differed among individuals (all F s ≥ 4.13 , all $ps \leq 0.001$). B and C notes, the rarest of note types in our sample, have the fewest differences among individuals. Of the 9 features reliably produced, only 5 B-note features differed among individuals: TD: ANOVA, $F = 9.26$, $p = 0.002$; AD: ANOVA, $F = 19.42$, $p \leq 0.001$; SF: ANOVA, $F = 15.81$, $p \leq 0.001$; PF: ANOVA, $F = 86.62$, $p \leq 0.001$; and

Fmax: ANOVA, $F = 9.27$, $p = 0.003$. Only 2 C-note features differed among individuals: PF and EF (ANOVA, $F = 39.02$, $p \leq 0.001$; $F = 45.92$, $p \leq 0.001$, respectively).

3.9. Study III – Syntactical Analysis

In Study III, we sought to describe the rules governing the syntax of the boreal chickadee *chick-a-dee* call. We expanded our sample of boreal chickadee calls to include all high quality calls obtained from the boreal chickadees recorded in our laboratory (as opposed to using only the subsample of 20 calls from each bird used in Studies I and II), as well as the sample of Macaulay Library boreal chickadee recordings. We used the note categories identified in Study I to accurately classify the notes within the larger sample of boreal *chick-a-dee* calls. Finally, we calculated the probability of note types appearing in certain positions within the calls and the probability that certain note types would follow other note types within a call.

3.10. Methods

a. Recordings and sound spectrograms. We used a total of 1,101 boreal *chick-a-dee* calls, composed of 3,584 notes, for inclusion in Study III (see Table 3-1 for a description of recordings). We eliminated calls that contained excessive noise, overlapping birds, were too faint to clearly identify notes, or contained only one note. The final analyses were conducted on the following sample: 349 calls from the Macaulay Library and 627 calls recorded from boreal chickadees in our laboratory for a total of 976 calls. These calls were composed of a total of 3,453 notes. Since it was not feasible to make 3,453 separate note cards, each whole call was saved to a separate sound file using Syrinx (Burt 2006) software and spectrograms of whole calls were made using SIGNAL 5.10.25 Sound Analysis Software (Engineering Design, Berkeley CA). All spectrograms

were 1,800 ms in duration (Hanning window = 512 points, cut-off amplitude -40dB relative to call peak amplitude). Image files were created from each individual call spectrogram, given a unique file name for later identification, printed, four spectrograms per page, on 8.5" x 11" white paper, and compiled into a binder for sorting. This method has been used for similar analyses in other chickadee species (Hoeschele et al. In press; Moscicki et al. In prep).

b. Note classification. All notes were sorted into categories, using the note-type descriptions and exemplars used in Study I, by the same three experienced boreal chickadee note sorters that classified notes in Study I. Note sorters were initially blind to the classifications of other sorters. Because the note-type classification procedure was slightly different between Studies I and III (seeing notes in the context of the whole call in the former and seeing notes in an isolated context in the latter), we compared the note-type classifications of the subsample of notes that were sorted using both the methodology of Study I and that of Study III to determine if sorting methodology affected note-type classification. Percent agreement among sorters was determined and a meeting was held to discuss any discrepancies in note-type classifications.

c. Probability calculations. After categorizing all 3,453 notes, we tallied the number of different syntax types and the number of each syntax type produced in this sample of boreal *chick-a-dee* calls. Following methods used with other brown-headed chickadees (Hoeschele et al. In press; Moscicki et al. In prep), we calculated conditional transition probabilities, or, the probability that a certain note type occurred in a call given that a certain note type had directly preceded it (e.g., the probability that a B note occurred given that an A note had just occurred within a call). To calculate this measure,

we tallied the number of transitions from A to B notes (using our previous example) and divided this by the total number of transitions from A notes. This probability was calculated for all possible note combinations as well as the probability that each note type would be the last note in the call (i.e., would be followed by no note type).

We also calculated note position probabilities. These probabilities included the probability that a certain note type occurred at a certain position within the call (i.e., that an A note occurred in the first position), or, on the contrary, that a certain position in the call contained a certain note type (e.g., the probability that the first note in a call was an A note). To calculate these probabilities, we tallied the total number of note types of interest (A notes in our example) in the position of interest (1st note in the call) and divided this by the total number of times the position occurred. The 1st position occurred in every call; however, if we were looking at notes in the 5th position, calls with only four notes would not have this position. To calculate the contrary probability, instead of dividing the number of A notes in the 1st position by the number of times the 1st position occurred, we instead divided by the number of A notes in any position in all calls. We calculated these probabilities to better understand the syntax of the boreal *chick-a-dee* call.

3.11. Results

Note-type percent agreement among sorters for all 3,453 notes was initially 95.42% (158 disagreements). We met to discuss note-type classification discrepancies and, upon further refining the criteria of B and D_h notes to ensure that D_h notes with a brief terminal portion were not misclassified as B notes, we arrived at 100% agreement. There was also 100% agreement when we compared notes sorted in Study I with the

same notes re-sorted using the methodology of Study III. This agreement suggests that seeing the note within the context of the whole call had little to no effect on the ability of experienced sorters to properly classify note types.

We report our syntax results for boreal *chick-a-dee* call types in two forms. In the expanded form, calls with repeated note types are considered distinct syntax types (i.e., call AAACCD is different from call ACCCDD); in the condensed form, note repetitions do not contribute to distinct syntax types (e.g., call AAACCD is not different from call ACCCDD and both calls are labeled as syntax type A, C, D). This was done to make our results comparable to those from bioacoustic studies of other chickadee species which have used one or both of the two methods listed above.

We identified 63 different expanded syntax types and 17 condensed syntax types in our sample of boreal *chick-a-dee* calls (see Table 3-5 for a complete list of syntax types of both forms). ‘AD_hD’ was the most prevalent expanded syntax type, occurring 175 times, and comprising 17.6% of our total sample. The five most prevalent expanded syntax types comprised 50.7% of calls in our sample. The majority of our total sample (79.4%) consisted of calls beginning with A notes; however, there was a discrepancy in the proportion of calls beginning with A notes between the birds recorded in our laboratory, with 89.3% of calls beginning with A notes, and the recordings from the Macaulay Library, where only 62.9% of the calls began with A notes. Calls in our sample were least likely to begin with B notes; only 1.0% of calls in our sample began with a B note. Every call in our sample followed a fixed pattern of note production; that is, notes were always produced in the order A → B → C → Dh → D within a call, though any note type may be omitted or repeated a variable number of times within this sequence.

In addition to overall syntax types, we also examined total transitions from one note type to another (see Table 3-6A). In our sample, the most common transitions were A notes followed by other A notes and D notes as the last note in a call (28.57% and 19.26% of all transitions, respectively). Again, there was a discrepancy between our two samples in the distribution of A notes; A notes followed by other A notes occurred 37.87% of the time in the calls of birds recorded in our laboratory, while this transition comprised only 6.28% of the total transitions in the Macaulay Library sample.

We next examined conditional transition probabilities (see Table 3-6B). We found that, in our sample, when an A note occurs it is most likely to be followed by another A note (54.0%), when a B note occurs it is most often followed by a D note (80.0%), C and D notes are most often the last note in the call (40.1% and 71.8%, respectively), and D_h notes are most often followed by D notes (92.9%). It is interesting to note that when A notes occur they are only followed by other typical introductory notes (B and C) 5.2% of the time; in addition, B notes are never followed by other B notes or by C notes in our sample.

When examining the probability of various note positions occurring within a call (see Table 3-7A) we can see that the longest call in our sample was 13 notes long (all A notes). There was again a discrepancy between our two subsamples with respect to call length. The longest call in the Macaulay Library sample consisted of 6 notes, while the birds recorded in our laboratory produced calls up to 13 notes in length. Finally, we found that when A notes are present they are usually the first note in the call (44.2%); when B, C, and D_h notes are present they are most often the second note in a call (69.1%,

43.4%, and 51.4%, respectively); and when D notes occur they are most often the third note in the call (47.5%; see Table 3-7B).

3.12. Discussion

Our studies here provide a detailed examination of the *chick-a-dee* call of the boreal chickadee. We identify the note types present in this call, measure and conduct detailed analyses on a variety of spectral and temporal features for each note type, and examine rules of note-type production in terms of call syntax. In this way, our work is a novel exploration of the *chick-a-dee* call of the boreal chickadee.

a. Call-note classification. The ability to accurately classify notes into different categories is important for birds to be able to correctly decode information contained in calls. There is increasing evidence that different note types in a call may convey different meanings (e.g., Mahurin and Freeburg 2009; Templeton et al. 2005), and that closely related species may use the same note types for different purposes (e.g., Ficken et al. 1994). These observations may lead some to ask whether closely related species can distinguish the note types of conspecifics and heterospecifics and decode the messages contained in their calls. To answer questions like these we must first examine the note types that comprise these calls.

It is important to note, however, that when considering comparisons across species the vocalizations of each species in question must first be studied individually; information about the vocalizations of one species cannot be assumed to apply to the vocalizations of closely related species. For example, when attempting to classify the note types in the *chick-a-dee* calls of boreal chickadees, we initially found it difficult to separate A and B notes. This is true of A and B notes in another brown-headed chickadee,

the chestnut-backed chickadee. Categories of A and B note types were so indistinguishable in this species' *chick-a-dee* calls that they were ultimately lumped into one category of A notes (Hoeschele et al. In press). This is markedly different from A and B notes studied in the Mexican chickadee, another brown-headed chickadee, where these note types are very distinct (Moscicki et al. In prep; Ficken 1990). These differences highlight the importance of individually studying the vocalizations of each species before attempting to assess more functional aspects of those vocalizations, such as messages encoded and the context in which those vocalizations are used.

It has been shown empirically in laboratory based operant experiments (Bloomfield and Sturdy 2008) that black-capped chickadees can distinguish conspecific calls from those of heterospecifics (mountain chickadees). In addition, statistical methods, namely linear discriminant analyses, have been used to successfully classify black-capped and mountain chickadee calls with 100% accuracy using only introductory notes (Dawson et al. 2006). With the boreal chickadee note type information gained from this study we can begin to examine whether conspecifics and heterospecifics can discriminate among boreal *chick-a-dee* note types in the same manner. Experiments such as these are important steps to gain a full understanding of the *chick-a-dee* call of this species and to provide insights for future work aimed at assessing the function of these vocalizations.

b. Quantitative note-type analysis. . In addition to knowing if birds are capable of discriminating among note types of conspecifics and heterospecifics, in order to achieve greater understanding of the *chick-a-dee* call we would also want to know how the birds perform these discriminations. In our sample of boreal *chick-a-dee* calls, we found many

features that may potentially be useful for discriminating among note types. It seems useful that many note features may provide note classification information; a combination of redundant, useful note features would circumvent problems of sound degradation encountered due to environmental factors such as wind, vegetation, and interfering vocalizations from other birds (Wiley and Richards 1982).

We found that total duration (TD) had the highest PNTC value in our sample and thus may be the most useful feature for discriminating among note types. All of the note types that were originally disagreed upon in the initial note sort in Study I were ultimately classified as either A, B, or D_h . One of the criteria used to distinguish among these note types (especially between B and D_h notes) was total duration. Total duration is also one of only two features (the other being F_{max}) that differed significantly among all three of these note types; therefore, it seems plausible that this feature would be important for note-type identification in this species.

Of the spectral features measured, frequency at maximum amplitude (F_{max}) had the highest PNTC value. This feature may be particularly important for discriminating between A and B notes as these two note types have few to no harmonics and thus the loudest frequency may be the most important component of the note. Start and end frequency also had relatively high PNTC values. Birds are able to detect changes in frequency much better than changes in duration (Dooling 1982); thus, it seems feasible that frequency measures have the potential to be used to discriminate among note types.

Another measured feature with a high PNTC value was ascending frequency modulation (FM_{asc}). Frequency modulation has been shown to be unaffected by degradation (Aubin 1989) and thus would be a useful feature to use for conveying note

type information. Frequency modulation was a main component used to discriminate A notes from B notes in the human sorting procedure described in Study I. Similarly, black-capped chickadees are capable of discriminating among the introductory notes of conspecific calls using only FM_{asc} (Charrier et al. 2005), though this remains to be tested in boreal chickadees. Thus, frequency modulation appears to be yet another useful feature in discriminating among boreal chickadee note types.

In addition to being able to discriminate among note types to gather important information, birds also need to be able to discriminate among individuals. It is important for many species to know whether an animal encroaching on its territory is its usual neighbour, to which it should not behave aggressively, or a stranger, to which it should behave antagonistically in order to defend its territory (e.g., bullfrogs (*Rana catesbeiana*), Bee and Gerhardt 2001; ants (*Formica xerophila*), Tanner and Alder 2009; little owls (*Athene noctua*), Hardouin et al. 2006). Individual recognition is important in this instance to conserve energy and engage only in useful conflict (Fisher 1954).

Like note-type discrimination, we found that many of the note features we measured may be useful for individual identification. An interesting result was that all features measured on the notes in the call type used most frequently, the AD_hD call type, were significantly different. The same was not true of B and C notes, with B notes having only five of nine features measured showing significant differences and C notes having only two of nine measured features showing significant differences. This may indicate that the AD_hD call is used most frequently because it conveys the most information about individual identity. For this to be true, we would want to verify that if we increased our

sample of B and C notes that we would not uncover more significant differences due solely to increased sample size and thus greater statistical power.

When examining individual note types, we found that the frequency measures (SF, PF, EF) consistently showed the highest PIC values and thus appear to be the most important features with respect to individual identification. It is logical that frequency characteristics would be highly individualized as these are controlled and dictated by the morphology of the songbird vocal apparatus, the syrinx (Suthers et al. 1999; Goller and Suthers 1996). Frequency in the *fee bee* song of black-capped chickadees has been shown to convey information about individual male quality (Christie et al. 2004). If the *chick-a-dee* call is also highly individualized, frequency features in this vocalization may also carry markers about the fitness of the bird producing it, though this has yet to be tested.

As with note-type coding, it is useful to have many features capable of predicting individual identity to overcome effects of environmental and behavioural interference that may prevent the accurate decoding of messages within a single feature (Wiley and Richards 1982). While we have shown which features could putatively be used to discriminate among individuals these features still require verification by the boreal chickadees themselves. Operant discrimination experiments have been conducted with great tits (*Parus major*) showing they can discriminate among conspecific individuals using vocalizations alone and this discrimination transfers to novel songs from those individuals (Weary and Krebs 1992). Similar individual recognition results have been shown for black-capped chickadees (Phillmore et al. 2002). This type of experiment could well be performed with boreal chickadees and the information presented in this

study could serve as a necessary starting point to determine which note features boreal chickadees attend to most in performing these kinds of essential discrimination tasks.

c. Syntactical analysis. In addition to examining the note types of boreal chickadee *chick-a-dee* calls individually, we also examined how those note types are assembled into the whole call. We looked at the syntax of boreal chickadee calls in two ways: in expanded form where note repetitions contribute to different syntax types, and in condensed form where they do not. It has been suggested that repetitions of the same note type within black-capped chickadee *chick-a-dee* calls serve to convey the signaler's motivation or sense of urgency and have little to do with the actual message of the call (Hailman et al. 1987; Templeton et al. 2005).

Our sample may reflect this finding of repetitious note types conveying urgency. There are differences in the number of A note repetitions observed in the Macaulay Library sample and the sample of birds recorded in our laboratory (see Table 3-5). This may reflect the context within which vocalizations were recorded for the laboratory birds (i.e., using a mirror to induce vocalizations, see Methods – Recordings, above). Proppe and Sturdy (2009) found that when black-capped chickadee calls were evoked in the laboratory (by an experimenter hand-waving at the bird) birds produced calls that differed from spontaneously-produced calls. Namely, evoked calls contained more high frequency notes, especially B notes. In our laboratory-recorded boreal chickadee call sample A notes may be used as an alarm call in the evoked call context and the number of repetitions may indicate the threat level, or level of urgency, perceived by the bird giving each call (Baker and Becker 2002). Numerous A note repetitions were not found in the Macaulay Library sample where calls were recorded under more natural conditions. This

is a putative example of how context can affect vocalizations. It is possible that recordings made under different contexts would yield even more syntax types than those found in our sample. For a more detailed description of the vocalizations of boreal chickadees given in different contexts see McLaren (1976).

In our examination of the syntax of the boreal *chick-a-dee* call, we found that all calls in our sample followed a general rule of note-type order: $A \rightarrow B \rightarrow C \rightarrow Dh \rightarrow D$, with the possibility that any note type could be repeated or omitted within this sequence. This rule applies to the *chick-a-dee* calls of all chickadee species studied to date (with some flexibility in mountain chickadees, Bloomfield et al. 2004). It seems advantageous to have similar rules of call composition across closely related species in order to share information about food location and predators (Thorpe 1961; Armstrong 1963). In addition, proper syntax is important for species identification in many songbird species, including the zebra finch (*Taeniopygia guttata*; Helekar et al. 2003), brown thrasher (*Toxostoma rufum*; Boughey and Thompson 1976), European starling (*Sturnus vulgaris*; Chaiken et al. 1993), song (*Melospiza melodia*), and swamp sparrows (*Melospiza georgiana*; Searcy et al. 1981). Boreal, black-capped, and Carolina chickadees have all shown decreased responsiveness to playback of conspecific calls with improper syntax (McLaren 1976; Charrier and Sturdy 2005; Clucas et al. 2004). These studies indicate that proper syntax production is an important feature of songbird vocalizations.

An interesting finding in our sample of boreal *chick-a-dee* calls was that B notes were never followed by other B notes. Although this may be due to our B note sample size, another interpretation could be that, since B notes begin with a tonal portion and end with a portion of high frequency modulation, it may be difficult for a bird's syrinx to

rapidly switch from producing highly frequency modulated sound to tonal sound. This phenomenon is found in other species with vocalizations involving trills (see Podos 1997 for a review of 34 species of the family Passeriformes). There is a trade-off, or vocal constraint, between the amount of frequency variation produced and the trill rate (Nowicki et al. 1992). Thus, the physical morphology of the boreal syrinx may contribute to the syntax of this species' *chick-a-dee* call.

In addition to physical constraints shaping the syntax of the *chick-a-dee* call of boreal chickadees, there is evidence from other species that learning may also play an important role in syntax formation. Faulty syntax learning has been shown to adversely affect other areas of song or call production. For example, white-crowned sparrows (*Zonotrichia leucophrys*) tutored with correct phonology (i.e., note structure), but incorrect syntax information, produced vocalizations deficient in both phonology and syntax (Plamondon et al. 2008). Further studies with white-crowned sparrows show that it is not sufficient to merely present call elements separately; in order to form the correct species-typical syntax these birds require at least two overlapping call elements (Plamondon 2008), thus highlighting that syntax is indeed a learned aspect of vocalizations in this species. We do not yet know if learning is important for the syntax of boreal *chick-a-dee* calls, or even if the *chick-a-dee* call is truly a learned vocalization in this species. The syntax information presented in this work could provide the groundwork for future studies aimed at testing these types of questions.

Our studies, presented here, provide a rigorous, detailed, and comprehensive examination of the boreal chickadee *chick-a-dee* call. This is the sixth of seven chickadee species to have their vocalizations analyzed in such a manner (the final species, the grey-

headed chickadee, is rare, has a small generally inaccessible range, and few calls have ever been recorded; Hailman and Haftorn 1995). Our work may serve as a foundation for future field and laboratory based experiments, some of which have been mentioned. Another important aspect of this work is that it adds to the body of knowledge of *chick-a-dee* calls from a variety of species, analyzed in a consistent way, which can be easily used for cross-species comparisons. Some cursory species comparisons have been described in this work; however, a more thorough comparison of the *chick-a-dee* call across all chickadee species remains to be undertaken. With the knowledge gained from this work it will be possible to look at in-depth differences between species in the black-headed and brown-headed chickadee subgroups. In this way, we may gain some insight into the evolutionary path of this genus, which has been debated (Gill et al. 2005), through the development, similarities, and differences in the species' respective name-sake *chick-a-dee* calls.²

² A version of this chapter has been submitted for publication.

3.13. Tables

Table 3-1. Sampling information for recordings of boreal chickadee (*Poecile hudsonica*) chick-a-dee calls.

Total Sample					
Recording Dates	Time of Day	Source	Location	Recording Equipment	Number of Recordings
June, 1953 - June, 2007	0446 - 1742	Macaulay Library of Natural Sounds	Alaska, Alberta, Maine, Manitoba, Minnesota, New Brunswick, New York, Nova Scotia, Ontario, Quebec, Vermont	Nagra IIIB recorder and AKG 200 microphone; SD744T recorder and Telinga Pro microphone	28
June, 2004 - July, 2004	0900 - 1700	Sturdy Laboratory	Edmonton, Alberta	Marantz PMD 670 digital recorder and C 1000 S condenser microphone	55
Subsample Used for Studies I and II					
Recording Dates	Time of Day	Source	Location	Recording Equipment	Number of Recordings
June, 1996 - June, 2007	0530 - 1038	Macaulay Library of Natural Sounds	Alaska, Manitoba, New York, Quebec	Nagra IIIB recorder and AKG 200 microphone; SD744T recorder and Telinga Pro microphone	6
June, 2004 - July, 2004	0900 - 1700	Sturdy Laboratory	Edmonton, Alberta	Marantz PMD 670 digital recorder and C 1000 S condenser microphone	55

Table 3-2. Potential for note-type coding (PNTC) for the 11 features measured on boreal chickadee note-types (A, B, C, D_h, and D).

Note: SF, start frequency; PF, peak frequency; EF, end frequency; AD, ascending duration; DD, descending duration; TD, total duration; FM_{asc}, ascending frequency modulation; FM_{desc}, descending frequency modulation; F_{max}, frequency at maximum amplitude; f₀, fundamental frequency; NPF, note peak frequency. See text for measurement descriptions.

* Significant differences. See text for adjusted *p* values.

**Significant differences among all note pairs in Games-Howell post-hoc tests.

^{ns} Non-significant differences.

	SF	PF	EF	AD	DD	TD	FM _{asc}	FM _{desc}	F _{max}	f ₀	NPF
CV _b	28.6	10.5	35.5	105.0	76.0	57.8	313.6	127.8	20.4	19.8	17.5
Mean CV _w	19.3	8.4	20.4	59.6	104.5	26.4	197.0	120.1	10.8	17.4	14.4
PNTC	1.5	1.2	1.7	1.8	0.7	2.2	1.6	1.1	1.9	1.1	1.2
<i>F</i>	315.5*	51.4*	190.0*	29.4*	103.8*	993.8*	4.4*	6.3*	686.0*	10.7*	11.7*
Games-Howell test	** except between B and D _h (<i>p</i> = .25)	** except between A and B and A and C (<i>p</i> = .80), (<i>p</i> = .14), B and C (<i>p</i> = .10)	** except between A and B (<i>p</i> = .19)	** except between A and B and A and Dh (<i>p</i> = .98), (<i>p</i> = .08), B and Dh (<i>p</i> = .06)	** except between A and B (<i>p</i> = .03)	** except between B and C (<i>p</i> = .59)	** except between A and C and B and D _h and C and D _h (<i>p</i> = .13), (<i>p</i> = .87), (<i>p</i> = .08)	^{ns} except between A and D _h (<i>p</i> = .001)	** except between D _h and D (<i>p</i> = .31)	** except between D _h and D (<i>p</i> = .64)	** except between C and D _h (<i>p</i> = .42)

Table 3-3. Potential for individual coding (PIC) values, coefficients of variation (CV_b and Mean CV_w), and F-values (* see text for significant alpha levels) for each acoustic feature measured on A, B, C and tonal D_h notes.

Note Type	TD	AD	DD	SF	PF	EF	FM _{asc}	FM _{desc}	F _{max}
A	CV_b	17.4	153.7	75.4	11.3	4.1	9.6	200.7	17.4
	Mean CV_w	12.7	214.7	52.5	8	3.6	7.2	265.1	3.2
	PIC	1.4	0.7	1.4	1.4	1.1	1.3	0.8	1.1
	F	13.8*	24.9*	7.49*	56.99*	14.05*	55.04*	14.33*	7.73*
B	CV_b	6.7	73.4	32.3	12.8	6.5	19.7	85.2	5
	Mean CV_w	4.7	84.3	25.1	7.3	2.2	26.8	97.4	5.3
	PIC	1.4	0.9	1.3	1.7	3	0.7	0.9	1
	F	9.26*	19.42*	4.34	15.81*	86.62*	1.01	2.33	0.49
C	CV_b	12.8	11.7	240.8	12.1	10	14.3	21.9	12.8
	Mean CV_w	10.2	11.9	-	12.4	5.4	7.4	20.3	11.8
	PIC	1.3	1	-	1	1.8	1.9	1.1	1
	F	2.65	0.52	-	0.62	39.02*	45.92*	5.97	0.04
D_h	CV_b	-	59.4	31.4	28.1	8	18.4	71.3	10.6
	Mean CV_w	-	60.5	26.5	21.6	6.3	15.1	83.5	9.1
	PIC	-	1	1.2	1.3	1.3	1.2	0.9	1
	F	-	41.26*	16.28*	34.39*	31.61*	10.63*	12.35*	15.58*

Table 3-4. Potential for individual coding (PIC) values, coefficients of variation (CV_b and Mean CV_w), and F values (*see text for significant alpha levels) for each acoustic feature measured on D and Dh notes.

Note	Type	TD	f_0	F_{max}	NPF
D	CV_b	7.1	10.4	7.4	16.2
	Mean CV_w	4.7	9.9	7.2	14
	PIC	1.5	1	1	1.2
	F	29.48*	4.60*	4.13*	12.09*
D_h	CV_b	22.3	49.8	16.6	16.6
	Mean CV_w	10.4	27.8	13.7	14
	PIC	2.1	1.8	1.2	1.2
	F	64.22*	6.99*	10.79*	9.91*

Table 3-5. Syntax types observed in our sample of boreal chickadee *chick-a-dee* calls. A) Calls with repeated note-types considered different syntax types (i.e., AAD is a different syntax type than AAAD; expanded version). B) Calls with repeated note types considered the same syntax type (i.e., AAD is the same as AAAD and is denoted as syntax type A, D; condensed version).

A.

Syntax	Number of Calls	Percentage of Sample
AAAAAAAAAAAA	1	0.10%
AAAAAAAAAAAA	1	0.10%
AAAAAAAAAAAA	1	0.10%
AAAAAAAAAAAA	3	0.30%
AAAAAAAAAAAA	3	0.30%
AAAAAAAAAAAA	3	0.30%
AAAAAADhD	1	0.10%
AAAAAAA	14	1.40%
AAAAAAA	14	1.40%
AAAAAC	1	0.10%
AAAAA	33	3.31%
AAAAC	1	0.10%
AAAADhDD	2	0.20%
AAAADhD	3	0.30%
AAAADh	1	0.10%
AAAA	66	6.61%
AAAC	4	0.40%
AAADhDD	3	0.30%
AAADhD	14	1.40%
AAADh	1	0.10%
AAA	76	7.62%
AABDhD	1	0.10%
AAB	2	0.20%
AACCC	1	0.10%
AACCCD	1	0.10%
AACD	2	0.20%
AAC	16	1.60%
AADD	6	0.60%
AAD	7	0.70%
AADhDD	18	1.80%
AADhD	78	7.82%
AADh	10	1.00%

B.

Syntax	Number of Calls	Percentage of Sample
AA	41	4.11%
ABDDD	1	0.10%
ABDD	4	0.40%
ABD	22	2.20%
AB	1	0.10%
ABDhD	1	0.10%
ACCD	2	0.20%
ACD	19	1.90%
AC	11	1.10%
ADD	3	0.30%
AD	5	0.50%
ADhDD	95	9.52%
ADhD	175	17.54%
Adh	23	2.30%
BDD	5	0.50%
BD	2	0.20%
BDhDD	1	0.10%
BDhD	1	0.10%
BDh	1	0.10%
CCCC	3	0.30%
CCC	11	1.10%
CCDDD	1	0.10%
CCDD	1	0.10%
CCD	3	0.30%
CC	2	0.20%
DDD	3	0.30%
DD	25	2.51%
DhDD	81	8.12%
DhD	62	6.21%
Dh	4	0.40%
DhDhD	1	0.10%
A	256	25.65%
A, B	3	0.30%
A, B, D	27	2.71%
A, B, Dh, D	2	0.20%
A, C	34	3.41%
A, C, D	24	2.40%
A, Dh	35	3.51%
A, Dh, D	389	38.98%
A, D	21	2.10%
B, Dh	1	0.10%
B, Dh, D	2	0.20%
B, D	7	0.70%
C	16	1.60%
C, D	5	0.50%
Dh	4	0.40%
Dh, D	144	14.43%
D	28	2.81%

Table 3-6. Transitions from one note type to another in our sample of *chick-a-dee* calls from boreal chickadees. A) Total number of transitions from each note type to each other note type. B) Conditional transition probabilities (i.e., the probability that one note type may occur given that a certain note type has occurred just previously).

A.

Transitions	Number	Percentage of Sample
A->A	929	27.57%
A->B	32	0.95%
A->C	58	1.72%
A->D	20	0.59%
A->D _h	424	12.59%
A->_	257	7.63%
B->A	0	0.00%
B->B	0	0.00%
B->C	0	0.00%
B->D	36	1.07%
B->D _h	5	0.15%
B->_	4	0.12%
C->A	0	0.00%
C->B	0	0.00%
C->C	43	1.28%
C->D	29	0.86%
C->D _h	0	0.00%
C->_	50	1.48%
D->A	0	0.00%
D->B	0	0.00%
D->C	0	0.00%
D->D	255	7.57%
D->D _h	0	0.00%
D->_	649	19.26%
D _h ->A	0	0.00%
D _h ->B	0	0.00%
D _h ->C	0	0.00%
D _h ->D	537	15.94%
D _h ->D _h	1	0.03%
D _h ->_	40	1.19%

B.

Conditional Transitions	Conditional Percentage
Given A first	A->A 54.01%
	A->B 1.86%
	A->C 3.37%
Total of 1720 transitions from A	A->D 1.16%
	A->D _h 24.65%
	A->_ 14.94%
Given B first	B->A 0.00%
	B->B 0.00%
	B->C 0.00%
Total of 45 transitions from B	B->D 80.00%
	B->D _h 11.11%
	B->_ 8.89%
Given C first	C->A 0.00%
	C->B 0.00%
Total of 122 transitions from C	C->C 35.25%
	C->D 23.77%
	C->D _h 0.00%
	C->_ 40.98%
Given D first	D->A 0.00%
	D->B 0.00%
	D->C 0.00%
Total of 904 transitions from D	D->D 28.21%
	D->D _h 0.00%
	D->_ 71.79%
Given D_h first	D _h ->A 0.00%
	D _h ->B 0.00%
	D _h ->C 0.00%
Total of 578 transitions from D _h	D _h ->D 92.91%
	D _h ->D _h 0.17%
	D _h ->_ 6.92%

Table 3-7. Note position probabilities. A) Probability of note types in each position in the call in our sample of boreal chickadee *chick-a-dee* calls (i.e., the probability that the 1st note in a call will be an A note). B) Probability of the position of each note type within our boreal chickadee *chick-a-dee* call sample (i.e., the probability that an A note will be the 1st note in a call).

A.

	Note 1	Note 2	Note 3	Note 4	Note 5	Note 6	Note 7	Note 8	Note 9	Note 10	Note 11	Note 12	Note 13
Total Notes	998	994	821	386	122	51	29	13	10	6	3	2	1
Prob. A	79.26%	43.16%	29.96%	38.34%	61.48%	80.39%	93.10%	92.31%	90.00%	100.00%	100.00%	100.00%	100.00%
Prob. B	1.00%	2.92%	0.37%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Prob. C	2.10%	5.33%	4.38%	2.33%	1.64%	1.96%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Prob. D	2.81%	18.71%	52.25%	54.40%	31.97%	17.65%	6.90%	0.00%	10.00%	0.00%	0.00%	0.00%	0.00%
Prob. D_h	14.83%	29.88%	13.03%	4.92%	4.92%	0.00%	0.00%	7.69%	0.00%	0.00%	0.00%	0.00%	0.00%

B.

	Prob. Note 1	Prob. Note 2	Prob. Note 3	Prob. Note 4	Prob. Note 5	Prob. Note 6	Prob. Note 7	Prob. Note 8	Prob. Note 9	Prob. Note 10	Prob. Note 11	Prob. Note 12	Prob. Note 13
A	44.19%	23.97%	13.74%	8.27%	4.19%	2.29%	1.51%	0.67%	0.50%	0.34%	0.17%	0.11%	0.06%
B	23.81%	69.05%	7.14%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
C	17.21%	43.44%	29.51%	7.38%	1.64%	0.82%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
D	3.10%	20.58%	47.46%	23.23%	4.31%	1.00%	0.22%	0.00%	0.11%	0.00%	0.00%	0.00%	0.00%
D_h	25.61%	51.38%	18.51%	3.29%	1.04%	0.00%	0.00%	0.17%	0.00%	0.00%	0.00%	0.00%	0.00%

3.14 Figures

Figure 3-1. Sound spectrograms (FFT window = 512 points) showing exemplars of each of the five note types identified in our sample of boreal chickadee *chick-a-dee* calls.

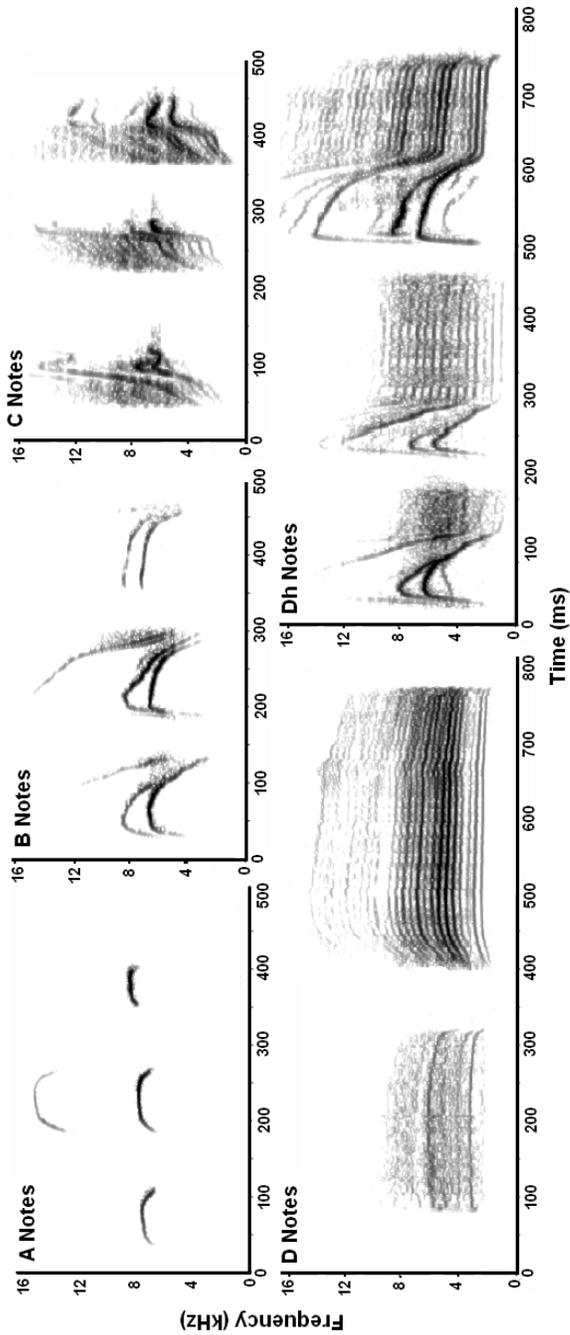
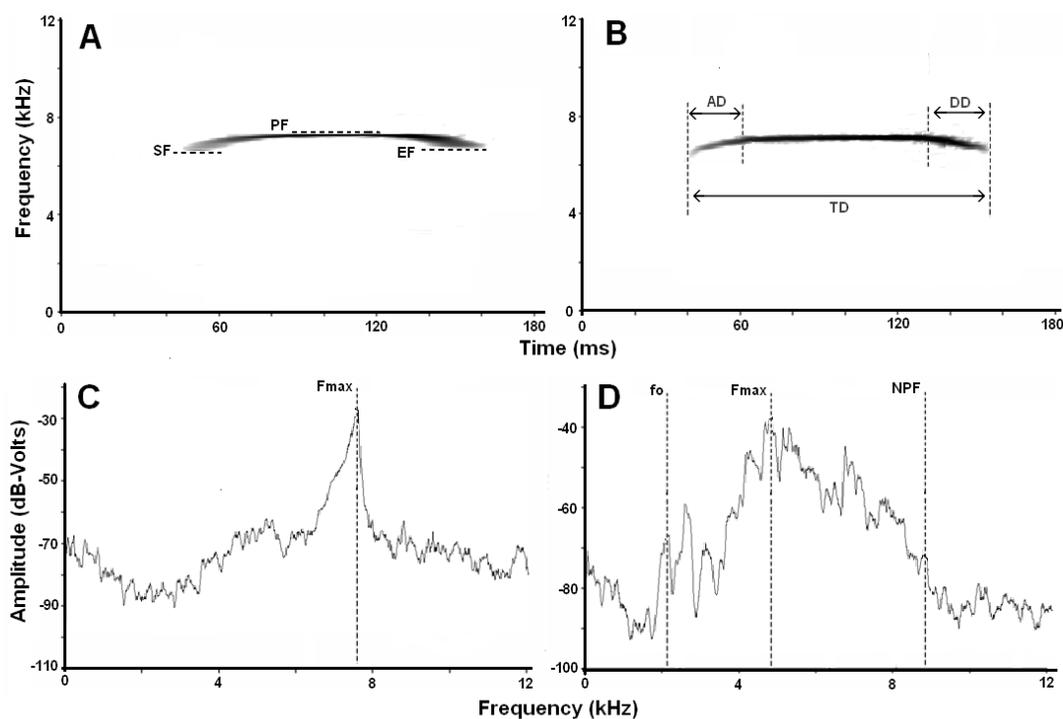


Figure 3-2. Sound spectrograms and spectra illustrating measurements of note-type features. Panels A, B, and C feature a representative A note as an example while panel D features a representative D note. A) Spectrogram (FFT window = 1,024 points) showing frequency measurements used on A, B, C, and the tonal portion of D_h notes. SF = start frequency; PF = peak frequency; EF = end frequency. B) Spectrogram (FFT window = 256 points) showing duration measurements; vertical lines indicate the boundaries of duration measurements. AD = ascending duration; DD = descending duration; TD = total duration. C) Spectrum (window size = 8,192 points) showing the frequency at maximum amplitude (F_{max} ; indicated by the vertical line). D) Spectrum (window size = 32,768 points) indicating the lowest visible frequency above -35dB relative to the note peak amplitude (f_0 ; indicated by the vertical line), F_{max} , and the highest frequency above -35dB from note peak amplitude (NPF; indicated by the vertical line).



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4. GENERAL DISCUSSION

The present studies have examined the *chick-a-dee* call of two closely related species of chickadee, Mexican and boreal. Although the *chick-a-dee* call is a fairly ubiquitous vocalization in all chickadee species, it had not yet been examined in this rigorous manner in these two species. Both species are from the brown-headed subgroup of the genus *Poecile* (Gill et al. 2005); this subgroup is in general less studied than the black-headed subgroup. To date, the *chick-a-dee* call of only one species in the brown-headed subgroup, the chestnut-backed chickadee, has been studied using methodology similar that that employed in the current studies (Hoeschele et al. In press). With information on the *chick-a-dee* call of more than one brown-headed subgroup species we can now compare aspects of this vocalization within this subgroup.

4.1 Proposed Species Comparisons

The species within the brown-headed subgroup of the genus *Poecile* have different degrees of relatedness. Boreal chickadees are most closely related to chestnut-backed chickadee and both are more distantly related to grey-headed chickadees. Mexican chickadees are the most distantly related to the rest of the brown-headed chickadees and there is some speculation that they may in fact be most closely related to some of the black-headed chickadees (Gill et al. 2005). It will be interesting to compare the *chick-a-dee* call among these species to determine if the similarities and differences in these vocalizations across species reflect the degree of relatedness among species.

In addition to comparing *chick-a-dee* calls within the brown-headed subgroup, it would also be informative to compare this vocalization among species in the two subgroups, brown- and black-headed. It would be interesting to see if the *chick-a-dee* call

is more similar within subgroups than between subgroups. It is already known that there are differences in the vocal repertoire between these two subgroups: black-headed chickadees produce a tonal, whistled *fee bee* song that brown-headed chickadees lack (Hailman 1989; Bent 1946); however, it is not known whether black-headed chickadees may have acquired this vocalization over time or if brown-headed chickadees lost the *fee bee* song. Perhaps studies comparing the *chick-a-dee* call produced by all chickadee species, and analyzing the similarities and differences in that call, will shed light on this question.

4.2 Proposed Frequency Comparisons

One feature of *chick-a-dee* calls that may be compared between subgroups is the importance of frequency information in this vocalization. The PNTC and PIC results presented in the current work show that frequency is important for note-type discrimination in both species studied, though Mexican chickadee note types appear to differ more on frequency features than boreal chickadee note types. Also, frequency measures in boreal *chick-a-dee* calls appear important for individual recognition. Information regarding individuals has already been found to be encoded in the *fee bee* song of the black-headed subgroup; the inter-note interval in this song conveys information about individual male quality (Christie et al. 2004). It would be interesting to determine if the frequency features in *chick-a-dee* calls also encode information about individual male quality. If the *chick-a-dee* calls of black-headed chickadees do not contain frequency features that indicate aspects of male quality, but the calls of brown-headed chickadees do, this may indicate that either the black-headed subgroup acquired the *fee bee* song to fill this function, or that the call of the brown-headed chickadee

evolved to take up this function upon the loss of the *fee bee* song. Whatever the outcome, many areas of potential study could follow from the information gained conducting these kinds of call comparisons across species.

4.3 Bioacoustics as a Foundation

In addition to using bioacoustics to examine similarities and differences in the *chick-a-dee* calls themselves, comparing them may illuminate a priori hypotheses for consideration in other areas of study. Bioacoustic information is a foundation for work aimed at understanding songbird vocal communication and thus is a necessary precursor to further studies investigating this complex process. Tinbergen's (1963) idea of examining a phenomenon from four perspectives, mechanistic, functional, phylogenetic, and ontogenetic, to best understand it may be applied to the studies of songbird communication that may now be possible using the bioacoustic information presented in the present work.

4.4 Bioacoustics as a Foundation for Mechanistic Studies

The bioacoustic work presented here may guide future studies aimed at further investigating the mechanisms of songbird vocal communication, the first of Tinbergen's (1963) perspectives. For example, we know that frequency characteristics are important for individual recognition in some of the chickadee species studied (Charrier et al. 2004; Bloomfield et al. 2004; Bloomfield et al. 2005), as well as other bird species (e.g., Long-tailed tits (*Aegithalos caudatus*), Sharp and Hatchwell 2005; White-faced whistling ducks (*Dendrocygna viduata*), Volodin et al. 2005; White-browed warblers (*Basileuterus leucoblepharus*), Aubin et al. 2004). We also know that frequency is controlled by the songbird vocal apparatus, the syrinx (Goller and Larsen 2002). Therefore, by comparing

the relative importance of frequency in discriminating note types and individuals, as well as basic differences in frequency measures, among the *chick-a-dee* calls of various species it would be possible to develop a priori hypotheses regarding aspects of the syrinx that may then be compared across species, such as size, musculature, and structure.

4.5 Bioacoustics as a Foundation for Functional Studies

Along with physical mechanistic comparisons, such as those proposed for the syrinx, the bioacoustic analyses presented in this work, and subsequent bioacoustic comparisons among chickadee species, may also lead to a priori hypotheses for studies focused on the function of various features of the *chick-a-dee* call, the second of Tinbergen's (1963) four perspectives. Examining the differences in the *chick-a-dee* calls among species may point to differences in how the chickadee species would perceive these vocalizations. For example, PNTC results presented here show that frequency measures were very different across the note types of Mexican chickadee calls while duration measurements were different, but less pronounced. This could indicate that this species may be better at duration discrimination and not be as adept at frequency discriminations; thus, the note types have evolved to be very different in frequency in order to allow for correct discrimination. Alternatively, perhaps duration is less important and frequencies are more distinct because frequency is a very important feature for this species to attend to and has become exaggerated over time. Experiments could be performed to determine the amount of neural activity after exposure to frequency differences compared to duration differences to determine if perception of calls is related to production. Studies have previously used the technique of measuring the expression of immediate early gene activity in the chickadee brain to examine the difference in

perception of calls and songs between males and females (Avey et al. 2008; Phillmore et al. 2003).

Another way to look at the perception of the *chick-a-dee* call across the *Poecile* species, and thus attempt to understand the function of the various frequency and duration aspects of that call, would be to perform operant discrimination tasks. Operant discrimination experiments aimed at understanding which aspects of the *chick-a-dee* call certain species attend to have been performed and described previously in this work (e.g., Bloomfield et al. 2008; Charrier et al. 2005). However, with the new information gained from the present studies on Mexican and boreal *chick-a-dee* calls, and the species comparisons this data will now allow, further operant experiments can be conducted to examine the similarities and differences in response learning across chickadee species. For example, for species known to be able to discriminate their own introductory notes based solely on ascending frequency modulation, like black-capped chickadees (Charrier et al. 2005) it could be tested whether they are still able to perform this discrimination with a species' *chick-a-dee* call that does not have as large a difference in ascending frequency modulation between note types, such as Carolina chickadees or Mexican chickadees (Charrier et al. 2004; Bloomfield et al. 2005; Moscicki et al. In prep). As well, the species with less ascending frequency modulation in its own vocalizations could be tested to see if capable of performing the discrimination based solely on ascending frequency modulation on the note types of conspecifics as well as on the note types of black-capped chickadees. Methods such as these could be employed to begin to understand whether the perception of vocalizations is influenced by the features of a species' own vocalization. Information pertaining to chickadee perception of various

components of the *chick-a-dee* call will guide experiments aimed at understanding the function of frequency and duration differences within this call. Experiments of this nature would not be possible without first having detailed bioacoustic analyses of the vocalizations of the species to be compared, analyses such as those presented in this work.

4.6 Bioacoustics as a Foundation for Phylogenetic Studies

The third of Tinbergen's (1963) perspectives, phylogenetic, pervades many of the experiments proposed here as they focus on comparing the *chick-a-dee* call across closely related species, an excellent method for drawing conclusion about common descent. One aspect of the bioacoustic work presented here, syntax information, provides ample material for species comparisons. While the syntax of the black-headed species has not yet been studied in quite the same manner as the syntax of the Mexican and boreal chickadees presented in this work, there is still a wealth of information on the syntax of those species' *chick-a-dee* calls (e.g., Hailman 1989; Charrier et al. 2004; Bloomfield et al. 2004; Bloomfield et al. 2005). One interesting difference that has become clear from studies of *Poecile* syntax is that species in the brown-headed subgroup do not produce as many, if any, B notes as do species in the black-headed subgroup (Hoeschele et al. In press; Charrier et al. 2004; Bloomfield et al. 2004; Bloomfield et al. 2005). Experiments could thus be undertaken to determine if species that do not possess B notes, like chestnut-backed chickadees (Hoeschele et al. In press), could determine if a B note was out of place in the syntax of a call that does naturally contain B notes. If capable of such a feat, this may point to other aspects of the call that may bear further study, such as if the note would still be recognized as out of place if the frequency or duration was altered.

This kind of study would provide information to help better understand why the *Poecile* species all appear to have similar rules for note-type production and why the notes are produced in a specific order.

There is already evidence that points to call syntax being important for species identification in a variety of songbird species (e.g., zebra finches (*Taeniopygia guttata*), Helekar et al. 2003; brown thrashers (*Toxostoma rufum*), Boughy and Thompson 1976), European starlings (*Sturnus vulgaris*), Chaiken et al. 1993; song (*Melospiza melodia*) and swamp sparrows (*Melospiza georgiana*), Searcy et al. 1981; black-capped chickadees, Charrier and Sturdy 2005). With detailed information now available on the syntax of many of the chickadee species it is possible to investigate whether these closely related species perceive and attend to the syntax of other chickadee species. A few studies have shown that when some chickadee species are exposed to calls of conspecifics in which the syntax has been altered to be incorrect they respond with fewer calls of their own (e.g., boreal chickadees, McLaren 1976; black-capped chickadees, Charrier and Sturdy 2005; Carolina chickadees, Clucas et al. 2004). Experiments can now be undertaken to see if closely related species can determine if syntax has been altered in the *chick-a-dee* calls of heterospecifics and if the birds are better at this task with the calls of the species more closely related to them (i.e., within their own subgroup). It would be important for birds to understand the message conveyed in calls of other species in order to take advantage of food resources found by these species and to avoid predators detected by other species (e.g., Mahurin and Freeberg 2009; Hurd 1996). This type of work could lead to a better understanding of if, and under what circumstances, chickadees attend to, or eavesdrop, on the calls of closely related species, and whether syntax contains

important information to be gained from eavesdropping. These types of experiments, aimed at understanding the chickadee call from a functional and phylogenetic perspective, can only be carried out by first having detailed knowledge of the syntax of the vocalizations of the closely related species, information gained from bioacoustic studies such as the work presented here.

4.7 Bioacoustics as a Foundation for Ontogenetic Studies

The last of Tinbergen's (1963) perspectives, ontogenetic, can also be examined through studies that may now be possible by utilizing the bioacoustic information presented in this work. For example, the syntax information gained from bioacoustic studies can be important not only for comparing syntax across species, but also for studying syntax learning. It is imperative that the correct syntax of a study vocalization first be known before attempting to study whether learning and exposure to different stimuli has any effect on the syntax ultimately produced. Some studies have already shown that learning is vital for correct syntax formation (e.g., Podos et al. 1999; Okanoya and Yamaguchi 1997), that songbirds such as white-crowned sparrows require a minimum exposure of at least two overlapping song elements to form the correct species-typical syntax (Plamondon 2008), and that this same species will produce deficient notes if tutored with deficient syntax (Plamondon et al. 2008). With the syntax information presented in this work, studies can be undertaken to attempt to tease out some aspects of nature verses nurture in syntax learning. For example, a chickadee species could be tutored with two types of calls in equal frequency, conspecific calls with altered syntax and heterospecific *chick-a-dee* calls with correct syntax. It could then be determined whether the species in question is more predisposed to learn its own species-typical note

types when given the wrong syntax or to learn a heterospecific call with correct syntax. It would be interesting to see if the call ultimately learned by chickadees in the proposed experiment changes depending on the degree of relatedness of the heterospecific chickadee call used. For these studies to be possible the syntax of the *chick-a-dee* call of all closely related species in question must be known; syntax information such as that provided in the current work.

Another aspect of syntax learning that could be investigated is altering the rules of note-type production. This could be done in order to better understand why the notes in the *chick-a-dee* call are produced in a particular order and why this order seems to be ubiquitous across species. Chickadees could be tutored with altered syntax such as higher pitched notes following lower pitched notes, contrary to what usually occurs within the *chick-a-dee* call, to determine if that type of syntax could be learned adequately. If not, this may help to explain why the notes in the *chick-a-dee* call of all species studied to date appear to follow a descending pitch contour (Charrier et al. 2004; Bloomfield et al. 2004; Bloomfield et al. 2005; Hoeschele et al. In press); perhaps the birds are physically incapable of producing notes in the opposite order. Also, chickadees could be tutored with repetitions of note types that are not generally repeated within their calls. For example, our sample of boreal chickadee calls revealed that there were no repeats of B note types within a single *chick-a-dee* call. If boreal chickadees tutored with repetitions of B note types within calls were unable to produce those repetitions it may again point to reasons such as vocal constraint that could explain the syntax rules of note-type production in this species. Bioacoustic studies provide information about the syntax of these calls; they are the foundation for ontogenetic studies such as those mentioned aimed

at understanding why note types are produced in a certain order and why this order seems to be ubiquitous among the chickadee species studied to date.

4.8 The Importance of Bioacoustic Analyses

As can be seen, bioacoustic studies of vocalizations can lead to the study of many other components of vocal communication, such as physiology, function, learning, and species comparisons, satisfying the four perspective outlined by Tinbergen (1963) to gain a thorough understanding of a phenomenon. Detailed descriptive studies are an important first step in the study of any phenomenon. This kind of inductive work leads to theories that can then be tested with a more deductive approach and may help illuminate not just information on individual vocalizations, individual species, or even multiple closely related species, but on vocal communication in general.

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