Note types and coding in Parid vocalizations: The chick-a-dee call of the chestnut-backed chickadee (Poecile rufescens)

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(Received 3 February 2009; revised 22 April 2009; accepted 13 July 2009)

A first step to understanding how a species communicates acoustically is to identify, categorize, and quantify the acoustic parameters of the elements that make up their vocalizations. The “chick-a-dee” call notes of the chestnut-backed chickadee (Poecile rufescens) were sorted into four call note categories, A, C, D, and Dh notes, based on their acoustic structure as observed in sound spectrograms, and evaluated based on the syntactical ordering of the note types within calls. The notes were then analyzed using quantitative measures and it was determined which features have the potential to convey information to discriminate note type, individual, and the geographic origin of the producer. The findings were comparable to previous research of congeners in that chestnut-backed chickadee calls were produced with a relatively fixed syntax and contained similarly structured note types across all geographic regions. Overall this information will form a base for future research on chestnut-backed chickadee vocalizations and will strengthen the foundation for future comparative evolutionary studies.

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PACS number(s): 43.80.Ka [MCH]

I. INTRODUCTION

In order to understand acoustic communication in songbirds, as in all animal species, we must first understand the acoustic structure and note composition that comprise their vocalizations. With this information we can begin to evaluate which aspects of the vocalizations are potentially important for individual recognition, species recognition, and to ascribing meaning. Further, by using similar methods across a number of closely related species, we can gain insights on the evolution of complex acoustic signals.

Chickadees (genus Poecile) are a frequently studied songbird genus for several reasons. First, chickadees are common in most areas of North America, making them readily available for scientific investigation. Second, chickadees are an excellent group for comparative study because there are many species of chickadees that all have unique, yet comparable, vocalizations such as the chick-a-dee call (e.g., Hailman and Ficken, 1996). Third, chickadees have a social structure that varies seasonally, whereby they form mated pairs in the spring and summer and in the fall and winter form cooperative flocks of typically six to eight individuals (Smith, 1991). These reasons, combined with the fact that chickadees have a complex and well-studied vocal repertoire, make them an excellent choice for studies of communication (Smith, 1991).

The North American clade of chickadees is often broken up into two sibling groups: black-headed and brown-headed chickadees based on both their appearance and their phylogenetic relationships (Gill et al., 2005). To date, the vocalizations of all the black-headed species of the North American chickadee clade [black-capped, mountain, and Carolina (atricapillus, gambeli, and Carolinensis) chickadees] have been studied extensively, including their whistled song (black-capped: Weisman et al., 1990; Kroodsma et al., 1999; mountain: Wiebe and Lein, 1999; and Carolina: Lohr et al., 1991, 1994) and chick-a-dee call (black-capped: Charrier et al., 2004; mountain: Bloomfield et al., 2004; and Carolina: Bloomfield et al., 2005). The whistled song is not part of the repertoire of brown-headed chickadees (chestnut-backed chickadee, Poecile rufescens, boreal chickadee, Poecile hudsonicus, gray-headed chickadee, Poecile cinctus, and Mexican chickadee Poecile sclateri), but they all produce chick-a-dee calls (Hailman, 1989). In fact, the chick-a-dee call of these species is used in social contexts normally reserved for the whistled song in the black-headed group. Specifically, the chick-a-dee call of the chestnut-backed chickadee is the most common vocalization of the dawn chorus, and is thought to be used for territory defense (Dahlsten et al., 2002). In con-
contrast to the black-headed group, chick-a-dee calls from members of the brown-headed group have not been studied nearly as extensively. Here we present the first in depth study examining the acoustic structure of the chestnut-backed chickadee chick-a-dee call.

In addition to examining the acoustic structure of the chestnut-backed chickadee call, we also looked at whether there was any geographic variation in the structure and syntax of the call; what some researchers refer to as different “dialects.” Vocal geographic variation has often been demonstrated for songbird populations separated by physical barriers (e.g., Slabbekoorn et al., 2003), and for populations lacking these barriers (e.g., Wright et al., 2008).

Because of the many regional and seasonal differences that occur in the vocalizations of many species, we examined and compared calls from a group of chestnut-backed chickadees recorded in May 2006 on Vancouver Island, as well as recordings of chestnut-backed chickadees recorded across many regions at different times of year. These regions contained areas of both sympatry and allopatry with other chickadee species. Our methodology for determining note types is similar to that used when studying the chick-a-dee calls of other chickadee species (Charrier et al., 2004; Bloomfield et al., 2004, 2005). We then measure and summarize several acoustic features from each note type to determine which aspects of the vocalizations the chestnut-backed chickadee could potentially use to discriminate among individuals and to discriminate among note types. Using this information, we made comparisons between notes, individuals, and geographic regions. We then postulate mechanisms by which the birds could extract information from conspecific calls. Finally, we examine syntactical trends across a vast library of calls recorded from several geographic areas.

II. STUDY 1: CALL NOTE CLASSIFICATION

The purpose of this study was to examine sound spectrograms of chick-a-dee call notes in order to determine the different note types present in the call. This information was then used as a basis for the subsequent studies.

A. Recordings

Recordings were obtained from two sources: a library of archived calls, and our own field recordings. Our field recordings from Vancouver Island in May 2006 (recorded by DEG) were used as a source from which we had detailed information about the nature of the recordings and individuals present in the recordings, which was important for some of our analyses. However, because this source contained recordings from only one location at one time of year, we also obtained recordings from Macaulay Library of Natural Sounds at the Cornell Laboratory of Ornithology, which consisted of recordings from many different people, with different recording equipment, in different months of the year, in different locations, and no detailed information regarding the individual identities of birds contained in the recordings.

The first sample (hereafter referred to as the Vancouver 2006 sample) of chestnut-backed chickadees was recorded in the field at eight different locations on Vancouver Island, Canada during May 2006 between the hours of 0500 and 1500 Pacific daylight time. All birds were unbanded, so sex was usually not known. A total of 43 pairs of chickadees were recorded. Because birds were unbanded, only recordings from one visit were used if locations were visited more than once. In these recordings it was clear which individual in the pair was vocalizing; this was important information for any analyses that required knowing which individual was calling. Recordings were made using a MiniDisc recorder (model MZ-N1, Sony Corp., Tokyo, Japan) connected to a Sennheiser omnidirectional microphone (model ME62, Sennheiser Corp., Wedemark, Germany), with a 20–20 000 Hz frequency response, mounted in a 60 cm parabola (Telinga Pro-universal model, Tobo, Sweden). The calls were then edited into individual wave files using SYRINX software, sampling at 22.05 kHz.

The goal was to obtain large samples of calls from each of several individuals with a representative sample of their call note type repertoire. In order to achieve this, there were two potential problems to overcome. First, calls were generally produced by birds high in the canopy at very low amplitudes, thus making for challenging sample acquisition in the field. Second, C and D notes in this species were relatively rare compared with other chickadee species studied to date (e.g., Charrier et al., 2004). To ameliorate these issues, we excluded calls from focal individuals if they had poor signal to noise ratio, high levels of background noise, a small sample of calls (<10), and/or had few (<5) calls that contained note types appearing similar to the C and D notes of other chickadee species. We had no numerical cutoff for poor signal to noise ratio, as this was determined by visually examining the spectrograms. However, all spectrograms had a cutoff of −35 dB below peak frequency (PF). Therefore, signals with noise that was louder than −35 dB from the peak of the signal and obscured our ability to properly distinguish the note from background noise were omitted. With all of these considerations in mind, nine individuals were selected from the Vancouver 2006 sample. From each of these individuals we then randomly selected ten calls such that the first five calls from each individual had to contain either a C or D type note, and additional five calls were randomly sampled from the remaining set of recorded calls such that at least five of the calls had notes resembling A or B type notes from other chickadee species. Thus, we sampled in total 10 calls each from 9 individuals for a total of 90 calls consisting of 490 notes.

The second set of calls was obtained from the Macaulay Library of Natural Sounds at Cornell Laboratory of Ornithology. A total of 564 calls and 2242 notes were obtained from this source, with recordings taken from a variety of regions (California, Washington, Oregon, and British Columbia) with various recording equipment (see Table 1 for details). Using the same procedure as was used for the Vancouver 2006 sample, we selected 12 individual recordings and randomly selected 10 calls from each of these such that at least 5 calls contained C or D type notes, and at least 5 calls contained A type notes for a total of 490 notes. These calls were evaluated after we had already established note types using the
Vancouver 2006 sample, to see if our results generalize to other regions and seasons. Recordings were from a broad range of years; however, for all analyses that required us to split the library into subgroups, year ranges were balanced as well as possible across subgroups (see Table II for a description of the total samples and the samples used in this study).

### B. Classification procedure

To classify the notes into note type categories, a method similar to that used in previously published papers was employed (e.g., Bloomfield et al., 2004). All 490 of the notes selected from the Vancouver 2006 sample were saved in separate sound files with a duration of 300 (non-D notes) or 500 ms (D notes) from which spectrograms were then generated using SIGNAL sound analysis software (Engineering Design, Berkeley, CA) at a window size of 512 points with a cut-off amplitude of −35 dB relative to the peak amplitude of the note. These spectrograms were then printed on glossy photo paper and arranged with 15 spectrograms per page, each accompanied with a random 4-digit number. The spectrograms were then cut out such that each note had its own small card.

In a preliminary analysis, we sorted the notes into six categories based on visual similarity. Exemplars were then identified for each of the note types by searching for notes with similar acoustic characteristics from the notes in the calls that were not selected for individual analysis. The exemplars were then printed on note cards in the same fashion as the 490 notes used for the analysis and were labeled as exemplars for each category. These exemplars, as well as a written description of each note type (the final version of which is provided in the results section), were presented to
two additional sorters (Sturdy and Moscicki) who then independently sorted the notes. Afterwards, the percent agreement was calculated between the sorters and the average agreement between two individuals was determined. The sorters then met to discuss any disagreements and refine the note type definitions.

After agreeing on and finalizing the note types of the chestnut-backed chickadee based on the Vancouver 2006 sample, this procedure was repeated with the sample obtained from the Macaulay Library to assess whether the same note types from one location and season are also found in other locations and seasons.

C. Results

In the first (i.e., preliminary) note sort, six note types were identified among the 490 notes in the sample of chestnut-backed chick-a-dee calls. However, due to less than desired percent agreement among sorters (<80%) on three of the note types, the six note types were collapsed into four. Specifically, three of the preliminary note types were collapsed into a single “A” note-type. The percent agreement among sorters after collapsing into four note types was 100%.

The same four note types were also found in the Macaulay Library sample as no notes were identified that did not clearly conform to the categories found in the Vancouver 2006 sample. However, there was slight disagreement among sorters (97% agreement) that resulted in refining the description of the Dh note, such that A notes with a noisy terminal portion would not be misclassified as Dh notes. Below are the final note descriptions that achieved consensus among the sorters. The nomenclature used for the note types observed here is similar to that used in previous studies with chick-a-dee calls. For a visual explanation, Fig. 1 shows exemplars of each note type.

1. A notes

The A note, much like A and B notes in other chickadee species, is highly tonal in nature. It increases in frequency, peaks, and then decreases in frequency, thus forming an inverted U shape, or, in some cases, an inverted V shape. The A note almost always occurs first in the call, if it occurs at all.

2. C notes

The C note of the chestnut-backed chickadee appears visually similar to the C notes of black-capped, mountain, and Carolina chickadees (Charrier et al., 2004; Bloomfield et al., 2004, 2005) in that it consists of a “stack” of frequency bands that ascend in frequency to a peak and are then occasionally observed to rapidly decrease over a very brief duration. The main ( loudest) amplitude band is frequency modulated from the beginning of the note to the peak and then occasionally decreases rapidly over a short duration. In addition, there are usually two parallel frequency bands that ascend prior to the main band (see Fig. 1). The C note typically appears in isolation from other call note types in the chestnut-backed chickadee.

3. D notes

The D note is also similar to the D notes of other chickadees in that they are composed of a stack of frequency bands that are relatively unmodulated in frequency over their duration. In the chestnut-backed chickadee, D notes have several harmonic-like bands that span a wide frequency range (approximately 2–9 kHz). The individual bands remain fairly constant in frequency, sometimes ascending slightly at the beginning and descending again at the end. D notes do not occur in every call, but when they do, they almost always appear at the end of the call.

4. D hybrid notes (Dh)

The D hybrid note resembles both the D note and A note, and could be considered a “hybrid” of the two note types, hence the name. It begins with a more tonal structure (like the A note) and ends with a harmonic-like structure (like the D note). It starts out much like the A note with an inverted U or V shape, but with a slightly longer descending than ascending frequency band. The end of the note uses the descending frequency band of the A note-like portion as the
III. STUDY 2: QUANTITATIVE NOTE ANALYSIS

After first determining and then classifying notes into types in the previous study, we made quantitative measurements of several measures of frequency and duration on each note. From the results of this analysis, it was possible to make quantitative acoustical comparisons between note types and individual birds.

A. Note measurement procedure

All measurements were completed using SIGNAL 5.10.25 software (Engineering Design, 2001–2007) according to the methods used with other chickadee species (Charrier et al., 2004; Bloomfield et al., 2004, 2005). Because all the Macaulay Library recordings were sampled at 44.1 kHz, which is also the standard sample rate used in other chickadee species, we resampled the Vancouver Island recordings from 22.05 to 44.1 kHz before conducting any measurements.

All frequency measurements were taken in a 1024-point window size spectrogram, which permitted a frequency precision of 43 Hz. We used this window to measure the start frequency (SF), PF, and end frequency (EF) of the frequency band with the highest amplitude for A, C, and the opening portion of D hybrid notes.

Duration measurements were taken in a 256-point window size spectrogram, which has a duration precision of 5.8 ms. Ascending durations (ADs) and descending durations (DDs) to and from the PF were measured in all notes with tonal portions (A, C, and Dh notes) as were the total durations (TDs) for each note type.

Based on the frequency and duration measurements for A, C, and the opening portion of D hybrid notes, we were also able to calculate ascending (FMasc) and descending (FMdes) frequency modulations. These were calculated as follows: FMasc=(PF−SF)/AD and FMdes=(PF−EF)/DD.

Finally, a spectrum was generated for each individual note with a smoothing width of 88.2 Hz, in which the loudest frequency (frequency of maximum amplitude, FMax) for all notes was measured. Additionally, the fundamental frequency ($f_0$) was measured for C, D, and D hybrid notes. See Fig. 2 for a visual explanation of each measurement.

B. Statistical analysis

All initial analyses of the two samples were conducted separately. This was because for the Vancouver 2006 sample, but not the Macauley sample, the same recordist made all of the field recordings using the same equipment. In the Macauley sample, some of the acoustic differences may have been due to different recordists and/or equipment. Thus, the Vancouver 2006 sample was ideal to set the standard for the quantification of chestnut-backed chickadee vocalizations. The Macaulay sample was examined to confirm that the results would generalize to chickadees in other regions and months of the year.

To compare the four note types separately for each sample, potential for note type coding (PNTC) (Charrier et al., 2004) was examined to see whether there was more variation of acoustic features between note types than within a note type. The PNTC is the ratio of the coefficient of variation for a particular acoustic feature, calculated between all note types (CVb) and the mean of the coefficients of variation (for the same acoustic feature) calculated within note types (CVw). The coefficient of variation between note types is calculated as $CV_b= (SD/\bar{x}) \times 100$ where SD is the standard deviation and $\bar{x}$ is the mean for an acoustic feature calculated on the total sample of call notes. The coefficient of variation within (CVw) is an average of the coefficients of variation for all the note types separately for a particular feature, calculated with the same formula. For example, the CVw for SF was calculated from the average coefficient of variation of SF for A, C, D, and Dh notes calculated separately. This allows us to look at the average variation within a note type to compare it to the total variation. If the variation for a given acoustic feature is greater between note types than within note types, then the ratio will be $>1$, and it is theoretically possible that these differences can be used by the birds to discriminate note types. Conversely, if similar amounts of variation exist between and within types, then the ratio will be $\sim 1$, indicating that the particular acoustic feature is unlikely to contribute in any meaningful way to note-type perception.

Similar to the PNTC, potential for individual coding (PIC) (Charrier et al., 2004) was examined. This allowed us to determine whether there are any acoustic features that are specific to an individual, and thus could be used by conspecifics for individual identification. We could distinguish individuals of the Vancouver 2006 sample, but not for the Macaulay Library sample, so only the Vancouver 2006 sample was used for this analysis. The PIC is calculated in the same manner as the PNTC (i.e., PIC=CVb/CVw). However, PIC values were calculated separately for each note type and feature, unlike the PNTC. CVb, therefore, instead of being calculated for each feature across all note types and individuals, was calculated for each feature separately for each note type but across all individuals. CVw is an average of the coefficients of variations within each individual, rather than note type like in PNTC. Because the sample of a single note type within an individual was small, an adjusted version of the CVw was used: $CV_w=(SD/\bar{x})(1+1/(4n)) \times 100$ where $n$ is the number of calls in each bird’s sample.

For each sample, a one-way analysis of variance (ANOVA) was also conducted using SPSS 11.5 (SPSS Inc. 1989–2002) to determine what measurements of each note type best predicted individual. A Bonferroni correction of alpha=0.005 (alpha of 0.05/10 measurements) was used to
account for the multiple measurements that could be used as predictors of individual.

Finally, we conducted linear discriminant analyses (LDAs) using Wilks’ lambda stepwise method, and multivariate analyses of variance (MANOVAs) on the Macaulay Library sample for each note type separately to determine whether within-region similarities and/or between-region differences could be observed. Three ad-hoc regions were formed and evaluated. The first region was the Vancouver Island chestnut-backed chickadees, which is an allopatric group of chickadees. No other chickadee species are present on the island (Dahlsten et al., 2002). The second region was the Northwestern United States that consisted of Washington, Oregon, and the very Northwestern tip of California. This region contains both black-capped chickadees and chestnut-backed chickadees, making it a region of sympathy for chickadees (Smith, 1993; Dahlsten et al., 2002). The final sample was chestnut-backed chickadees in other regions of California, which live in a region separate from black-capped chickadees. No calls were sampled from chestnut-backed chickadees north and east of Vancouver Island, because none were available from the Macaulay Library. Both United States regions also contain some mountain chickadees in the more mountainous regions of the states (McCallum et al., 1999). However, based on the locations that recordings were obtained (when this information was available), there was likely minimal overlap between mountain chickadees and chestnut-backed chickadees in this study since most of the recordings in each of the United States appeared to be taken by the coast rather than in the mountains. Additionally, because the Vancouver 2006 sample was larger than the entire sample received from the Macaulay Library, and since the Macaulay Library contained far less recordings from Vancouver Island than the other two regions, a subsample of calls from the Vancouver 2006 sample was chosen to boost the Vancouver Island region in the regional comparisons. Because we wanted to use samples with the largest potential amount of acoustic variation, we looked for the individuals that had the largest sample of calls from which we pseudo-randomly chose the ten calls for analysis. Four birds had ≥40 (40–73) calls and the other five had <20 (13–17) calls. We therefore included only these four birds. See Table II for a full description of the recordings used.

C. Sample specific results

PNTC values indicated that there were numerous acoustic features that the birds could potentially use to discriminate among note types. Both the Vancouver 2006 sample and the Macaulay Library sample had PNTC values >1 for TD, AD, DD, SF, EF, FMasc, and FMdes, suggesting that these measures differ for all note types in both samples. The Van-
TABLE III. PNTC values for both the Vancouver 2006 sample and the Macaulay Library sample. A value >1 indicates a potential for note type coding.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Vancouver 2006 sample</th>
<th>Macaulay Library sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>CVb</td>
<td>Mean CVw</td>
<td>PNTC</td>
</tr>
<tr>
<td>TD</td>
<td>64.5</td>
<td>55.8</td>
</tr>
<tr>
<td>AD</td>
<td>29.9</td>
<td>24.0</td>
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<tr>
<td>DD</td>
<td>64.6</td>
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</tr>
<tr>
<td>SF</td>
<td>25.6</td>
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</tr>
<tr>
<td>EF</td>
<td>21.5</td>
<td>20.1</td>
</tr>
<tr>
<td>PF</td>
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<td>8.2</td>
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<td>FMax</td>
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<tr>
<td>f0</td>
<td>17.5</td>
<td>21.0</td>
</tr>
<tr>
<td>FMasc</td>
<td>33.6</td>
<td>27.7</td>
</tr>
<tr>
<td>FMdes</td>
<td>36.5</td>
<td>29.6</td>
</tr>
</tbody>
</table>

The LDAs conducted for each note type on the three regions suggested that A notes are similar across the three regions. In spite of this, the model was able to sort them at a better than chance level. The other three note types (i.e., C, D, and Dh) form clearly distinguishable categories based on region. In agreement with these results, all MANOVAs conducted on all note types showed significant differences across regions for all note types. A notes were correctly classified by location of origin by the LDA model an average of 56.5% of the time. However, California A notes were classified correctly 68.4% of the time and Vancouver Island and Northwestern United States A notes were only classified as being Californian 14.4% and 13.2% of the time, respectively. When looking at the MANOVA to try and further evaluate the differences among groups, we found that the model returned a significant result \( F(18,942)=11.858, p<0.001 \). There were main effects for all A note measurements across regions except FMasc and FMdes \( F(2,478)=5.108, p \leq 0.006 \). To look at these further, we conducted Tukey post-hoc analyses and found that, for all significant measurements except FMax, PF, and FMdes, California was significantly different from the other two regions \( p \leq 0.001 \). That said, the two more northerly regions were not significantly different from each other. For SF only Vancouver Island and California were significantly different from each other \( (p=0.003) \), and for PF and FMasc the opposite was true: All regions except Vancouver Island and California were different from each other \( p \leq 0.035 \).

C notes were classified correctly 77.8% of the time by the LDA model. In this case, both Vancouver Island and the Northwestern United States group were classified correctly frequently (81.0% and 83.3% of the time, respectively) whereas California classified correctly 66.7% of the time. The MANOVA was significant \( F(20,140)=6.527, p<0.001 \), with main effects for all measurements except DD, FMax, and FMdes \( F(2,78)=9.147, p \leq 0.001 \). When looking at the results of Tukey post-hoc comparisons for all measurements with significant main effects, Vancouver Island was significantly different from the other two regions \( (p \leq 0.008) \) with the exception of SF, while California was significantly different from the other two regions only for SF \( (p<0.001) \).

D notes were classified correctly 74.4% of the time by the LDA model. Interestingly, Northwestern United States and Vancouver Island D notes were least likely to be misclassified as Californian (0.00% and 3.8%, respectively). In general, the LDA had the highest accuracy at classifying the Northwestern United States region, with an accuracy of 90.5%. Vancouver Island and California had 65.4% and 71.0% accuracies, respectively. This suggests that the Northwestern United States D notes were the least variable, but they were intermediate between Vancouver Island and California D notes, which are more distinct from one another. The MANOVA for D notes was again significant \( F(6,146)=15.258, p<0.001 \) and showed main effects for all measurements \( F(2,75)=8.831, p<0.001 \). Tukey post-
<table>
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<th>Note type</th>
<th>TD</th>
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<th>SF</th>
<th>EF</th>
<th>PF</th>
<th>Fmax</th>
<th>$f_o$</th>
<th>FMasc</th>
<th>FMdes</th>
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<td>23.7±5.9 ms</td>
<td>28.5±8.6 ms</td>
<td>4996.4±997.7 Hz</td>
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<td>7853.3±684.0 Hz</td>
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<tr>
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<td>1.2</td>
<td>0.5</td>
</tr>
<tr>
<td>$F$</td>
<td>5.050</td>
<td>9.818</td>
<td>1.832</td>
<td>0.436</td>
<td>2.730</td>
<td>4.372</td>
<td>3.255</td>
<td>7.681</td>
<td>4.862</td>
<td>1.626</td>
</tr>
<tr>
<td>df</td>
<td>35</td>
<td>35</td>
<td>35</td>
<td>35</td>
<td>35</td>
<td>35</td>
<td>35</td>
<td>35</td>
<td>35</td>
<td>35</td>
</tr>
<tr>
<td>D</td>
<td>Mean±SD</td>
<td>175.5±21.9 ms</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>CVb</td>
<td>12.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>5731.4±375.2 Hz</td>
<td>2648.8±507.0 Hz</td>
</tr>
<tr>
<td>Mean CVw</td>
<td>8.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6.5</td>
<td>19.1</td>
</tr>
<tr>
<td>PIC</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.0</td>
<td>8.7</td>
</tr>
<tr>
<td>$F$</td>
<td>9.373</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>24.960</td>
<td>8.650</td>
</tr>
<tr>
<td>df</td>
<td>63</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>63</td>
<td>63</td>
</tr>
<tr>
<td>Dh</td>
<td>Mean±SD</td>
<td>149.0±20.0 ms</td>
<td>25.5±4.4 ms</td>
<td>107.6±21.6 ms</td>
<td>3682.0±767.7 Hz</td>
<td>2303.6±299.6 Hz</td>
<td>6432.5±579.5 Hz</td>
<td>5999.6±294.9 Hz</td>
<td>2529.8±210.0 Hz</td>
<td>110.6±39.3 Hz</td>
</tr>
<tr>
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<td>17.4</td>
<td>20.1</td>
<td>20.9</td>
<td>13.0</td>
<td>9.0</td>
<td>4.9</td>
<td>8.3</td>
<td>35.5</td>
<td>25.4</td>
</tr>
<tr>
<td>Mean CVw</td>
<td>9.3</td>
<td>13.7</td>
<td>17.2</td>
<td>19.5</td>
<td>12.9</td>
<td>4.4</td>
<td>5.4</td>
<td>8.0</td>
<td>24.2</td>
<td>14.3</td>
</tr>
<tr>
<td>PIC</td>
<td>1.4</td>
<td>1.3</td>
<td>1.2</td>
<td>1.1</td>
<td>1.0</td>
<td>2.1</td>
<td>0.9</td>
<td>1.0</td>
<td>1.5</td>
<td>1.8</td>
</tr>
<tr>
<td>$F$</td>
<td>4.141</td>
<td>0.918</td>
<td>0.781</td>
<td>1.824</td>
<td>0.503</td>
<td>22.440</td>
<td>0.654</td>
<td>3.488</td>
<td>2.299</td>
<td>7.115</td>
</tr>
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<td>18</td>
<td>18</td>
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<td>18</td>
<td>18</td>
<td>18</td>
<td>18</td>
<td>18</td>
</tr>
</tbody>
</table>

*Significant with $p < 0.005$.
hoc comparisons revealed that for TD, Vancouver Island was significantly different from the other two regions \((p < 0.001)\). For FMax and \(f_o\), California was significantly different from the other two regions \((p \leq 0.002)\).

The LDA model classified Dh notes by region correctly 63.8\% of the time. The model was high for California (83.3\%) and did less well with Vancouver Island (64.3\%) and even less with the Northwestern United States region (52.4\%). There were no misclassifications of Vancouver Island as California, or California as the Northwestern United States. Only the Northwestern United States was misclassified as both other regions, suggesting that these notes were intermediate between the other two. Because, in this case, the Northwestern United States was more likely to be misclassified than both the other two regions together, it appears that this region was the most variable. The MANOVA looking at the differences in measurements across regions was, again, significant \([F(20, 72) = 3.958, p < 0.001]\). However, only AD, SF, PF, and FMax showed significant main effects \([F(2, 44) = 3.880, p \leq 0.028]\). When examining the post-hoc tests with these variables, Vancouver Island and Northwestern United States differed on AD \((p = 0.027)\), California differed from the other two for SF and PF \((p \leq 0.039)\), and Vancouver Island differed from the other two for FMax \((p \leq 0.035)\).

In summary, for the majority of the measurements for the notes, Vancouver Island and California were the most different with the Northwestern United States falling somewhere in between, suggesting that the acoustic differences may be correlated with geographic distance between the populations.

**IV. STUDY 3: SYNTACTICAL ANALYSIS**

After distinguishing note types and analyzing their features, the next step was to examine their ordering, or syntax, within the call. The subsamples in our studies were pseudorandomly selected; that is, we purposefully selected calls that contained a variety of note types. Because of this, and because we wanted as large a sample as possible to determine call syntax trends, we analyzed every usable call (i.e., high quality, low noise with discernable note types) in both samples. This not only gave us descriptive information of the call, but also allowed us to evaluate how our large Vancouver 2006 sample compared to a more general sample, and whether there are any differences in syntax types and rules present. If there are differences between the samples, this would suggest that regional or seasonal differences could also play a role in syntax.

**A. Call note ordering procedure**

Whole calls were printed with 4 spectrograms per page on 8.5\times 11 pages of paper in a binder of calls. Sorters recorded the note type ordering observed within each call. All three sorters were blind to the classifications from the other sorters, and were the same sorters from study 1. The sorts were then compared, and any disagreements discussed together in a group until the group came to a general consensus to determine the final agreed syntax.

From the data obtained from the full call sets, all syntactical arrangements were analyzed and the total number of times a call was produced was examined. Additionally, we looked at probabilities within the samples of note type order and placement in order to evaluate whether there are standard syntactical rules followed in both samples. First we looked at the probability of notes occurring given the previous note type. For example, what is the probability that the next note is a C note given that the previous note is an A note? These probabilities were calculated by summing up the total number of all occurrences (e.g., total occurrences of A followed by C notes) and finding the proportion of each occurrence given the preceding note (e.g., total number of A followed by C occurrences/total transitions from A notes).

We then looked at the probabilities of note type placement within individual calls. For example, what is the probability that the first note in a call will be an A note? Or, vice versa: What is the probability that an A note will be the first note in a call? These were calculated in the same way as the order probabilities, e.g., the total number of A notes that are the first note in the call/the total number of notes that are first in the call. An example for the opposite calculation would be the total number of A notes that were the first note in the call/the total number of A notes. Comparable studies have been conducted in both black-capped chickadees (Hailman et al., 1987) and Mexican chickadees (Ficken et al., 1994) that found both species have fixed syntactical rules used to generate calls based on Markov chain analyses.

Finally, Pearson correlations were conducted to compare the proportions of each syntax type between the Vancouver 2006 sample and the Macaulay Library sample to see whether there are any syntactical differences between a specific and more general sample. Similar correlations were conducted on the probabilities of each note type followed by each other note type, as well as the probabilities of the placement for each note type within the call.

**B. Results**

The percent agreement in classifying note types was extremely high (99.6\%). Sixty-eight specific syntax patterns were found in the two samples together, suggesting that there is a wide range of patterns the birds can use in communicating. However, 55.6\% of all chick-a-dee calls contain just A notes, and another 22.7\% contained just A notes that terminate in either a single D note or a single Dh note. Overall, 88.7\% of all calls in our sample begin with A notes and most of the remaining calls contain either just C notes (5.4\%) or just D notes (4.8\%). Only 1.1\% of the calls (17/1532) have any other syntax not described above. The chestnut-backed chickadee does, therefore, appear to have a more primitive syntactical structure to its call than any of the black-headed chickadee species (Bloomfield et al., 2004, 2005; Charrier et al., 2004), although there is still room for variation within these parameters.

The frequency of each syntactic sequence was significantly correlated between the two samples, but the correlation was not high \((r = 0.534, p < 0.001)\). When looking again at the data, it is apparent that the Vancouver 2006...
sample is dominated by certain vocalizations, whereas the Macaulay sample seems to have more variation, which makes sense considering that the Macaulay sample is more varied in terms of location and season. In fact, 34.3% of the calls in the Vancouver 2006 sample have identical syntax (six A notes) whereas the most common call in the Macaulay sample (four A notes) only makes up 11.7% of the total calls. See Table V for detailed information on the call types and their proportions in the different samples.

However, when looking at what proportion of the time a note, e.g., an A note, is followed by every other note, the two samples are extremely similar ($r=0.949$, $p < 0.001$). This suggests that the difference between syntax types is not due to different syntactical rules about which note should follow which other note. Overall, A notes are most commonly followed by more A notes, C notes are most commonly followed by more C notes, while D and Dh notes are most commonly the last notes within the call. See Table VI for more information on the proportions of the note types following each note type.

V. DISCUSSION

This paper provides the first detailed acoustic description of the note types of the chick-a-dee call of the chestnut-backed chickadee. This species is the first member of the brown-headed chickadee clade to have its chick-a-dee calls studied in such depth, which opens up new opportunities for comparative study. We looked at both a specific and broad sample of calls in terms of location and time of year, making our study the most comprehensive yet.

We found that the chestnut-backed chick-a-dee call was composed of 4 distinct note types (A, C, D, and Dh) that were arranged in 68 syntactical call types in our sample of 1532 calls with 7628 notes. Based on the 68 call types, we described syntactical rules based on the probabilities of note types being followed by all the other note types, and on the probabilities of the different placements within the call. For all note types there were several acoustical features that could be used by listening birds to differentiate between note types, as well as the individual producing the note. We also found regional differences in the structure of all note types suggesting that, although all regions use the same note types, the way they are produced varies from region to region.

A. Individual discrimination

Based on the PIC results of the Vancouver 2006 sample, there appear to be many potential mechanisms for birds to be able to differentiate between individuals. This information provides us with numerous possible hypotheses on how chickadees could discriminate between individuals. As one example, a listener might distinguish between individuals by attending to the fundamental frequency of D notes, and this possibility could be tested using operant conditioning paradigms (Sturdy et al., 2000). However, because we recorded unbanded birds, it was only possible to record each bird used for analysis once, and it is possible that the current motivational and contextual states of the birds may have contributed to the differences we found among individuals. We believe...
that this is most likely not the case, as other chickadee species that were recorded on multiple occasions in the laboratory also showed similar PIC values (Bloomfield et al., 2004; Charrier et al., 2004).

B. Note discrimination and syntax

The PNTC results suggest that all note types found in our study can be distinguished using several features. The Vancouver 2006 sample shows that many features measured on the notes can be used to tell note types apart. Fewer features can be used across populations as shown through the PNTC values for the Macaulay sample, possibly because of variations between regions. However, there are two features, namely, TD and FMDes, which stand out in the Macaulay Library sample with extremely high PNTC values, which suggests that these two features are especially important in differentiating note types across all regions.

We found numerous syntactical arrangements of the chestnut-backed chick-a-dee call, which might also be used in different contexts, as in other chickadee species. For example, black-capped chickadees produce more D notes when a model of a more threatening species of predator is presented (Templeton et al., 2005), and Carolina chickadee respond to calls rich in C notes at feeders (Freeberg and Lucas, 2002). By determining what features of the notes the bird could potentially use to discriminate between note types, potential mechanisms for processing meaning of call syntax have also been described. This has been shown with both black-capped and mountain chickadees, which are able to discriminate each other's vocalizations into categories (Bloomfield and Sturdy, 2008) and the mechanisms for which are currently being explored in our laboratory.

In addition to this, our findings from study 3 on the syntax of the calls suggest that once a note type has been generated in a call, the probability for the next note type is the same across samples. Thus, the differences in frequencies of specific call syntax between the Vancouver 2006 sample and the Macaulay Library sample seem not to be due to different syntactical rules; instead they may be due either to sampling error, or to different contexts, which could be seasonal contexts such as food availability. This is interesting because even though the chestnut-backed chickadee appears to use its call for the same functions that song usually serves (Dahlsten et al., 2002), and components of songs that are present often vary across regions (e.g., Slabbekoorn et al., 2003), the birds appear capable of producing the same call set in all regions. This finding is not trivial and was not necessarily to be expected from the outset; gargle calls in chickadees have been shown to vary significantly across regions, with more syllable sharing within than between regions (Baker et al., 2000).

C. Regional differences

The LDAs conducted for each note type on the three regions suggested that all note types except A notes were easily differentiated across regions, and A notes were also distinguished based on region at a greater than chance level. In addition, the MANOVAs showed that all notes were significantly different across regions. Thus it is possible that these differences were indicative of different dialects in different regions that chestnut-backed chickadees inhabit, in line with other research on geographic variation in avian vocalizations. C, D, and Dh notes were the most different between the Vancouver Island and California samples, suggesting a geographic correlation, such that, as geographic distance increases, so do differences in call note production. However, the reasons for these differences are not yet clear. Thorough comparative investigations of sympatrically living species could help us determine whether these differences are due to acoustic character displacement (Brown and Wilson, 1975). Alternatively, by evaluating whether the different regions consist of different major habitat types, we could evaluate whether differences in vocalizations are due to acoustic adaptation (Morton, 1975). Finally, regional differences might reflect genetics differences (Burg, 2007). Given our sample, it was not possible to address other potential vocal differences due to season or time, or look at the regions in more depth, but this is something that could be looked at with a more controlled sample in the future.

<table>
<thead>
<tr>
<th>Syntax pattern</th>
<th>Grand total</th>
<th>Vancouver Island (%)</th>
<th>Macaulay (%)</th>
</tr>
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<tbody>
<tr>
<td>CCCCCC</td>
<td>7</td>
<td>0.6</td>
<td>0.2</td>
</tr>
<tr>
<td>CCCCCCC</td>
<td>1</td>
<td>0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>DADh</td>
<td>1</td>
<td>0.0</td>
<td>0.2</td>
</tr>
<tr>
<td>DD</td>
<td>64</td>
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<td>11.5</td>
</tr>
<tr>
<td>DDAAAA</td>
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</tr>
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<td>DDDD</td>
<td>3</td>
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<td>0.5</td>
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<tr>
<td>DDDDD</td>
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</tr>
<tr>
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TABLE V. (Continued.)

<table>
<thead>
<tr>
<th>Probability of next note (%)</th>
<th>A</th>
<th>C</th>
<th>D</th>
<th>Dh</th>
<th>Call end</th>
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<td>Preceding note</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>78.90</td>
<td>0.59</td>
<td>3.70</td>
<td>3.50</td>
<td>13.31</td>
</tr>
<tr>
<td>C</td>
<td>2.39</td>
<td>68.90</td>
<td>0.72</td>
<td>0.00</td>
<td>27.99</td>
</tr>
<tr>
<td>D</td>
<td>0.37</td>
<td>0.00</td>
<td>24.86</td>
<td>0.37</td>
<td>74.39</td>
</tr>
<tr>
<td>Dh</td>
<td>0.00</td>
<td>0.00</td>
<td>33.19</td>
<td>0.00</td>
<td>66.81</td>
</tr>
</tbody>
</table>

TABLE VI. Probability of the next note type given the preceding note. These probabilities are based on the entire sample.
VI. Conclusions

Overall, our results can be used as a starting point for further investigations of the chick-a-dee call. In addition, the chestnut-backed chickadee is an especially important addition to current knowledge on chickadee vocalizations because it will allow us to conduct comparative evolutionary studies between black-headed and brown-headed chickadees, which were not possible before.

ACKNOWLEDGMENTS

This research was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant, an Alberta Ingenuity New Faculty grant, Canada Foundation for Innovation (CFI) New Opportunities and Infrastructure Operating Fund grants, and start-up and CFI partner funding from the University of Alberta to C.B.S. M.H. was supported by the Queen Elizabeth II master’s scholarship (QEII) scholarship (University of Alberta). D.E.G. was supported by a Faculty Development grant from St. Edwards University in Austin, Texas. M.K.M. was supported by NSERC post-graduate scholarship (PGS) and Alberta Ingenuity Fund scholarship.


