

Variation in chick-a-dee calls of tufted titmice, *Baeolophus bicolor*: Note type and individual distinctiveness

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The chick-a-dee call of chickadee species (genus *Poecile*) has been the focus of much research. A great deal is known about the structural complexity and the meaning of variation in notes making up calls in these species. However, little is known about the likely homologous “chick-a-dee” call of the closely related tufted titmouse, *Baeolophus bicolor*. Tufted titmice are a prime candidate for comparative analyses of the call, because their vocal and social systems share many characteristics with those of chickadees. To address the paucity of data on the structure of chick-a-dee calls of tufted titmice, we recorded birds in field and aviary settings. Four main note types were identified in the call: **Z**, **A**, **D_h**, and **D** notes. Several acoustic parameters of each note type were measured, and statistical analyses revealed that the note types are acoustically distinct from one another. Furthermore, note types vary in the extent of individual distinctiveness reflected in their acoustic parameters. This first step towards understanding the chick-a-dee call of tufted titmice indicates that the call is comparable in structure and complexity to the calls of chickadees. © 2007 Acoustical Society of America. [DOI: 10.1121/1.2749459]

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I. INTRODUCTION

The “chick-a-dee” call of the genus *Poecile*, the North American chickadees, is a structurally complex vocal signal. Calls are composed of distinct note types, and note composition is guided by rules of note ordering (Hailman *et al.*, 1985). By using these rules of note ordering an extremely large number of distinct calls can be produced by varying the number of note types within a call. A great deal has been discovered about variation in note composition and acoustic structure and how these relate to possible messages and meanings of chick-a-dee calls (Hailman, 1989; Hailman and Ficken, 1996; Lucas and Freeberg, 2007; Sturdy *et al.*, 2007; Templeton *et al.*, 2005). For example, variation in acoustic structure of notes or in note composition in chick-a-dee calls, or both, may potentially encode information about individuals (Bloomfield *et al.*, 2004, 2005; Charrier *et al.*, 2004), flock membership (Mammen and Nowicki, 1981; Nowicki, 1983), local population membership (Freeberg *et al.*, 2003), energetic status of the signaler (Lucas *et al.*, 1999), food detection and flight behavior of the signaler (Freeberg and Lucas, 2002; Smith, 1972), detection of predator by, and distance of predator to, the signaler (Baker and Becker, 2002; Ficken *et al.*, 1994), and level of threat related to predator size (Templeton *et al.*, 2005).

These efforts at understanding the chick-a-dee call have been directed towards chickadee species (and some *Parus* tit species, e.g., willow tit, *P. montanus*, Haftorn, 1993, 2000; black-lored tit, *P. xanthogenys*, Hailman, 1994). As described in Hailman and Ficken (1996) and Freeberg *et al.* (2007), however, very little is known about the likely homologous chick-a-dee call of the closely related titmice (genus *Baeolo-*

phus). The aim of this study is to begin to understand the structure of the chick-a-dee call of tufted titmice, *B. bicolor*, and to assess some of the potential information that may reside in the notes of the signal.

Recent work by Bloomfield and Sturdy and colleagues (mountain chickadees, *Poecile gambeli*, Bloomfield *et al.*, 2004; Carolina chickadees, *P. carolinensis*, Bloomfield *et al.*, 2005; black-capped chickadees, *P. atricapillus*, Charrier *et al.*, 2004), has used a consistent approach to analyzing call structure across these different species. This approach involves assessing multiple acoustic parameters of the different note types that construct calls, to determine the potential for those acoustic characteristics to be used by the birds in note type and individual perceptual discriminations. Another study of Carolina chickadees found relationships between acoustic structure of notes in a call and the local population of the signaler, as well as the note composition of the rest of the call (Freeberg *et al.*, 2003). In the present study, we have taken approaches used by these earlier studies to assess call and note variation in tufted titmice. We aimed to address the paucity of data on the chick-a-dee call of tufted titmice by classifying their note types into natural categories using acoustic features, by determining which spectral and temporal features of each note type may be used in note type and individual discrimination, and by beginning to describe the effects of note composition of calls and sex of signaler on note structure. The current study is our first step to a more comprehensive analysis of structural and functional variation of this call system in titmouse species.

II. METHODS

A. Subjects

Chick-a-dee calls used in the current study were recorded from 16 individually color-banded tufted titmice that

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served as subjects in two separate aviary studies or were part of naturalistic field studies from December of 2005 through April of 2006. For aviary studies, 14 titmice were housed in social groups with other titmice and some also with Carolina chickadees. All birds in the aviaries could see and hear wild birds in the wooded areas around the aviaries. High quality vocalizations were also recorded from two color banded free-range birds. One aviary individual, after being released from the aviary study, was recorded at the field site mentioned above. One call from this bird's field recordings is included in this analysis.

We captured birds recorded in the aviaries at several different sites at the University of Tennessee Forest Resources, Research, and Education Center (UTFRREC), Ijams Nature Center, and a residential site, all within Knox and Anderson counties, TN. After capture with potter (treadle) traps set on platform feeding stations or with mist nets set near the feeding stations, all titmice were individually color marked with unique color combination leg rings and then placed in one of three-outdoor aviaries ($6 \times 9 \times 3.5$ m) located at UTFRREC. Although ages of birds were not known, no birds used in this study produced the highly variable and plastic vocal signals characteristic of young birds first learning their vocalizations. We measured wing chord length of birds as a criterion for estimating sex. We were able to classify sex of most of the tufted titmice in our sample based upon wing chord measurements—we categorized birds with wing chords of ≤ 77 mm as females and birds with wing chords of ≥ 80 mm as males, with birds falling between 77 and 80 mm being classified as unknown (based upon Thirakthupt, 1985). In our set of 16 birds, six were classified as males, five as females, and six as unknown (five of the unknown birds had wing chord measures that fell in the range of overlap between females and males, and one was never measured). This wing chord criterion for sexing birds was supported with capture data of 11 titmice (none were subjects in this study) in May of 2007. At this time of year, titmice are nesting and incubating young (Grubb and Pravosudov, 1994), with females exhibiting complete brood patches and males exhibiting fairly swollen cloacal protuberances with minimal brood patch presence (Pyle, 1997). Using brood patches and cloacal protuberances as our means of sexing these 11 birds, we found that two of three females had wing chords ≤ 77 mm (with the third female having a wing chord of 78.5 mm, which would have resulted in her being classified as “unknown” in our study), and eight of eight males had wing chords ≥ 80 mm.

In the aviaries, diet was composed of *ad libitum* black-oil sunflower seed and safflower seed, mixed songbird seed, suet, and crushed oyster shell. In addition, birds were provided with Bronx Zoo diet for omnivorous birds, chopped fresh vegetables or fruit, and fresh vitamin treated water each day. We also added to the aviary feeding bowls roughly 2–3 mealworms per bird each day. We acclimated the titmice to human presence for at least the first two weeks they were in captivity. During the acclimation period JO or TF or both would enter the aviary and sit where they would during a recording session and/or walk around the aviary. Recording began after this acclimation period. After recording was

completed birds were recaptured in the aviaries using potter traps and transported back to their sites of capture and released.

B. Recording of chick-a-dee calls

We recorded chick-a-dee calls using Sennheiser ME-64 and ME-66 microphones and either Fostex FR-2 digital field memory recorders (with a sampling rate of 22 050 and a 16 bit resolution) or a Marantz-PMD 22 portable cassette recorder on Maxell-XLII tape. In the aviaries the microphone was mounted on a stand approximately 3 m off the ground and angled toward nearby perches. The observer sat as motionless as possible at a far end of the aviary and documented the identity of the bird after it called directly on the sound file. For field recordings the microphone was set up roughly 1 m from the platform feeding station and was aimed up at the feeding station. The feeding stations were stocked with a 1:1 ratio of black-oil sunflower seed and safflower seed to attract birds. The observer sat as motionless as possible roughly 10 m away and partially concealed by vegetation.

C. Call selection and note categorization

Chick-a-dee calls included in this analysis were chosen based first on recording quality: we chose calls that were produced within 45° of the axis of the microphone and within 3 m of the microphone (as stated by the observer on the recording file), and that had minimal wind and background noise. Once we had compiled a group of high quality calls from a bird, we semirandomly picked ten calls from the bird to go into subsequent analyses. Before random picking of calls, we first attempted to increase the diversity of note types included in the call sample for each individual. If a note type was rare for a particular individual, we specifically chose 1 or 2 calls that included that note type from its set of calls. After we had selected 1 or 2 calls for the rare note type of an individual, we used a random number generator to pick the remaining calls needed to reach ten calls per bird. Calls with only one note were omitted from the current study; for our purposes here, a call is defined as having two or more notes.

To classify call notes JO scored all 508 notes from 160 calls and assigned each to either a **Z**, **A**, **D_h** or **D** note-type category (described below; Fig. 1). These categories are similar to those used in the chick-a-dee call descriptions of chickadees. TF independently scored notes for all 160 calls, and agreement was high (Cohen's Kappas for inter-rater reliability on note classifications: **Z**=0.94, **A**=0.95, **D_h**=1.00, **D**=1.00; JO's note classifications were used for analyses). **Z** and **A** are whistled note types that begin at a high frequency and differ in duration and extent of frequency change. **A** notes are shorter in duration than **Z** notes and frequently have a pronounced drop in ending frequency, whereas **Z** notes are longer and do not typically drop below 4 kHz. **D** notes are harsh sounding note types that appear as stacked harmonics in spectrogram form (similar to the **D** note types in several chickadee species). **D_h** notes are a hybrid category. These notes begin at an upper frequency similar to an **A**.

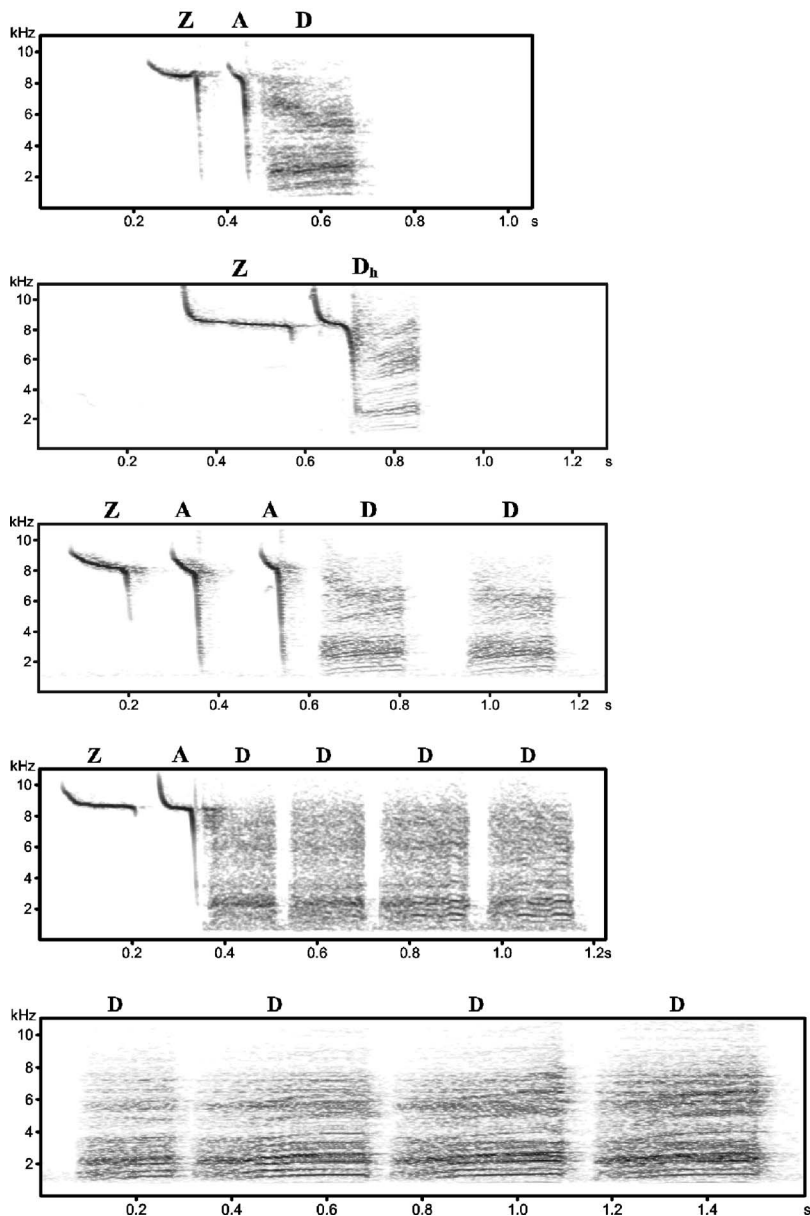


FIG. 1. Sound spectrograms of examples of chick-a-dee calls from tufted titmice. *Y* axis=frequency (kHz); *X* axis=time (s). Spectrograms were generated in Avisoft SASLab Pro, with a FFT length of 512, frame 75%, and Blackman window. Note type classifications (*Z*, *A*, *D_h*, and *D*) for each note are indicated above the note in each spectrogram.

However, the ending frequency drop does not terminate, but levels off and is joined by the harmonic-like structure of a *D* note.

D. Analyses of the chick-a-dee calls

Calls recorded with the Marantz PMD-22 cassette recorder were digitized using Cool Edit Pro (version 2) run on a Windows XP platform, with a sampling rate of 22 050 at 16 bit resolution. Once all recording files were digitized or uploaded to the computer, Cool Edit Pro (version 2) was used to assess the large (5–15 min) sound files for high quality calls. All calls were viewed in the Blackman-Harris window with a resolution of 256 bands. Individual calls were separated in Cool Edit and acoustical analyses were completed using SASLab Pro sound analysis and synthesis laboratory software (version 4.2; Avisoft, hereafter, SASLab). All of our parameter measurements of notes of calls were made in a 512 pt fast Fourier transform (FFT) Blackman spectrogram window using the automatic parameter settings feature

within SASLab. We used a volume range of 25–45% in the Normalize window of the “Change Volume” menu in SASLab. We used this volume range to adjust the volume of individual files to make note types of calls recorded at different distances and orientations from the microphone comparable to one another for automatic parameter measurements by SASLab. To decrease low frequency background noise in the sound files we applied a high pass Butterworth filter set at 0.8 kHz, and occasionally at 1.0 kHz, depending on the nature of background noise in the individual call file. Within the automatic parameter settings we selected for automatic two threshold measurements, and therefore could manually change the “threshold” and the “start/end threshold” options. To ensure that all note types within a call were individually measured by SASLab, we used a threshold range of –34 to –40 dB, and a start/end threshold range of –10 to –20 dB, depending on the specific quality of each call. We used the same 17 automatic parameter measures for each note type. The automatic parameter measures included

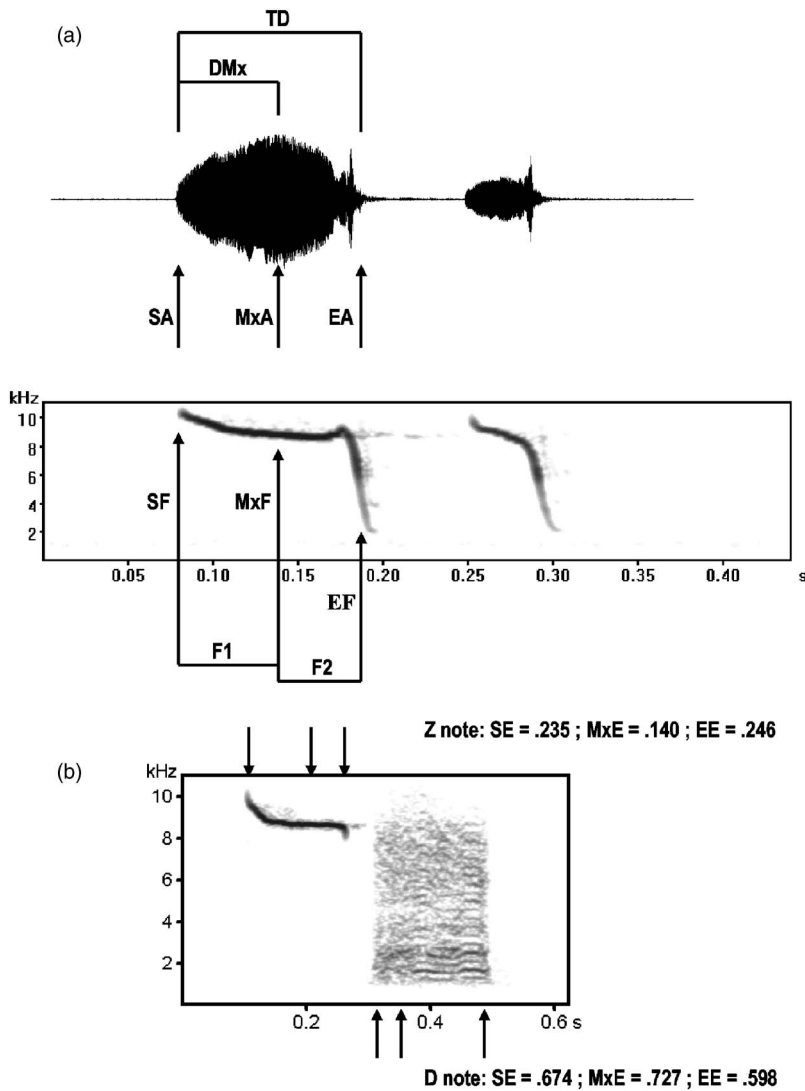


FIG. 2. Illustration of some of the parameters measured in notes of chick-a-dee calls in this study, (a) Wave form and sound spectrogram of a **ZA** call, illustrating the temporal and some of the amplitude and frequency measures. (b) Sound spectrogram of a **ZD** call, illustrating some of the entropy measures. TD=total note duration; DMx=distance to maximum amplitude; SA =amplitude at start of note; MxA=amplitude at point of maximum amplitude; EA=amplitude at end of note; SF=frequency at start of note; MxF=frequency at point of maximum amplitude; EF=frequency at end of note; F1=frequency difference between SF and MxF; F2=frequency difference between MxF and EF; SE =entropy at start of note; MxE=entropy at point of maximum amplitude; EE=entropy at end of note. Not illustrated are the mean measures of frequency, amplitude, and entropy for the entire note, and RMS of the entire note.

two temporal, six frequency, five amplitude, and four entropy parameters (Fig. 2; several of our measures are adapted from those described in Bloomfield *et al.*, 2004, 2005; Charrier *et al.*, 2004; Freeberg *et al.*, 2003).

1. Temporal parameters

We assessed two different temporal parameters: *total note duration* (TD) which measures the duration (s) of each note from start to end, and *distance to max* (DMx) which measures the duration (s) from the start of a note to the point of maximum amplitude in the note.

2. Frequency parameters

We assessed six frequency-based parameters: *start frequency* (SF), *end frequency* (EF), *max frequency* (MxF), *mean frequency* (MnF), *frequency change 1* (F1), and *frequency change 2* (F2), each measured in Hz. SF is a measure of the frequency at the start of the note, and EF is the same measure at the end of the note, based upon the threshold settings described above. MxF is the frequency in the note at the point with maximum amplitude. MnF is a parameter derived from the averaged spectrum of the entire note. F1 measures change in frequency from SF to MxF (calculated as

SF–MxF), and F2 measures change in frequency from MxF to EF (calculated as MxF–EF).

3. Amplitude parameters

The five amplitude parameters are *start amplitude* (SA), *end amplitude* (EA), *max amplitude* (MxA), *mean amplitude* (MnA), each measured in dB, and *root mean square* (RMS), measured in 1 V units. SA is a measure of the amplitude at the start of the note, and EA is the same measure at the end of the note, based upon the threshold settings described above. MxA measures the maximum amplitude of the note. MnA is a derived parameter that averages the amplitude across the spectrum of the entire note; rms is a wave form parameter derived from the entire note.

4. Entropy parameters

Entropy measures provide an assessment of structural disorder or “noisiness” within a note. For example, a relatively pure tone note would have entropy fairly close to 0, whereas a harsh, noisy note or syllable spanning a wide range of frequencies would have an entropy closer to 1 [see Fig. 2(b) for typical entropy differences seen in comparisons of **Z** notes and **D** notes]. We measured *start entropy* (SE), the

entropy at the beginning of the note, *end entropy* (EE), the entropy at the end of the note, based upon the threshold settings described above. *Max entropy* (MxE) is the entropy at the point in the note of maximum amplitude, and *mean entropy* (MnE) is the entropy averaged across the entire note.

E. Statistical analyses

The basic goal of our study was to describe the structure of note types of the chick-a-dee call of the tufted titmouse. Our high inter-rater agreement in categorizing note types into *Z*, *A*, *D_h* and *D* notes (discussed above), suggested these note categories may be natural categories. We next aimed to determine which acoustic features of each note type may be useful in note type and individual discrimination, and to begin to describe the effects of a call's note composition on these acoustic features. We first sought to establish which acoustic features of these note types would have the potential to allow receivers to discriminate note types, and possibly individuals, from one another. As a converging measure of this approach, and since many of our measured parameters were likely highly correlated with one another, we reduced the 17 parameters using factor analysis, and then used the factors that emerged to test for effects of note type, individual, and sex and note composition of call on factor scores.

1. Potential for note-type coding (PNTC): Can acoustic features help discriminate between note types?

We determined which spectral and temporal features of notes of the chick-a-dee call may be used to discriminate between note types by examining the potential for note type coding (PNTC, Bloomfield *et al.*, 2004, 2005; Charrier *et al.*, 2004). PNTC is a variance measure. Specifically, it is the ratio of the coefficient of variation (Sokal and Rohlf, 1995) between note types (CV_b) and the mean of the coefficients of variation within note types (CV_w). This measure indicates which spectral and temporal features are less variable within note types than between note types, and therefore which of these parameters can potentially be used in note type discrimination. A parameter with a PNTC value greater than 1 (i.e., $CV_b > CV_w$) means it may be useful in note-type discrimination (Bloomfield *et al.*, 2004, 2005; Charrier *et al.*, 2004). If a PNTC value for an acoustic parameter is greater than two, it is considered to be a parameter that may be highly useful in note-type discrimination (Robisson *et al.*, 1993). We used the small samples formula to determine PNTC:

$$PNTC = (CV_b * 100) / [CV_w * 100 * (1 + 1/4n)].$$

CV_b is the SD for the acoustic parameter across all the note types, divided by the mean for that acoustic parameter across all note types. CV_w , calculated for each note type, is the SD for the acoustic parameter of the note type, divided by the mean for that acoustic parameter for that note type. The $(1 + 1/4n)$ at the end of the equation is the correction for small samples (e.g., Sokal and Rohlf, 1995). The “*n*” denotes the number of cases analyzed for each note type. The PNTC analysis was applied to all 508 notes.

2. Potential for individual coding (PIC): Can acoustic features help discriminate between individuals?

We tested whether note-type acoustic characteristics may be useful in individual discrimination (PIC, Bloomfield *et al.*, 2004, 2005; Charrier *et al.*, 2001, 2002, 2004). For individual discrimination to be possible, acoustic parameters must have lower intra-individual variation than inter-individual variation. This means that for an individual titmouse to be distinguishable via one of its note types, it would have to produce reliably distinctive features in that note type that are less variable within its repertoire than in the total set of that note type produced in calls of members of the entire group of birds. To test for this possibility we examined, for each note type, which of the 17 parameters were less variable within an individual than across individuals, to determine which parameters could potentially be useful for each note type in discriminating across individuals. For each note type separately, we examined the PIC using the small samples formula as described above:

$$PIC = (CV_b * 100) / [CV_w * 100 * (1 + 1/4n)].$$

CV_b is the SD for the acoustic parameter across all the individuals, divided by the mean for that acoustic parameter across all individuals. CV_w , calculated for each individual, is the SD for the acoustic parameter, divided by the mean for that acoustic parameter. The $(1 + 1/4n)$ at the end of the equation is the correction for small samples. The “*n*” denotes the number of cases analyzed for each individual. For a parameter to be useful in individual discrimination the PIC value must be greater than 1, which would indicate that the parameter's variation among individuals is greater than variation within an individual bird (Bloomfield *et al.*, 2004, 2005; Charrier *et al.*, 2004). A PIC value greater than 2 is considered to be highly useful at permitting individual discrimination (Robisson *et al.*, 1993). The PIC analysis was run on all individuals by note type. *Z* and *A* note types were produced by all 16 individuals within the sample. The *D_h* note type was only produced by three individuals. The *D* note type was produced by all birds, but one was excluded from the PIC analysis because it produced only one *D* note.

3. Factor analysis: Are note types and individuals distinct?

As a converging measure of note type and individual distinctiveness in the chick-a-dee call of titmice, we reduced the 17 parameters using factor analysis (SPSS, Statistical Package for the Social Sciences, version 13.0). We used the principal components method with a varimax rotation. Factor scores for each note of each call of each bird were then used in analyses of variance (ANOVAs) to evaluate the effects of note type and individual. When significant effects of note type or individual were found for a particular factor, post hoc tests with corrections for multiple comparisons were used to test for significant contrasts between note types or between individuals. If error variance was equal across groups we used Tukey's Honestly Significant Difference (HSD) post hoc test. If error variance was not equal across groups we used Dunnett's *C* post hoc test.

TABLE I. Prevalence of note types in our sample of chick-a-dee calls of tufted titmice.

| Unit | Mean No. \pm SD | Maximum No. | Percent of calls with ≥ 1 of note type |
|-------------|-------------------|-------------|---|
| Total notes | 3.17 \pm 1.63 | 18 | |
| Z | 0.92 \pm 0.55 | 2 | 80.6 |
| A | 0.81 \pm 0.60 | 2 | 71.3 |
| D_h | 0.10 \pm 0.30 | 1 | 10.0 |
| D | 1.34 \pm 2.02 | 18 | 64.4 |

4. Effect of note composition and signaler sex on a note's factor scores

To examine the possible effects of note composition or sex of signaler we conducted two tests. Only Factor 1 and Factor 2 scores (see below) were analyzed in this analysis since these two factors account for most of the variation. First, for Z, A, and D note types separately, we tested whether the factor scores for the first note to occur in a call was different if it were the only note, compared to if it were followed by at least one more of the note type in a string in the call, as in Freeberg *et al.* (2003) for Carolina chickadees. This addressed, for example, whether a Z note followed by non-Z notes in the call was acoustically different from a Z note followed by one or more Z notes (and possibly other note types) in the call. Our second test of an effect of note composition on the first Z, A, and D note types to occur in calls addressed whether the overall number of notes in a call affected factor scores for those notes. Note numbers were grouped into three classes: two note calls, three note calls, four+ note calls. The D_h note type was excluded from note composition analysis because of small sample size and the fact that it was never repeated within a call in this sample. We also tested for an effect of sex on Z, A, and D note types, and excluded the D_h note because of the small sample size for that note type.

III. RESULTS

We analyzed a total of 508 notes from 160 calls (ten calls per bird). Our final call sample had 145 Z, 132 A, 16 D_h , and 215 D note types. The average tufted titmouse call in our sample had 3.2 notes, and averaged 0.9 Z, notes, 0.8 A notes, 0.1 D_h notes, and 1.3 D notes (Table I). Calls containing at least 1 Z note occurred with the highest frequency (roughly 80% of the calls in our sample; Table I) and calls containing at least 1 D_h note were least common (10% of the calls in our sample). Over half the calls in our sample had ZAD or ZA note compositions, and nearly 80% of the calls were composed of two or three total notes (Table II). We observed only one case (0.006 of the sample) of a call structure violating the Z-A- D_h -D rule of note ordering, a call with AZAD note composition.

A. Potential for note-type coding

The PNTC analysis assessed which acoustic parameters of the tufted titmouse chick-a-dee call notes may potentially be useful in distinguishing between note types (Table III). All parameters had PNTC scores greater than 1, indicating the

potential for note types to be discriminated from one another on the basis of each parameter. Parameters with the greatest potential to be useful in note-type discrimination—that is, those with PNTC values >2 (Robisson *et al.*, 1993)—are TD, SF, MxF, MnF, and SE. Thus, three of the four frequency measures, note duration, and “noisiness” at the start of the note, appear to be best at potentially allowing discrimination of these four note types from one another.

TABLE II. The different call structures (note compositions) and their frequencies observed in titmouse chick-a-dee calls.

| Note composition | Percent in sample | Cumulative percent |
|-----------------------|-------------------|--------------------|
| ZAD | 33.8 | 33.8 |
| ZA | 17.5 | 51.3 |
| ZZD _h | 5.0 | 56.3 |
| DDD | 3.8 | 60.0 |
| ZD _h | 3.8 | 63.8 |
| ZZ | 3.8 | 67.5 |
| DDDD | 3.1 | 70.6 |
| ZAA | 2.5 | 73.1 |
| AAD | 2.5 | 75.6 |
| ZADD | 1.9 | 77.5 |
| ZAAD | 1.9 | 79.4 |
| ZADDD | 1.9 | 81.3 |
| AA | 1.9 | 83.1 |
| ADDD | 1.9 | 85.0 |
| ZD | 1.3 | 86.3 |
| DDDDD | 1.3 | 87.5 |
| DDDDDD | 1.3 | 88.8 |
| ZZA | 0.6 | 89.4 |
| ZZAD | 0.6 | 90.0 |
| ZZADDDD | 0.6 | 90.6 |
| ZZD | 0.6 | 91.3 |
| ZADDDD | 0.6 | 91.9 |
| ZAADD | 0.6 | 92.5 |
| ZD _h DDD | 0.6 | 93.1 |
| ZD _h DDDDD | 0.6 | 93.8 |
| ZDD | 0.6 | 94.4 |
| ZDDDDD | 0.6 | 95.0 |
| AD | 0.6 | 95.6 |
| ADD | 0.6 | 96.3 |
| AADD | 0.6 | 96.9 |
| AZAD | 0.6 | 97.5 |
| DD | 0.6 | 98.1 |
| DDDDDDD | 0.6 | 98.8 |
| DDDDDDDD | 0.6 | 99.4 |
| DDDDDDDDDDDDDDDDDD | 0.6 | 100.0 |

TABLE III. Potential for note-type coding (PNTC) values of our 17 acoustic parameters.

| Parameter | PNTC |
|-----------|------|
| Duration | |
| TD | 2.04 |
| DMx | 1.45 |
| Frequency | |
| SF | 3.79 |
| EF | 1.36 |
| MxF | 2.98 |
| MnF | 2.21 |
| F1 | 1.34 |
| F2 | 1.47 |
| Amplitude | |
| SA | 1.26 |
| EA | 1.22 |
| MxA | 1.38 |
| MnA | 1.08 |
| RMS | 1.23 |
| Entropy | |
| SE | 2.01 |
| EE | 1.28 |
| MxE | 1.70 |
| MnE | 1.93 |

B. Potential for individual coding

The PIC analysis assessed for each note type which acoustic parameters could be useful in distinguishing between individuals. We found that all parameters are >1 for the **Z** note type, which suggests it may be the note type most likely to carry individual signature features, followed by **D_h** (14 parameters), **A** (13 parameters), and **D** (5 parameters) note types (Table IV). Even though all 17 parameters for **Z** notes are >1 , none of these parameters are considered to be highly useful in individual distinction, though TD, with a PIC value of 1.91, may be fairly useful. **D_h** notes do present PIC values >2 , but this may be an effect of small sample size and should be interpreted with caution.

C. Factor analysis

A factor analysis on the 17 parameters generated four factors with eigenvalues >1 (Table V). We determined that a parameter loaded onto the factors if it had a value of 0.6 or greater. Of the 17 total parameters, 14 loaded onto the four factors. Factors 1 and 2 together account for 60.9% of the total variation, and are our main factors for analyses of possible note composition and sex effects described below. Frequency and entropy parameters load heavily onto Factor 1, amplitude measures load heavily onto Factor 2, duration parameters load heavily onto Factor 3, and an entropy and frequency change measure associated with the ending of the notes load heavily onto Factor 4.

D. Factor analysis: Are note types distinct?

We found a significant effect of “note type” on all four factors (Fig. 3; Factor 1: $F_{3,33}=242.9$, $P<0.001$; Factor 2: $F_{3,34}=8.5$, $P<0.001$; Factor 3: $F_{3,31}=31.0$, $P<0.001$; Factor 4: $F_{3,34}=79.3$, $P<0.001$). Post-hoc analyses (corrected

for multiple comparisons) indicated that all four note types were significantly different from one another for Factor 1 (factor scores: $D_h > Z > A > D$) and for Factor 4 (factor scores: $D_h > A > D > Z$). For Factor 2, **Z** notes had significantly higher factor scores than did **D** and **D_h** notes. For Factor 3, **D_h** notes had significantly higher factor scores than did **D** and **Z** notes, and those three notes had significantly higher factor scores than did **A** notes. Taken together, all four factors do a reasonably good job of potentially discriminating the note types, with Factors 1 and 4 (frequency and entropy parameters) providing the strongest potential discrimination.

E. Factor analysis: Are individuals distinct?

“Individual” had a significant effect on at least one factor score for each note type (Table VI). For both **Z** and **D** note types, individual had a significant effect on all four factor scores. Factor 1 produced the largest number of significant individual-individual distinctions for **Z** notes and Factors 1 and 3 produced similar numbers of such individual-individual distinctions for **D** notes. In these cases, there were typically two or three birds with factor scores very different from other birds, accounting for most of the significant bird \times bird comparisons.

F. Note composition and sex effects

Overall there was little effect of note composition detectable within this call set. Factor 2 scores for first **A** notes in calls were significantly affected by the number of **A** notes in calls ($F_{1,7}=48.55$, $p<0.001$; Fig. 4). The overall amplitude of the first **A** note in a call is higher when it is followed by 1 or more **A** notes than if it is the only **A** note in a call. Factor 1 scores for **A** notes were not significantly affected by the number of following **A** notes in the call ($F_{1,9}=2.98$, $p=0.118$). Factor scores for **Z** and **D** note types were also not significantly impacted by the number of **Z** notes or **D** notes, respectively, to follow (**Z** notes: Factor 1 $F_{1,12}=2.64$, $p=0.130$; Factor 2 $F_{1,14}=1.75$, $p=0.208$; **D** notes: Factor 1 $F_{1,12}=0.02$, $p=0.889$; Factor 2 $F_{1,9}=2.33$, $p=0.161$). Similarly, we found no effect of the total number of notes in a call on factor scores for either **Z** (Factor 1 $F_{2,22}=1.07$, $p=0.361$; Factor 2 $F_{2,22}=0.02$, $p=0.978$), **A** (Factor 1 $F_{2,22}=0.85$, $p=0.44$; Factor 2 $F_{2,22}=0.10$, $p=0.905$) or **D** notes (Factor 1 $F_{2,17}=0.16$, $p=0.854$; Factor 2 $F_{2,18}=0.04$, $p=0.961$; Fig. 5). Finally, sex had no detectable effect on Factor 1 or Factor 2 scores for either **Z** (Factor 1 $F_{1,9}=0.09$, $p=0.769$; Factor 2 $F_{1,9}=0.60$, $p=0.458$), **A** (Factor 1 $F_{1,8}=0.08$, $p=0.780$; Factor 2 $F_{1,8}=0.01$, $p=0.944$), or **D** note types (Factor 1 $F_{1,9}=0.04$, $p=0.850$; Factor 2 $F_{1,9}=0.04$, $p=0.853$).

IV. CONCLUSIONS

In this study we used the acoustic parameters measured from chick-a-dee calls of tufted titmice to classify their note types into categories, to determine which of the note types may potentially be useful in note type and individual discrimination, and to describe possible effects of note composition or sex of signaler on note type acoustic structure. Simi-

TABLE IV. Potential for individual coding (PIC) values of our 17 acoustic parameters for each note type (first row for each parameter), and means \pm SD (second row for each parameter). PIC values greater than 1 are potentially useful for discriminating individuals.

| Parameter | Note type | | | |
|-----------|-------------------|-------------------|-------------------|-------------------|
| | Z | A | D_h | D |
| TD | 1.91 | 0.99 | 1.17 | 1.01 |
| (s) | 0.12 \pm 0.04 | 0.05 \pm 0.01 | 0.24 \pm 0.02 | 0.17 \pm 0.02 |
| DMx | 1.29 | 1.08 | 1.04 | 0.87 |
| (s) | 0.07 \pm 0.03 | 0.03 \pm 0.01 | 0.04 \pm 0.02 | 0.09 \pm 0.05 |
| SF | 1.69 | 1.56 | 3.73 | 1.02 |
| (kHz) | 9.21 \pm 0.51 | 8.94 \pm 0.46 | 9.56 \pm 0.76 | 2.52 \pm 0.68 |
| EF | 1.14 | 1.01 | 1.43 | 1.03 |
| (kHz) | 7.34 \pm 0.95 | 5.54 \pm 1.74 | 2.92 \pm 1.44 | 2.75 \pm 0.98 |
| MxF | 1.47 | 1.04 | 1.64 | 1.06 |
| (kHz) | 8.36 \pm 0.38 | 8.08 \pm 0.76 | 8.28 \pm 0.68 | 2.79 \pm 0.80 |
| MnF | 1.64 | 1.07 | 1.25 | 1.03 |
| (kHz) | 8.36 \pm 0.40 | 8.16 \pm 0.73 | 5.75 \pm 2.80 | 2.56 \pm 0.41 |
| F1 | 1.54 | 1.11 | 2.14 | 0.92 |
| (kHz) | 0.85 \pm 0.51 | 0.86 \pm 0.74 | 1.28 \pm 0.89 | -0.35 \pm 1.24 |
| F2 | 1.24 | 1.03 | 1.26 | 0.95 |
| (kHz) | 1.02 \pm 1.02 | 2.53 \pm 1.75 | 5.36 \pm 1.69 | -0.04 \pm 1.37 |
| SA | 1.31 | 1.03 | 0.99 | 0.87 |
| (dB) | -31.93 \pm 4.65 | -34.47 \pm 4.81 | -36.56 \pm 3.67 | -39.51 \pm 5.49 |
| EA | 1.35 | 1.03 | 1.20 | 0.86 |
| (dB) | -31.92 \pm 4.77 | -34.82 \pm 4.77 | -38.34 \pm 4.11 | -39.59 \pm 6.17 |
| MxA | 1.18 | 0.98 | 0.95 | 0.90 |
| (dB) | -18.34 \pm 4.27 | -21.71 \pm 4.30 | -22.04 \pm 3.74 | -27.78 \pm 5.21 |
| MnA | 1.20 | 0.98 | 1.44 | 0.88 |
| (dB) | -30.47 \pm 4.83 | -32.15 \pm 4.98 | -40.49 \pm 3.71 | -36.38 \pm 5.04 |
| RMS | 1.24 | 1.09 | 0.87 | 0.95 |
| (V) | 0.08 \pm 0.04 | 0.07 \pm 0.03 | 0.05 \pm 0.02 | 0.04 \pm 0.02 |
| SE | 1.69 | 1.20 | 1.46 | 0.97 |
| | 0.27 \pm 0.09 | 0.30 \pm 0.07 | 0.45 \pm 0.08 | 0.64 \pm 0.05 |
| EE | 1.13 | 1.05 | 2.19 | 0.98 |
| | 0.49 \pm 0.15 | 0.68 \pm 0.09 | 0.61 \pm 0.07 | 0.60 \pm 0.05 |
| MxE | 1.32 | 1.11 | 1.52 | 0.97 |
| | 0.17 \pm 0.04 | 0.28 \pm 0.14 | 0.32 \pm 0.10 | 0.54 \pm 0.07 |
| MnE | 1.13 | 0.95 | 2.99 | 0.96 |
| | 0.38 \pm 0.08 | 0.58 \pm 0.12 | 0.81 \pm 0.06 | 0.70 \pm 0.05 |

lar analyses have been completed on the chick-a-dee call of chickadee species for many years (see reviews in Sturdy *et al.* (2007) and Lucas and Freeberg (2007)). Our study was prompted by the fact that *Baeolophus* and *Poecile* are closely related, and share many features of their natural histories and social organizations (Grubb and Pravosudov, 1994; Mostrom *et al.*, 2002), but very little is known about the structure and nature of the chick-a-dee calls of titmice.

We classified the notes of the chick-a-dee call of the tufted titmouse into four distinct note types: **Z**, **A**, **D_h** , and **D**, with high inter-observer agreement. Like chickadee (*Poecile*) species that have been documented, tufted titmouse chick-a-dee calls obey basic rules of note ordering, with over 99% of our call sample obeying a **Z** \rightarrow **A** \rightarrow **D_h** \rightarrow **D** rule (see Table II). The potential for note-type coding (PNTC) analysis indicated that all of our 17 measured parameters could potentially be useful in note-type discrimination. ANOVAs used here to detect an effect of note type on factor score can be considered a converging method of potential note-type distinctiveness. We found that note type had a significant effect

TABLE V. Factor loadings and variance explained for the factor analysis of the 17 acoustic parameters. See text for definitions of factor properties.

| Parameter | Factor 1 | Factor 2 | Factor 3 | Factor 4 |
|---------------------|----------|----------|----------|----------|
| SF | 0.904 | | | |
| SE | -0.776 | | | |
| MxF | 0.917 | | | |
| MxE | -0.816 | | | |
| MnF | 0.869 | | | |
| RMS | | 0.882 | | |
| SA | | 0.898 | | |
| EA | | 0.906 | | |
| MxA | | 0.868 | | |
| MnA | | 0.922 | | |
| TD | | | 0.812 | |
| DMx | | | 0.829 | |
| EE | | | | 0.744 |
| F2 | | | | 0.676 |
| Eigenvalue | 5.34 | 5.01 | 1.97 | 1.79 |
| Variance explained | 31.42 | 29.45 | 11.59 | 10.53 |
| Cumulative variance | 31.42 | 60.87 | 72.46 | 82.99 |

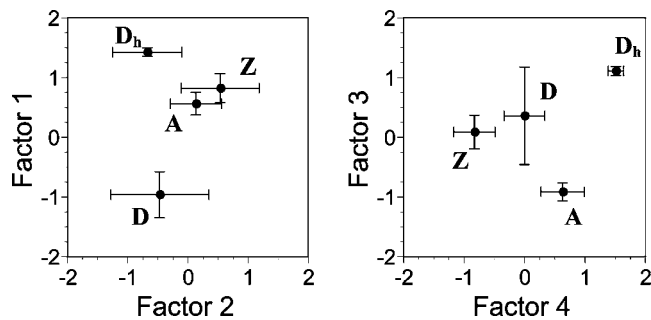


FIG. 3. Means (± 1 SD) for each of the four factors emerging from factor analysis for Z, A, D_h , and D note types.

on factor scores for all four factors that emerged in our analysis. Taken together, these two tests show, unsurprisingly, that acoustic characteristics vary reliably with note type (see also Dawson *et al.*, 2006 for a recent example of using artificial neural networks to distinguish note types of chick-a-dee calls of black-capped chickadees, *P. atricapillus*). Experiments like those by Sturdy *et al.* (2000), now need to be conducted to determine if titmice actually perceive the difference between note types, and which perceptual mechanisms guide this discrimination.

The chick-a-dee call of tufted titmice is also capable of encoding individual identity information, as seen in chickadee species (Bloomfield *et al.*, 2004, 2005; Charrier *et al.*, 2004). The potential for individual coding (PIC) analysis, as well as ANOVAs run on factor scores, indicate that individuals in our sample can potentially be discriminated on the basis of acoustical features of the note types. However, the results of the PIC analysis offer some different interpretations than the results of the ANOVAs run on factor scores. For example, for our 17 parameters, all 17 provided PIC scores greater than 1 (suggesting the potential for individual distinctiveness) for Z notes, but only five provided PIC scores greater than 1 for D notes (Table IV). This would suggest that Z note types in tufted titmice may allow for strong individual-level discrimination, but D notes would be more limited in their ability to do so (i.e., limited to note

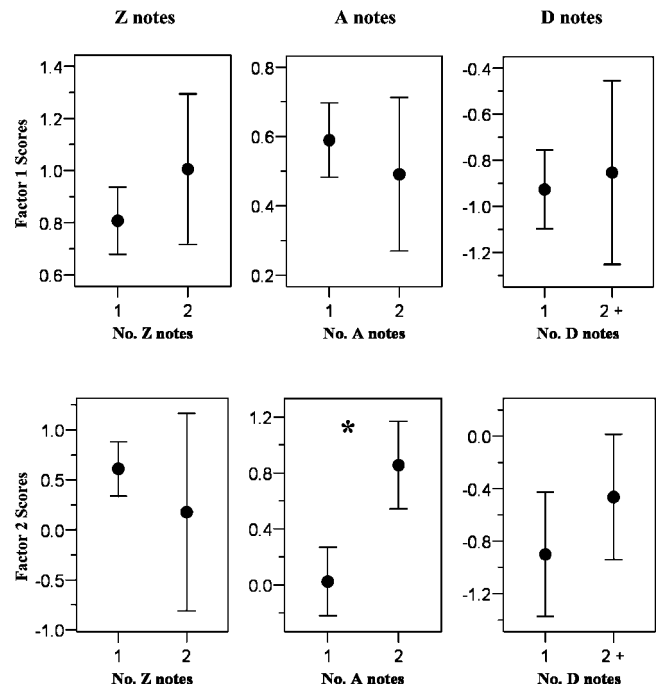


FIG. 4. Effect of note composition on factor scores for Z, A, and D notes: for the first Z, A, and D note type to occur in a call, the effect of one or more Z, A or D note (respectively) on its factor 1 and factor 2 scores. Data are plotted as means and 95% confidence intervals.

duration and some frequency measures). However, analysis of variance of factor scores for D and Z notes indicate that both provide a strong potential for individual distinctiveness (Table VI). Additionally, ANOVAs indicated a fairly weak effect of individual on the factor scores for both A and D_h notes note types (Table VI), but PIC analysis indicated that these note types should allow for fairly strong individual-level discrimination (Table IV). The explanation for these differences in PIC analyses compared to the factor score analyses will, as described above, need to be addressed with perceptual discrimination studies as conducted by Sturdy *et al.* (2000) or with call playback studies as conducted by Nowicki (1983). However, both analyses indicate that indi-

TABLE VI. Effect of individual on factor score for each note type. The F statistic for the influence of individual on factor score for each note type is displayed on line one with its p-value below it, and line three is the number of unique individual (bird \times bird) comparisons that are significantly different, given that a significant effect of individual was detected. Individual comparisons were significant after corrections for multiple comparisons.

| | Z | A | D_h | D |
|-----------------------------|-----------------------------|---------------------------|---------------------------|------------------------------|
| (<i>ndf</i> , <i>ddf</i>) | (15, 129) | (14, 117) | (2, 13) | (14, 199) |
| Factor 1 | $F=6.70$ $p<0.001$ 19 | $F=2.04$ $p<0.05$ 0 | $F=0.16$ $p<0.85$ | $F=10.99$ $p<0.001$ 17 |
| Factor 2 | $F=7.96$ $p<0.001$ 8 | $F=1.94$ $p<0.05$ 0 | $F=4.95$ $p<0.05$ 0 | $F=5.83$ $p<0.001$ 7 |
| Factor 3 | $F=4.70$ $p<0.001$ 5 | $F=0.83$ $p=0.64$ | $F=0.55$ $p=0.59$ | $F=13.32$ $p<0.001$ 20 |
| Factor 4 | $F=1.82$ $p<0.05$ 2 | $F=1.55$ $p=0.11$ | $F=0.13$ $p=0.88$ | $F=2.29$ $p<0.05$ 1 |

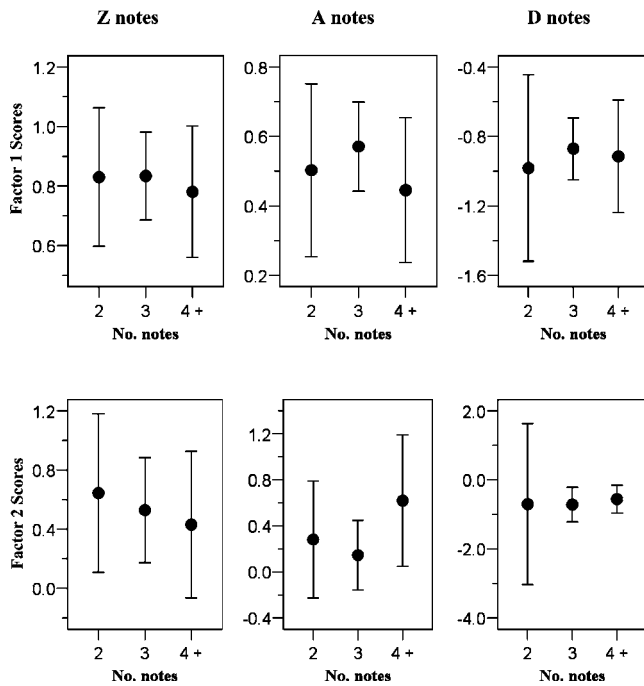


FIG. 5. Effect of note composition on factor scores for *Z*, *A*, and *D* notes: for the first *Z*, *A*, and *D* note type to occur in a call, the effect of the total number of notes in the call on its factor 1 and factor 2 scores. Data are plotted as means and 95% confidence intervals.

viduals are potentially distinguishable from one another by the acoustic characteristics of the note types of their chick-a-dee calls.

We suggest that the *Z* note type may be the primary note type to encode individual identity in tufted titmouse chick-a-dee calls, taking a number of lines of evidence into consideration. For example, the *Z* note occurs in the highest percentage of calls (Table I), and if it is present in a call, it virtually always occurs first (Table II). Also, PIC values for *Z* notes were >1.0 for all 17 acoustic parameters we measured (Table IV) and strong effects of individual were detected for all four factors that emerged from our factor analysis (Table VI). Playback studies manipulating *Z* note types (as well as other note types) are now needed to test this assertion.

We detected very little effect of note composition (call structure) on the acoustic structure of notes of calls. This finding contrasts with the pervasive effects of note composition on the acoustic structure of notes of the chick-a-dee call observed in Carolina chickadees (Freeberg *et al.*, 2003). Differences in call length between tufted titmice and Carolina chickadees are a likely contributor to the differences in the effect of note composition seen in these two species. The average number of note types in a Carolina chickadee chick-a-dee call is roughly twice that seen in tufted titmouse chick-a-dee calls. As described by Hailman *et al.* (1985), calls with more note types or more notes may be physiologically more difficult for an individual to produce than calls with fewer note types or fewer notes. Physiological constraints therefore may be an important causal factor in the note composition effect seen in Freeberg *et al.* (2003). Unlike Carolina chickadees, however, most tufted titmouse calls have few notes. In

our sample, roughly 80% of the calls were composed of only two or three total notes. If the production of a four-note call is physiologically no more taxing to a titmouse than production of a two-note call, then this could well explain our finding of a general lack of a note composition effect. Larger samples of chick-a-dee calls of tufted titmice, that would uncover larger numbers of calls with greater numbers of notes, may yet reveal an effect of note composition on acoustic features of note types.

We also detected no effects of sex on Factor 1 or Factor 2 scores for the *Z*, *A*, and *D* note types in our sample. The earlier study with Carolina chickadees likewise found minimal sex effects on acoustic parameters of note types (Freeberg *et al.*, 2003). The lack of a strong sex effect on acoustic features of notes of chick-a-dee calls may not be too surprising, though, given the fact that sexes in these two species are highly monomorphic, and the call is used by both sexes throughout the year in facilitating social cohesion (Grubb and Pravosudov, 1994; Hailman, 1989; Hailman and Ficken, 1996; Mostrom *et al.*, 2002).

Individual distinctiveness in vocal signals is common in many avian (and nonavian) species (Stoddard, 1996). Individual distinctiveness has been hypothesized to be useful to birds with fairly stable social organization, like the Parids, in which individuals of a group may frequently be out of sight from one another and need to communicate (e.g., Marler, 1960). Note type and individual discrimination have been demonstrated in a few chickadee species, and we have now extended these findings to tufted titmice, a species related to chickadees, but one whose vocal behavior is much less understood. Given the complexity of the chick-a-dee call, including its structural similarities with human language (e.g., Hailman and Ficken, 1986; Hailman *et al.*, 1985), increased effort is needed to understand variation in structure and function of chick-a-dee calls of titmouse species, as well as other under-studied Parid species.

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