Variation in chick-a-dee calls of a Carolina chickadee population, *Poecile carolinensis*: Identity and redundancy within note types

Todd M. Freeberg,[a] Jeffrey R. Lucas, and Barbara Clucas[b]
Department of Biological Sciences, Lilly Hall, Purdue University, West Lafayette, Indiana 47907

Chick-a-dee calls of chickadee species are structurally complex because calls possess a rudimentary syntax governing the ordering of their different note types. Chick-a-dee calls were recorded in an aviary from female and male birds from two field sites. This paper reports sources of variation of acoustical parameters of notes in these calls. There were significant sex and microgeographic differences in some of the measured parameters of the notes in the calls. In addition, the syntax of the call itself influenced characteristics of each of the notes. For example, calls with many introductory notes began with a note of higher frequency and longer duration, relative to calls with few introductory notes. Furthermore, the number of introductory notes influenced frequency and duration components of notes later in the call. Thus, single notes are predictive of the note composition of the signaler's call. This suggests that a receiver might gain the meaning in the call even if it hears only part of the call. Further, single notes within these complex calls can contain information enabling receivers to predict the sex of the signaler, and whether it is from the local population. © *2003 Acoustical Society of America.* [DOI: 10.1121/1.1559175]

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I. INTRODUCTION

There are several potential conflicts between various functions of the vocal signals of animals. For example, the need to generate signals that effectively transmit information about individual identity will possibly limit the amount of song or vocal sharing that would facilitate the maintenance of group or population markers. Furthermore, when information is being transferred by vocal signals, it is often necessary for the signaler to provide redundant information, particularly as the noise level in the environment increases (Bradbury and Vehrencamp, 1998; Wiley, 1983). Redundancy of information can be achieved by using other signal modalities in parallel with vocal signals, by repeating the same or similar vocal signals, or by providing the same information in different ways within the same vocal signal (Bateson, 1968; Endler, 2000; Hauser, 1996; Smith, 1977; Uetz, 2000). This latter notion could be facilitated by the use of different note, syllable, or phrase types within a vocal system that were probabilistically associated with one another, such that the detection of one note type by a receiver might allow it to predict, for example, other note types in the signal to follow. As with the trade-offs between individual and group identification in vocal signals, redundancy of information within signals may limit the amounts of different information regarding identity or external referents that could be conveyed.

The chick-a-dee call system in avian species of the genus *Poecile* is produced in a variety of primarily social contexts (Ficken *et al.*, 1978; Hailman, 1989; Smith, 1972, 1991). The chick-a-dee call has a high acoustic variability with a rudimentary syntax that governs the ordering of its note types (Hailman, 1989). In black-capped chickadees, *Poecile atricapillus*, for example, there are four note types (A, B, C, and D) that follow a general A-B-C-D ordering. Any given note type may or may not be present in a given chick-a-dee call and, if present, can occur multiple times. These calls are said to be "combinatorial" in that they follow a simple and relatively fixed syntax but nonetheless could vary enormously in the number of different call types that could be produced (Hailman and Ficken, 1986; Hailman *et al.*, 1987). The chick-a-dee call system of Carolina chickadees, *P. carolinensis*, also obeys these simple syntactic rules. The chick-a-dee call of Carolina chickadees typically begins with relatively high-frequency A notes ["high-see" and related notes in Smith (1972); see also Hailman (1989)], occasionally followed by a single B note (variants of "high-tee" note) or by more structurally complex C notes ("chick" notes), and ends with lower-frequency D notes ("dee" notes). The numbers and even presence of each note type is variable in these calls, although calls virtually always follow an "A-B-D" or "A-C-D" ordering [Fig. 1(a)]. This variable, yet rule-governed, system of notes in chick-a-dee calls means that the call system theoretically could convey a large amount of information (Hailman *et al.*, 1985, 1987).

The presence of identity information in the chick-a-dee call system has primarily been studied in black-capped chickadees. Mammen and Nowicki (1981) found that frequency and duration properties of the first D note in calls, as well as characteristics of the complete call such as call duration and number of D notes (which relate to the "syntax" or note composition of the call), varied among different

[a] Author to whom correspondence should be addressed. Department of Psychology, Austin Peay Building 303A, University of Tennessee, Knoxville, TN 37996. Electronic mail: tfreeber@utk.edu
[b] Current address: Animal Behavior Graduate Group and Department of Psychology, University of California at Davis, One Shields Avenue, Davis, CA 95616. Electronic mail: baclucas@ucdavis.edu
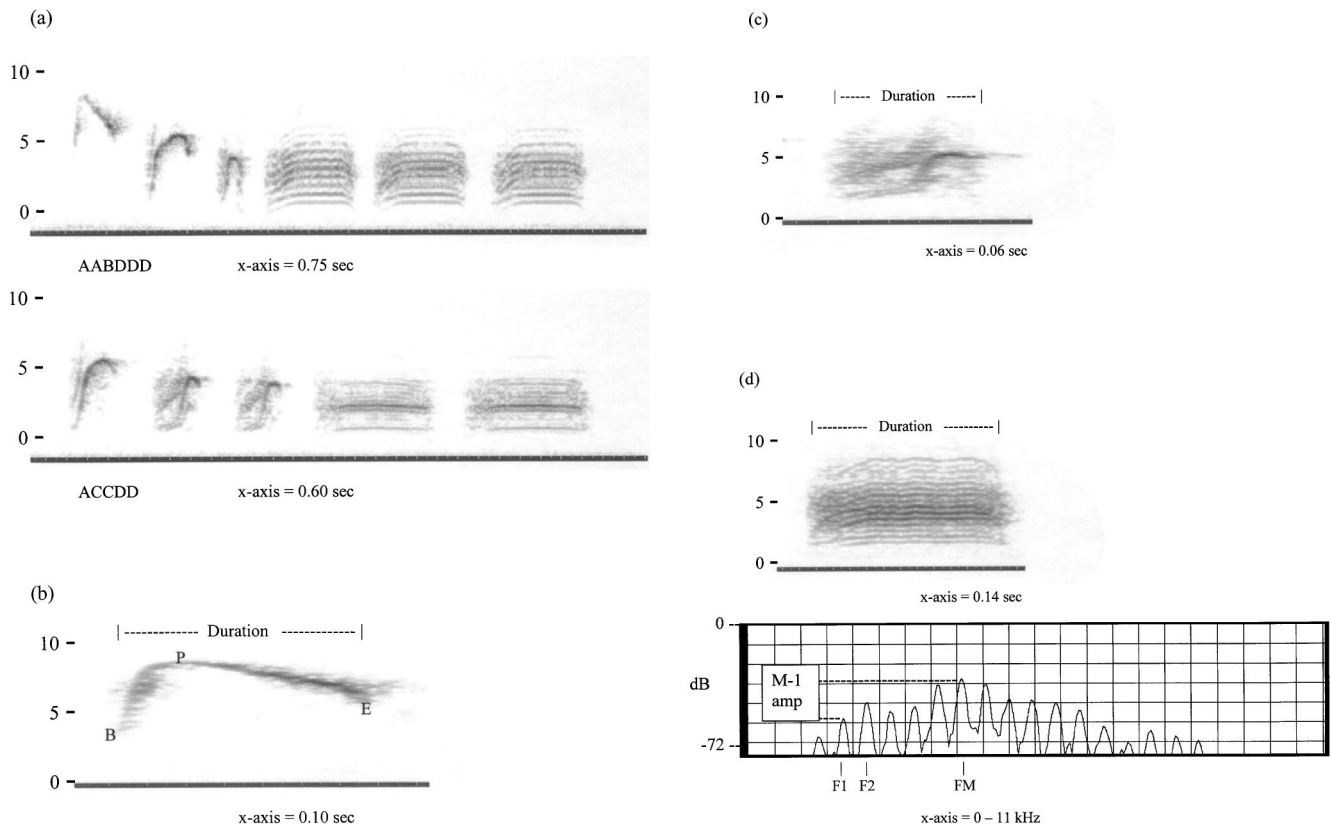
FIG. 1. Examples of note types comprising chick-a-dee calls of Carolina chickadees, and illustration of some of the parameters measured in the study. For each example, frequency (kHz) is depicted on the Y axis. (a) Sonagrams of chick-a-dee calls containing 2 A, 1 B, and 3 D notes (top figure) and 1 A, 2 C, and 2 D notes (bottom figure). The X axis in the top figure is 750 ms and in the bottom figure is 600 ms. (b) Example of some A note measures. B =beginning frequency. P=peak frequency. E=end frequency. (c) Example of C note measure. (d) Example of some D note measures. The bottom figure in (d) is an amplitude spectrum with relative amplitude (dB) on the Y axis and frequency (Hz) on the X axis. F1=frequency of the first peak. F2=frequency of the second peak. FM=frequency of the maximum amplitude peak. M-1 amp=the relative amplitude difference between the maximum peak amplitude and the first peak amplitude.

flocks. That study did not consider the possibility that acoustic properties of notes might be affected by the note composition of the entire call. Therefore, a potential confound between note composition and note properties may bias conclusions drawn about flock differences. We consider this possibility here using the calls of Carolina chickadees.

To our knowledge, no analysis of variation in note parameters within calls in Carolina chickadees exists comparable to the work of Mammen and Nowicki (1981) on black-capped chickadees. Some recent work has focused on the production and perception of chick-a-dee calls in different situations, including testing whether different note compositions in calls correspond with different social or physical contexts. For example, Carolina chickadees signalers produce chick-a-dee calls at higher rates during times of temporary energetic stress (Lucas *et al.*, 1999). Further, Carolina chickadees respond differently to field playbacks of chick-a-dee calls that vary in note composition, suggesting that calls with different note compositions might convey different meanings to receivers (Freeberg and Lucas, 2002). Finally, in other chickadee species, different usage of note types in different contexts has been documented (Mexican chickadees, *Poecile sclateri*, Ficken *et al.*, 1994; mountain chickadees, *P. gambeli*, Gaddis, 1985).

Here we present data on sources of acoustic variation in

several characteristics of the notes of calls we recorded from female and male Carolina chickadees from two capture sites (separated from one another by at most 5 km). Geographic variation in vocalizations has long been studied in songbirds (e.g., Baker and Cunningham, 1985; Kroodsma and Miller, 1996; Mundinger, 1982), and sex differences in acoustic characteristics of the same vocal types have been demonstrated in some species (Ballintijn and ten Cate, 1997; Okanoyak, 1993; Yamaguchi, 1998a). One of our goals was to establish a first step towards uncovering micro-level variation (between sites close in proximity, and between birds from the same sites that differ in sex) in the structures of this call. We asked whether characteristics of individual note types in chick-a-dee calls (after syntax effects are statistically removed) might provide information about the identity of the signaler. We characterized notes in our analyses using a number of frequency and amplitude measurements, in addition to whole-note properties such as duration, internote interval, entropy, continuity, and modulation (see ''C notes'' and ''D notes'' below).

In addition to testing for this micro-level of geographic variation, we sought to determine whether properties of the first A, C, and D notes in a call predicted (or were predicted by) syntactic characteristics of the rest of the call. In chick-a-dee calls, a note can occur more than once in a string of the

same note type—for example, a call containing A, C, and D notes can vary from ACD to AAAAAACD to ACCCCCCD to ACDDDDDDD to AACCCDDDDD, and so on. It has been hypothesized that each of the four note types may encode different information about signaler motivation to approach or withdraw from an area (e.g., Ficken *et al.*, 1994; Freeberg and Lucas, 2002; Gaddis, 1985). Further, the number of notes may encode information about the intensity of those tendencies (Hailman *et al.*, 1985, 1987; Smith, 1972). Thus, an AAACCC call may signal the same general message as an AAACCCCCCC call, but the latter call would indicate a higher intensity on the part of the signaler for the particular message conveyed by C notes. In the present study, we sought to test whether the properties of certain notes could predict other notes in the call. If so, a receiver might be able to determine probabilistically a call's composition of notes, even if the receiver were to hear only part of the call. This would suggest an interesting form of redundancy of information in these structurally complex calls.

II. METHODS

A. Experimental animals and recording of chick-a-dee calls

We captured individual Carolina chickadees from flocks at the Ross Biological Reserve (hereafter, Ross) and the Martell Forest Reserve (hereafter, Martell) in West Lafayette, IN. Ross and Martell females and males were captured for recording from late fall to early spring, from 1997 to 1999. We tried to capture only adult birds [aged according to Pyle (1997)], and time of year for recording birds was balanced across sex and microgeographic capture site (Table I). All birds used in this study were banded with unique combinations of colored leg rings to permit individual identification. In addition, we had banded a number of the birds in months or years prior to their use in this study and this served as an aid for aging these previously banded birds. Birds were captured using baited seed stands with Potter (treadle) traps. After capture, birds were placed in individual 1-m^3 cages in the laboratory. All birds were maintained with mixed seeds, grit, shredded carrot, one to three mealworms, and fresh vitamin-treated water daily. Lights in the aviary were set to the natural light/dark cycle that the birds would experience in the wild, given the time of year when the birds were captured and recorded. After recording (or, for some birds, after their use in a different study), birds were released at their site of capture.

We recorded all the birds in the same 1-m^3 cage, to standardize the recording conditions across birds, in a room whose walls were made of acoustic tiling covered with polyurethane foam padding to minimize reverberation. All birds were recorded within a week of capture. During recording, chickadees could hear chickadees housed in the same room and in adjoining rooms. We recorded chick-a-dee calls with Saul Mineroff directional electret microphones, placed within 1 m of the bird, on Maxell XLII tape using a Marantz PMD 222 portable cassette recorder.

We attempted to record at least ten chick-a-dee calls

TABLE I. Capture site, sex, age, and recording date of Carolina Chickadees. AHY = ''After Hatch Year'' (see Pyle, 1997), indicating a bird that had been hatched at least as early as the summer of the year prior to recording. ASY = ''After Second Year,'' indicating a bird that had been hatched at least as early as two summers before recording. U = ''Unknown,'' indicating a bird we were unable to age successfully, and so could not determine whether it was older than HY (''Hatch Year'').

Capture site	Sex	Bird no.	Age	Recording date
Ross	F	5	AHY	12/97
Ross	F	7	AHY	03/98
Ross	F	11	AHY	10/99
Ross	F	14	AHY	09/99
Ross	F	16	U	10/99
Ross	F	22	AHY	10/99
Ross	M	1	AHY	11/97
Ross	M	9	AHY	04/98
Ross	M	15	ASY	12/98
Ross	M	19	AHY	02/99
Ross	M	20	AHY	09/98
Martell	F	2	AHY	11/97
Martell	F	4	AHY	11/97
Martell	F	6	AHY	02/98
Martell	F	10	AHY	09/98
Martell	F	13	ASY	02/99
Martell	F	17	AHY	09/98
Martell	F	21	AHY	12/98
Martell	F	23	U	12/98
Martell	F	25	AHY	02/99
Martell	M	3	AHY	11/97
Martell	M	8	AHY	03/98
Martell	M	12	AHY	09/98
Martell	M	18	U	12/98
Martell	M	24	AHY	02/99

from each individual for later analyses. We obtained an average of 8.7 (range 3–15) calls from six females and an average of 12.6 (range 10–20) calls from five males from the Ross capture site, and an average of 10.6 (range 3–20) calls from nine females and an average of 11.8 (range 10–18) calls from five males from the Martell capture site. In our population, sex is strongly predicted by wing chord, the length of the bird's unflattened wing from the bend of the wing to the end of the longest primary feather [the cutoff between the sexes in our area is 62 mm, with males being larger than females (Thirakhupt, 1985)]—we used this size criterion to determine sex in this study.

B. Analyses of chick-a-dee calls

Recorded calls were digitized using the Cool Edit sound analysis program (version 96 run on the Windows 95 platform), with a sampling rate of 22 050 at 16-bit resolution. We measured several aspects of the notes in the calls, some of which were based on measures reported in earlier studies of black-capped chickadees (Mammen and Nowicki, 1981; Nowicki, 1989; Nowicki and Nelson, 1990). The first two note types (A and B notes) tend to be frequency modulated, relatively pure-tone whistled notes. We measured acoustic parameters of all of the introductory whistled notes in each call, although most of our analyses below focused on only the first introductory note (in this north-central Indiana population, this is virtually always an A note, rather than a B note, and, in the sample here, all were A notes).

We also measured properties of all of the C notes and the first, second, and last D notes within calls containing one or more of each note type, although, as was the case with A notes, most of our analyses concentrate on parameters of the first C note and first D note in calls. We used different acoustic parameters for the three different note types (A, C, and D) because the notes are structurally quite distinct (see Fig. 1).

1. A notes

Six parameters were used to characterize A notes [Fig. 1(b)]: *duration* (ms), *beginning frequency* (at the onset of the note, Hz), *peak frequency* (highest frequency in the note, Hz), *end frequency* (at the offset of the note, Hz), *position of peak amplitude* ([time at peak amplitude-note start time]/note duration), and relative *shape* ([time at peak frequency-note start time]/note duration).

2. C notes

Six parameters were used to characterize C notes [Fig. 1(c)]: *duration* (ms), *peak frequency* (Hz), *entropy, continuity, modulation*, and *pitch* (Hz). All of these parameters were obtained by using Sound Analysis [Version 1.4; see Tchernichovski *et al.* (2000)]. *Peak frequency* is a frequency measure derived from the spectrogram. *Entropy* provides a measure of the randomness or amount of ''noise'' in the waveform of a note; white noise, which by definition is completely random, has an entropy of 1, and a pure tone, which is by definition completely nonrandom, has an entropy of 0. *Continuity* is a measure of the extent to which frequency contours in a note type are stable across consecutive sampling windows. As Tchernichovski *et al.* (2000) note, continuity and entropy are correlated but not perfectly so—adding unbroken harmonics to a sound will not change continuity but will cause an increase in entropy. *Modulation* provides a measure of the relative frequency changes within the note. *Pitch* indicates the fundamental frequency of the note.

3. D notes

Twelve parameters were used to characterize D notes [Fig. 1(d)]. Six of these 12 parameters were whole-note characteristics: *duration* (ms), *internote interval* preceding the D note (ms), *entropy, continuity, modulation*, and *pitch* (the last four were obtained using Sound Analysis, described above). The other six parameters were characteristics of the frequencies and amplitudes of the stack of overtonelike structures that make the note. Frequency parameters (all Hz) were *freq max peak*, the frequency of the overtone with the maximum amplitude; *freq first peak*, the frequency of the lowest overtone within 30 dB of the maximum amplitude peak; and *freq second peak*, the frequency of the second overtone within 30 dB of the maximum amplitude peak. This 30-dB criterion for first peak and second peak measures is based on Nowicki (1989). Relative amplitude parameters were *position of maximal amplitude* ([time at peak amplitude-note start time]/note duration), *max to first peak amplitude difference* (the difference in amplitude from the max peak to the first peak

measured at 50% of the duration of the note), and 75%–50% *amplitude modulation* (the average of measures for first, second, and max peaks measured from 50% to 75% of the duration of the note).

C. Statistical analyses

The bulk of the analysis presented here focuses on the first A, first C, and first D notes in calls. However, to provide some context for the structure of these notes relative to the rest of the notes in the calls, we measured A and C note parameters for every A and C note in the calls, and D note parameters for the first, second, and last D note (when more than one D note occurred). We report general trends within strings of notes below, but carried out statistical tests only for the first A, C, and D notes in strings of A, C, and D notes, respectively. Since calls vary in the number of notes present within a string of the same note type (one of the components of the rudimentary syntax of the chick-a-dee call system), the power we have to detect syntax-specific note properties will obviously be highest with a detailed analysis of the first note in a sequence. Additionally, we analyzed in detail parameters for only these first notes of strings because there is a precedent for analyzing the first note in a series of the same note type (e.g., Mammen and Nowicki, 1981; Nowicki, 1989), and because one of the goals of the study was to determine whether information in the first note of a series of notes was predictive of the other notes in the call, as well as of sex or capture site.

We evaluated the source of variation in the properties of the chick-a-dee call in three ways. First, we ran a factor analysis of the parameters used to describe each note [PROC FACTOR; SAS Institute (1990)]. We then performed repeated-measures ANCOVA on the first factor for the first A note and first C note, and on the first two factors for the first D note in each call [PROC MIXED; SAS Institute (1990)]. Five independent variables were used in each ANCOVA: sex, capture site, number of A+B notes, number of C notes, and number of D notes in the call. Two-way interactions were added to the model and removed in order of increasing F statistic until all remaining interactions were significant ($\alpha=0.05$). For analysis of A notes, *duration* was log-transformed, and for analyses of D notes, *internote interval, pitch*, and *freq first peak* were log-transformed, to normalize the residuals of the ANCOVA models.

The factor scores were generally a robust index of the properties of a note, but they obviously did not explain all the variability in our measured note parameters. To ensure that no parameter-specific trends were missed, we also ran separate repeated-measures ANCOVAs for each measured note variable to determine the extent to which a bird's sex or capture site influenced specific properties of notes of the calls. Because we measured several variables for each of the notes (6 for A and C notes, and 12 for D notes), we corrected for multiple tests in these significance tests of single parameters using a sequential Bonferroni adjustment (Rice, 1989). The adjusted α value is provided with each of the reported significant tests. We carried out these sequential Bonferroni adjustments separately for sex and capture site.
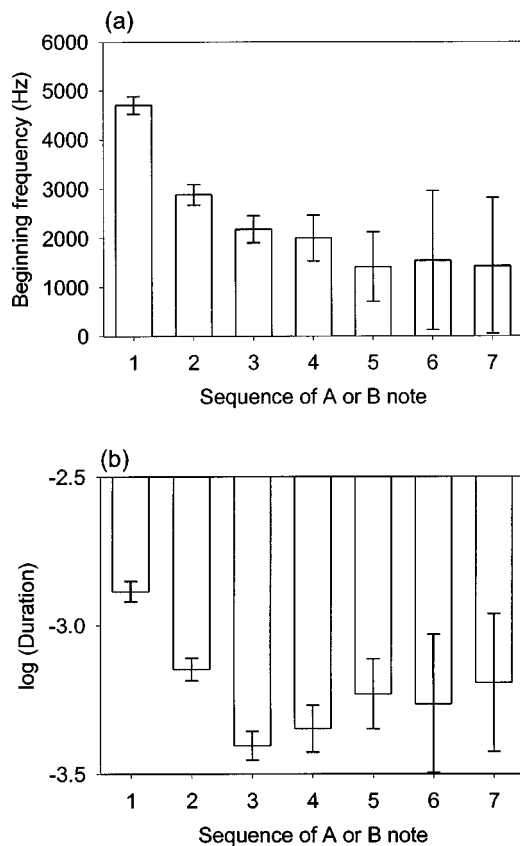
(a)

(b)

FIG. 2. Frequency and duration (log-transformed) characteristics of A notes within a string of A notes. Data are illustrated as means ±s.e.

III. RESULTS

In total, we analyzed 269 calls and 674 notes. Martell calls ($N=154$) contained on average ($\pm$s.d.) 2.1 ± 1.1 A $+$B notes (range in analyzed calls 0–8), 0.4 ± 0.9 C notes (range 0–6), and 3.6 ± 2.2 D notes (range 1–14). Ross calls ($N=115$) contained on average 2.4 ± 1.2 A+B notes (range 0–8), 0.2 ± 0.6 C notes (range 0–3), and 3.1 ± 1.9 D notes (range 1–12).

A. A notes

To provide some context for understanding variation in note structure between calls, it is important to realize that strings of introductory whistled notes (A and B notes) tend to start with high-frequency, long-duration notes. Subsequent notes show a decrease in both beginning frequency ($F_{6,43}=21.1, p<0.0001$) and duration (log-transformed, $F_{6,43}=17.3, p<0.0001$), as is generally the case with the chick-a-dee call in *Poecile* species (Fig. 2; see also Hailman, 1989). These trends are similar between sexes and between populations. This is illustrated by a lack of significant interaction between sex and the position of a note in a sequence of A/B notes (frequency: $F_{4,39}=0.22$, $p=0.92$; duration: $F_{4,58}=0.59$, $p=0.67$), and no significant interaction between population and note position (frequency: $F_{4,58}=0.49$, $p=0.74$; duration: $F_{4,58}=2.4$, $p=0.06$). Note that multiple notes of the same type are always clustered together in a string, and are never interdigitated with other note types in the call.

A factor analysis of the first A note in calls indicates that

TABLE II. Factor loadings for the first two factors of a factor analysis of the properties of the first A note in the chick-a-dee call. See text for definitions of properties.

Parameter	Factor 1	Factor 2
Log (Duration)	0.416	−0.312
Position of peak amplitude	0.584	−0.292
Beginning frequency	0.805	−0.260
Peak frequency	0.882	−0.023
End frequency	0.646	0.688
Shape	−0.629	0.530
Eigenvalue	2.75	1.01
Variance explained	46%	17%

the six parameters used to characterize the notes are all correlated with one another (Table II). Factor 1 (46% of the variance explained) is positively correlated with note duration, position of peak amplitude, and note frequencies (beginning, peak, and end), and is negatively correlated with note shape. Thus, longer notes (compared to shorter notes) tend to have higher frequencies, an amplitude peak relatively late in the note, and the peak frequency relatively early in the note. Only 17% of residual variance is explained by factor 2, and this residual variance is most strongly correlated with shape and end frequency (Table II).

We used factor 1 as an index of the properties of each note in a repeated-measures ANCOVA. Both sex category and capture site had an effect on factor 1 through a significant interaction between these parameters (sex: $F_{1,18}=1.2$, $P=0.29$; capture site: $F_{1,18}=0.5$, $P=0.48$; sex $\times$ capture site: $F_{1,18}=8.8$, $P=0.008$; Fig. 3). A multiple comparisons analysis shows that the interaction results from two different effects: (1) a significant effect of sex in birds from the Ross capture site ($t_{18}=2.8$, $P=0.013$), with male birds having lower factor 1 scores, and (2) a significant population difference between males ($t_{18}=2.6$, $P=0.02$), with Martell males showing higher scores than Ross males. Analysis of individual parameters found the duration of the first A note (log-transformed to normalize variance) to be significantly different between populations ($F_{1,19}=9.9$, adjusted $\alpha=0.0083$, $P=0.0054$): Martell A notes are longer than Ross A notes. Furthermore, there was a significant interaction between capture site and sex on beginning frequency ($F_{1,18}=10.86$, adjusted $\alpha=0.0083$, $P=0.004$). A multiple comparisons analysis shows that the interaction re-

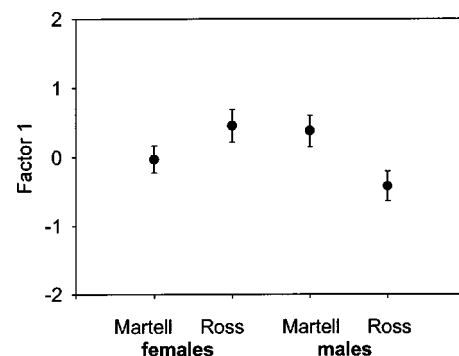FIG. 3. Factor 1 scores for Martell and Ross females and males. Data are illustrated as means ±s.e.

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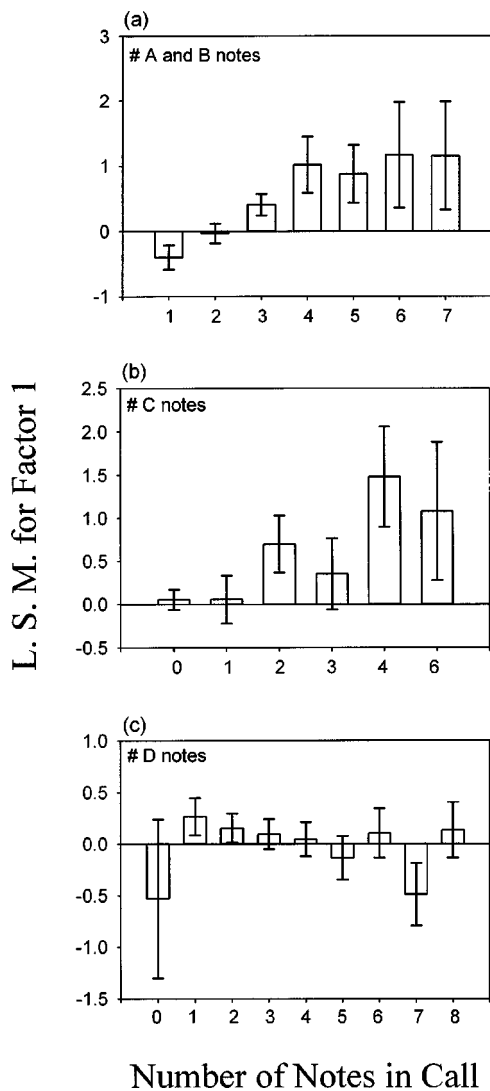
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FIG. 4. Factor 1 for the first A note as a function of the number of introductory whistled A and B notes in the call (a), the number of C notes in the call (b), and the number of D notes in the call (c). Data are illustrated as least squares means ±s.e.

TABLE III. Factor loadings for the first two factors of a factor analysis of the properties of the first C note in the chick-a-dee call. See text for definitions of properties.

Parameter	Factor 1	Factor 2
Duration	−0.849	−0.283
Pitch	0.282	0.604
Continuity	−0.860	0.409
Entropy	0.891	−0.324
Peak frequency	0.901	0.096
Modulation	0.467	0.307
Eigenvalue	3.36	0.82
Variance explained	80%	18%

notes. In other words, the parameters we measured for C notes are not significantly different whether the note is the first, second, or last in a long string of C notes.

A factor analysis of the six parameters used to characterize C notes generated one factor with an eigenvalue greater than 1 (80% variance explained: Table III). Factor 1 was negatively correlated with C note duration and continuity, and positively correlated with entropy and peak frequency. Thus, short C notes (compared to long C notes) tend to be noisy (low continuity and high entropy), and have a high peak frequency.

Repeated measures ANCOVA suggests that factor 1 scores do not vary with bird sex category or with the site from which the birds were sampled (Factor 1: sex, $F_{1,10}=0.84$, $P=0.38$; site, $F_{1,10}=1.41$, $P=0.26$). Analysis of single parameters of the C notes found a significant effect of capture site on duration of the note ($F_{1,10}=31.51$, adjusted $\alpha=0.0083$, $P=0.0002$): Martell C notes are longer in duration than Ross C notes.

Also unlike series of A notes, the structure of the first C note does not appear to change appreciably with the syntax of the call. We detected no effect on factor 1 of the number of introductory whistled notes [number A+B notes: $F_{1,5}=0.97$, $P=0.37$; Fig. 5(a)], number of C notes [$F_{1,3}=0.21$, $P=0.68$; Fig. 5(b)], or number of D notes [$F_{1,2}=1.78$, $P=0.31$; Fig. 5(c)].

C. D notes

As with series of C notes, the structure of D notes does not appear to change greatly in a series of D notes. We collected measurements for the first, second, and last D note in each call (assuming the call had more than a single D note in it). Only note duration changed significantly, with the first D note being significantly shorter than the following notes ($F_{2,47}=16.1$, $p=0.0001$; Fig. 6). These trends were similar between sexes and between populations, as indicated by a lack of significant interaction between sex and the position of the note in the sequence of notes ($F_{2,45}=0.02$, $p=0.98$) and no significant interaction between population and note position ($F_{2,45}=2.58$, $p=0.09$).

A factor analysis of the 12 parameters used to characterize the first D note in each call generated two factors with eigenvalues greater than 1.0. Factor 1 (46% of the variance explained) primarily represents whole-note traits, showing positive correlations with the internote interval (log-

sults from two different effects: (1) a significant population difference between males ($t_{18}=3.17$, $P=0.005$), with Martell males showing higher frequency A notes than Ross males, and (2) a significant effect of sex in birds from the Ross capture site ($t_{18}=3.04$, $P=0.007$), with male birds having lower frequency A notes than females.

Following the first A note in a call, the subsequent note composition of the call had a significant effect on the structure of that first A note. Factor 1 scores increased significantly with an increase in the number of introductory whistled notes (A and B notes) in the call [$\beta=0.39\pm0.06$; $F_{1,17}=43.5$, $P<0.0001$; Fig. 4(a)], and showed a marginally significant increase with an increase in the number of C notes [$\beta=0.20\pm0.09$; $F_{1,20}=5.0$, $P=0.048$; Fig. 4(b)]. We did not detect an effect of the number of D notes in the call on factor 1 scores for the first A note [$F_{1,20}=1.2$, $P=0.30$; Fig. 4(c)].

B. C notes

Unlike series of A notes, the structure of the first C note does not appear to change appreciably within a string of C
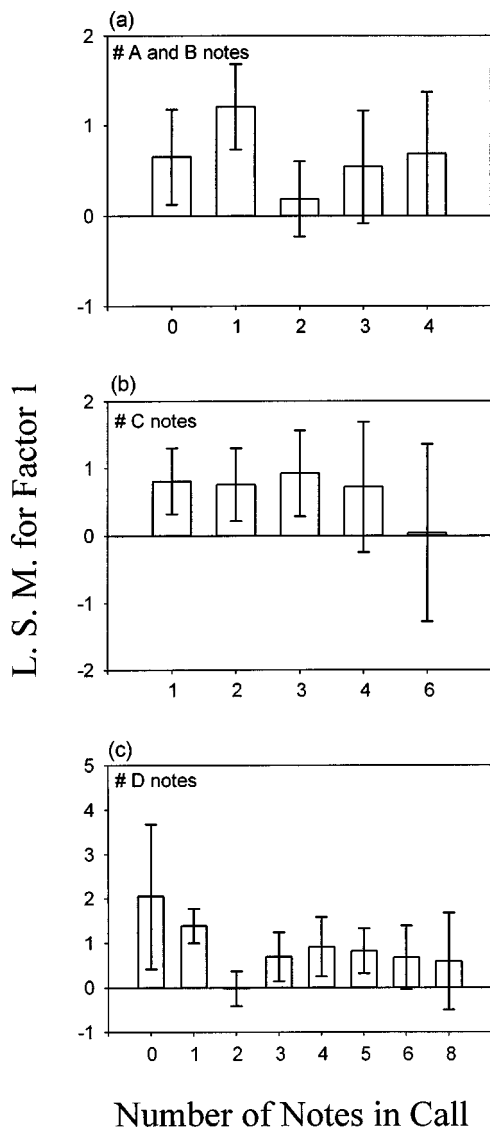
FIG. 5. Factor 1 for the first C note as a function of the number of introductory whistled A and B notes in the call (a), the number of C notes in the call (b), and the number of D notes in the call (c). Data are illustrated as least squares means ±s.e.

transformed), entropy, and modulation, and negative correlations with note duration, continuity, and the amplitude difference between the first and maximal frequency peaks (Table IV). Thus, long notes (compared to short notes) tend to have high continuity, low entropy, low modulation, a large ampli-
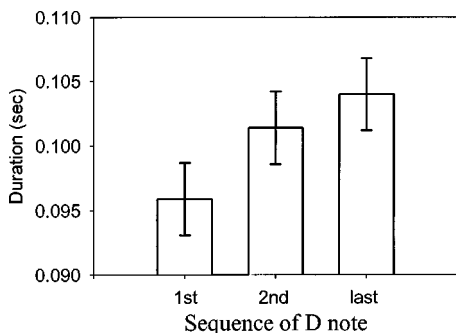

FIG. 6. Duration of D notes as a function of the sequence of D notes. Data are illustrated as means ±s.e.

TABLE IV. Factor loadings for the first two factors of a factor analysis of the properties of the first D note in the chick-a-dee call. See text for definitions of properties.

Parameter	Factor 1	Factor 2
duration	−0.478	0.056
Log (Freq 1st peak)	0.249	0.857
Freq 2nd peak	0.134	0.892
Freq max. peak	0.074	0.512
Position of maximal amplitude	0.015	0.159
Log (Inter-note interval)	0.529	0.128
75%–50% amplitude modulation	0.135	−0.270
Max to first peak amplitude difference	−0.598	−0.183
Entropy	0.610	0.074
Continuity	−0.852	0.282
Log (Pitch)	−0.284	−0.113
Modulation	0.598	−0.287
Eigenvalue	2.54	2.09
Variance explained	46%	38%

tude difference between the maximal amplitude frequency peak and the first peak, and a short internote interval. Factor 2 (38% variance explained) is strongly correlated with the frequency properties of the note, showing a positive correlation with the first, second, and maximal frequencies (Table IV).

Repeated measures ANCOVAs indicate that neither factor 1 nor factor 2 scores vary with bird sex or with the site from which the birds were sampled (factor 1: sex, $F_{1,22}=0.90$, $P=0.35$; capture site, $F_{1,22}=2.0$, $P=0.17$; factor 2: sex, $F_{1,22}=0.06$, $P=0.81$; capture site, $F_{1,22}=2.7$, $P=0.12$). While the composite properties derived from the factor analysis did not differ between birds of different capture sites or sex categories, two individual note parameters did differ between capture sites. There was a significant effect of capture site on amplitude modulation ($F_{1,22}=13.5$, adjusted $\alpha=0.0042$, $P=0.0013$) and an effect of capture site on frequency modulation ($F_{1,22}=5.2$, adjusted $\alpha=0.0045$, $P=0.0026$). D notes from the Martell site show stronger frequency modulation and stronger amplitude modulation than D notes from the Ross site.

Note composition had a significant effect on the properties of the first D note. For factor 1 scores, this includes the number of introductory whistled notes preceding the first D note [number of A+B notes, $F_{1,21}=16.3$, $P=0.0006$; Fig. 7(a)], the number of C notes preceding the first D note [$F_{1,11}=8.8$, $P=0.013$; Fig. 7(b)], and the number of D notes following the first D note [$F_{1,23}=19.9$, $P=0.0002$; Fig. 7(c)]. For all note types, an increase in the number of notes increased the factor 1 score (number of A+B notes: $\beta=0.32\pm0.08$; number of C notes: $\beta=0.18\pm0.06$; number of D notes: $\beta=0.20\pm0.04$). Thus, as the number of any single note type increased, the first D note became noisier (higher entropy, lower continuity), shorter in duration and with a longer internote interval, and more strongly frequency modulated.

Note composition had a different effect on factor 2 scores than it had on factor 1 scores. The number of introductory whistled notes and the number of C notes had no

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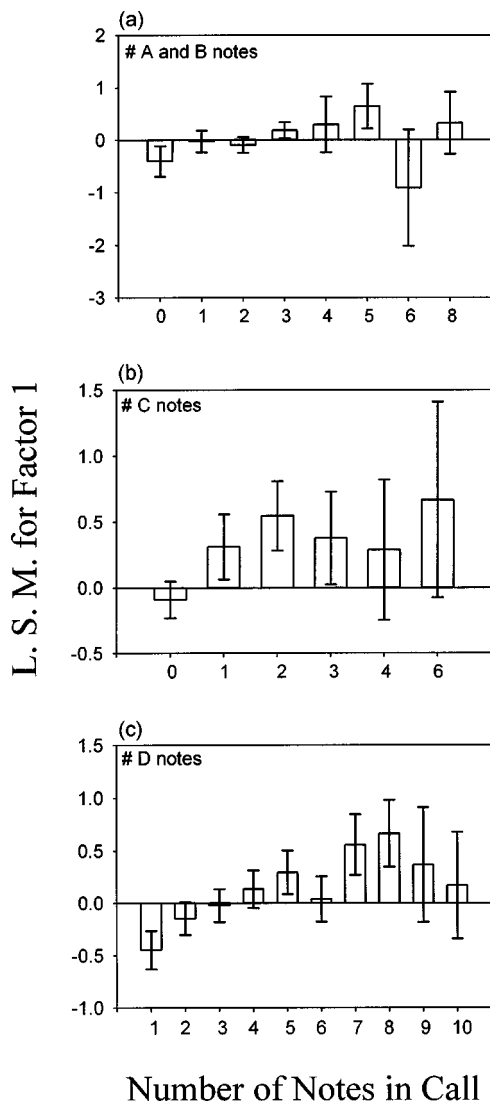Freeberg *et al.*: Variation in chick-a-dee calls   2133

FIG. 7. Factor 1 for the first D note as a function of the number of introductory whistled A and B notes in the call (a), the number of C notes in the call (b), and the number of D notes in the call (c). Data are illustrated as least squares means ±s.e.

effect on factor 2 scores (A+B notes: $F_{1,21}=0.13$, $P=0.72$; C notes: $F_{1,11}=3.4$, $P=0.09$). In contrast, factor 2 scores decreased significantly with an increase in the number of D notes ($F_{1,23}=5.3$, $P=0.031$; $\beta=-0.066\pm0.029$). Thus, first D notes tended to be lower in frequency when followed by a large number of D notes, compared to first D notes followed by few D notes.

IV. CONCLUSIONS

In the present study, we found that single elements within chick-a-dee calls (the first note in a string of A, C, or D notes) were predictive of a bird's local capture site. In one case we found a significant interaction between capture site and sex for a note type parameter, suggesting that at least some sex-specific characteristics of elements of a call can vary. However, at least for this Indiana population of Carolina chickadees, it appears that chick-a-dee calls are structurally much more sexually monomorphic than are vocalizations that have been tested for sexual differences in other

species—such as song in Northern cardinals (Yamaguchi, 1998a), contact calls in Bengalese finches (Okanoyak, 1993), and the vocal signals of collared doves (Ballintijn and ten Cate, 1997).

Most of the studies done to determine markers of identity in chick-a-dee calls of black-capped chickadees have focused on properties of the D notes (e.g., Mammen and Nowicki, 1981; Nowicki, 1989). Here, we found evidence of properties of D notes being predictive of a bird's capture site, but we also found that parameters in A and C notes were predictive of capture site. Factor analyses of A notes indicated an interaction between capture site and sex of bird for factor 1. Looking at individual parameters, both A note and C note duration predicted capture site. These microgeographic differences (5 km or less) suggest that chickadees learn these variations in note properties, as chickadees can easily disperse this distance within their lifetimes. Evidence of call learning has been documented in black-capped chickadees (Hughes et al., 1998; Nowicki, 1989), and, in addition, the Nowicki (1989) study suggested that adult birds could modify call parameters. Call learning and vocal plasticity in both females and males would appear to be advantageous for chickadee species in that flocks may differ in parameters of their chick-a-dee calls, so newly-independent young chickadees dispersing some distance from their parents' territory might have to modify their calls. Moreover, even adult individuals may be in different flocks from one winter to the next (see Dixon, 1963; Mammen and Nowicki, 1981; Odum, 1941, 1942; Weise and Meyer, 1979).

A previous study on micro-level geographic differences in black-capped chickadee calls (Mammen and Nowicki, 1981) failed to control for the note composition of calls when considering identity markers, despite the fact that note composition characteristics of the chick-a-dee calls differed between some of the flocks studied. Our results suggest that note composition has to be statistically controlled to remove the statistical confound between note composition (syntax) and note structure. As such, the nature of flock differences in the structure of the D note of black-capped chickadees needs to be reexamined.

The first A and D notes in a string of A and D notes were largely predictive of the note type composition of the call as a whole—i.e., of other notes (both of the same and of different note types) in the call. This suggests possible redundancy of information in this call system—whatever the meaning of a complete chick-a-dee call, the receiver potentially could ascertain that meaning by hearing only a portion of the call. Signal redundancy can result from multiple signals that refer to the same information [e.g., visual and vibrational mating cues (Uetz, 2000)] or from multiple dimensions of a single signal each of which refers to the same information, such as individual identity cued by multiple overtones and several frequency-modulated elements within a note (Jouventin et al., 1999). The chick-a-dee call provides a third type of redundancy where the properties of single notes provide cues about the syntactical structure of the entire call. Several studies have suggested that syntax (or more generally, note composition) is a critically important property of the chick-a-dee call (Ficken et al., 1994; Freeberg and Lucas, 2002;

Smith, 1972). These studies provide a context for why redundancy might evolve in the chick-a-dee vocal system.

Redundancy increases the ability of a receiver to detect correctly the relevant properties of a vocal signal (Wiley and Richards, 1982). A recent study on penguin vocal patterns illustrates this point well. King penguins, *Aptenodytes patagonicus*, increase both the number of calls given and the number of syllables per call under windy conditions, compared to vocalizations given under calm conditions (Lengagne *et al.*, 1999). Thus, the high background noise generated by wind causes these birds to give signals that are more redundant, and this increases the probability that receivers of those signals will be able to detect signal-specific cues (here individual recognition cues). We should emphasize that while note repetition is a form of redundancy in species like the king penguin, in the chick-a-dee call note repetition is more likely to be a part of the information encoded in the signal (here the entire call) than a simple redundant repetition of information encoded in a single note (see Smith, 1972).

In some chickadee species, longer strings of D notes have been hypothesized to function in "mobbing" behaviors in the context of a predator (Odum, 1942). In addition to hearing the long string of harsher D notes used in these "scolding" calls (or if due to background noise, the entire string of D notes is not heard), the results from our study indicate that a receiver might gain the information from individual parameters of the first D note heard [Fig. 7(c)]. Alternatively, if individual parameters of the first A note in a call (or of the string of A notes in general) convey information about alarm level, as suggested by a study of a structurally similar note type in Mexican chickadees, *P. sclateri*, by Ficken (1989), then a call possessing redundant information in the form of individual parameters of the first D note could convey a similar meaning [Fig. 7(a)]. As A notes are highly directional note types and appear to degrade in the environment more quickly than do the other note types (Witkin, 1977), this redundancy could be of adaptive significance (see also Marten and Marler, 1977).

It is important to stress, however, a limitation of the present study—we have assessed note type variation and call differences only from the standpoint of signal production. Playback tests are needed to determine whether receivers do respond to the note differences we have detected (e.g., Ratcliffe and Otter, 1996; Searcy and Nowicki, 1999; Yamaguchi, 1998b). This has been done, for example, at the level of flock differences in chick-a-dee calls in black-capped chickadees (Nowicki, 1983).

Physiological and anatomical constraints may provide a mechanistic explanation for this "redundancy" hypothesis in notes in chick-a-dee calls. A signaler about to produce a long string of A notes may need to begin that string at a higher frequency and with different relative amplitude characteristics, due to requirements of muscular processes or neuroanatomical structure at the level of the syrinx (Gaunt, 1996; Lambrechts, 1996). Physical constraints on vocal production have been documented in a number of avian taxa (Larsen and Goller, 1999; Podos, 1997; Suthers, 1999). Limits on the production of chick-a-dee calls in black-capped chickadees have been suggested. Hailman *et al.* (1987) argued that call

length and a general frequency decrease over the course of the call are likely constrained by a process similar to "breath groups" in human speech, whereby fundamental frequencies of speech decrease as alveolar pressure drops before another breath is taken. Learning experiments could be useful in determining whether frequency drops in chick-a-dee calls (and the gargle vocalization of *Poecile* species), and therefore parameters of individual notes, are constrained by physiological process (Lambrechts, 1996), or are constrained by the acoustical and social environment of young birds (Hughes *et al.*, 1998).

The chick-a-dee call in many species of the genus *Poecile* is a combinatorial communicative system. Because of this combinatorial nature, it has been hypothesized that call types with different numbers and proportions of individual notes could convey different meanings to call receivers (Hailman and Ficken, 1986; Hailman *et al.*, 1985). Hailman and Ficken (1996) suggested that chickadee signalers use chick-a-dee calls under situations of mild alarm, but in a diversity of contexts. Different *Poecile* species, furthermore, may use similar chick-a-dee calls in different contexts (Hailman and Ficken, 1996). These relationships between call composition and calling context in *Poecile* species would seem to be a fruitful area for comparative studies. Data from the present study suggest that the redundancy between call composition and single note properties might be widely distributed in the *Poecile*—comparative work on identity and redundancy in this complex call system might help elucidate the relationships between call composition and meaning.

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