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Note types and coding in parid vocalizations. I: The chick-a-dee call of the black-capped chickadee (*Poecile atricapillus*)

Isabelle Charrier, Laurie L. Bloomfield, and Christopher B. Sturdy

Abstract: The chick-a-dee call of the black-capped chickadee, *Poecile atricapillus* (L., 1766), consists of four note types and is used in a wide variety of contexts including mild alarm, contact between mates, and for mobilizing members of winter flocks. Because note-type composition varies with context and because birds need to identify flock mates and individuals by their calls, it is important that birds are able to discriminate between note types and birds. Moreover, previous experiments have shown that black-capped chickadees are able to discriminate their four note types, but the acoustical basis of this process is still unknown. Here, we present the results of a bioacoustic analysis that suggests which acoustic features may be controlling the birds' perception of note types and of individual identity. Several acoustic features show high note type and individual specificity, but frequency and frequency modulation cues (in particular, those of the initial part of the note) appear more likely to be used in these processes. However, only future experiments testing the bird's perceptual abilities will determine which acoustic cues in particular are used in the discrimination of note types and in individual recognition.

Résumé : Le chant « chick-a-dee » de la mésange à tête noire, *Poecile atricapillus* (L., 1766), est composé de quatre types de notes et il est utilisé dans de nombreux contextes, comme l'alarme, le contact entre partenaires et entre membres du groupe. La composition en notes variant avec le contexte et les oiseaux ayant besoin de s'identifier entre eux par leurs vocalisations, il est important qu'ils soient capables de discriminer à la fois les différents types de notes, mais aussi les divers individus du groupe. La mésange à tête noire perçoit les différents types de notes de son chant comme des catégories ouvertes, cependant la base acoustique de cette catégorisation est encore inconnue. Nous rapportons ici les résultats d'une analyse acoustique qui présente les paramètres acoustiques susceptibles de contrôler la perception des types de notes et la reconnaissance individuelle. Plusieurs paramètres sont spécifiques à chaque type de note et à chaque individu, cependant seuls les paramètres relatifs aux fréquences et à la modulation de fréquence, en particulier ceux de la partie initiale, semblent les plus susceptibles d'être utilisés dans ces processus. De futures expériences testant les capacités de perception de l'oiseau permettront de déterminer les paramètres acoustiques effectivement utilisés dans la discrimination des types de notes et dans la reconnaissance individuelle.

Introduction

Songbirds (the oscines) are an increasingly popular model system for understanding the proximate mechanisms and ultimate functions underlying vertebrate acoustic communication (for a review see Slater 2003). This popularity is due to a number of factors, not the least of which is that songbirds learn song from a model in a manner considered analogous to human language learning (Doupe and Kuhl 1999). Moreover, male songbirds use song as an acoustic ornament to attract females and females select mates using song quality as an indicator of male fitness (Catchpole and Slater 1995). However, songbirds learn, produce, and perceive vocalizations other than song (namely, learned calls), and use these vocalizations in the context of specific behavioural interactions. Therefore, if one seeks a comprehensive understanding of acoustic communication, the analysis must not focus exclusively on learned song. Rather, all modes of acoustic signaling, including the mechanisms and function of communication via learned calls, must be considered (for others following this broadening of scope see Hailman and Ficken 1996; Hughes et al. 1998; Vicario et al. 2002).

One of the most well-understood examples of learned calls is the chick-a-dee call of the black-capped chickadee, *Poecile atricapillus* (L., 1766). Black-capped chickadees are small songbirds native to North America that possess a large, well-studied vocal repertoire. Two of the most well studied of their suite of vocalizations, both of which are learned, are the whistled fee-bee song (e.g., Ficken et al. 1978; Ratcliffe and Weisman 1985), which is used to attract and maintain a mate and defend a territory, and the aforementioned chick-a-dee call, which is used to raise mild

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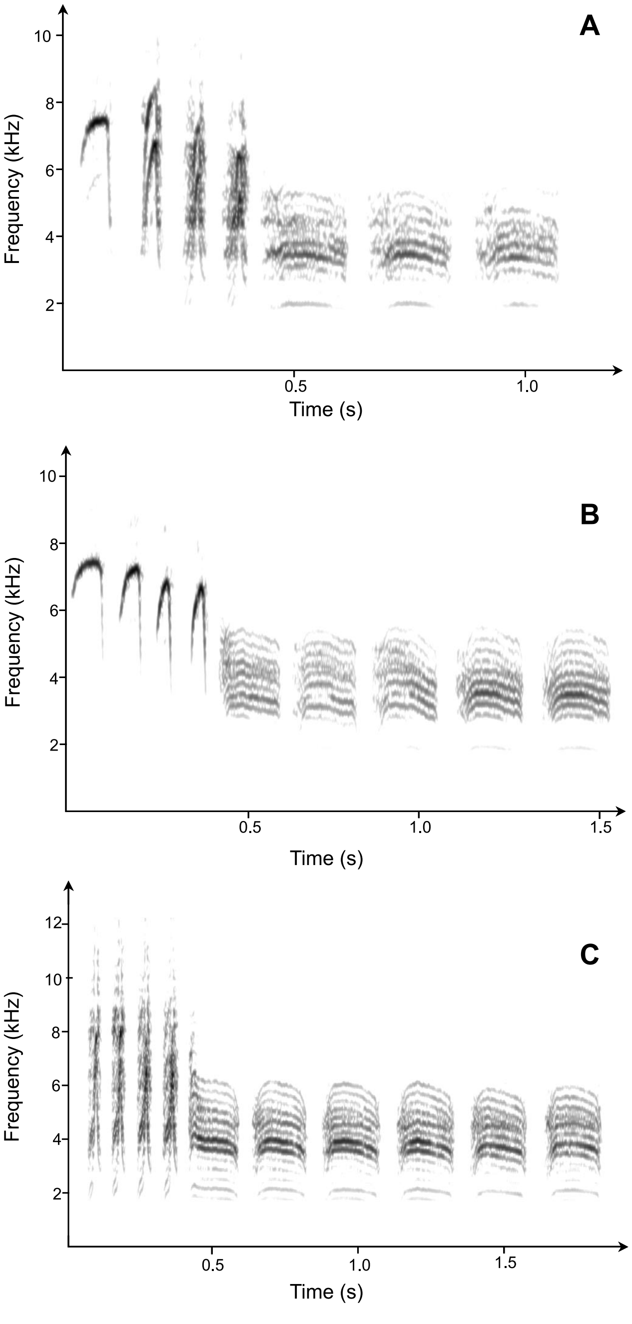
alarm and coordinate flock activities (Ficken et al. 1978; Hailman et al. 1985). In contrast to the songs of many songbird species, the song of the black-capped chickadee is significantly less acoustically complex than their chick-a-dee call. The fee-bee song consists of two whistled notes that are sung at a constant pitch interval relative to each other (Weisman et al. 1990). Chick-a-dee calls contain four note types (A, B, C, and D) sung in a fixed order (A→B→C→D), but note types can be repeated or omitted to produce chick-a-dee calls with seemingly infinite combinations of notes (e.g., ACCCCD, ABDDD; see Fig. 1). The combinatorial nature of this call shares many features with human speech (Hailman et al. 1985). Therefore, not only is the chick-a-dee call "learned" in a comparative manner to human speech, but unlike learned song, it also appears to be "used" in a comparative manner to human speech. That is, the number of notes and note-type occurrence between renditions of the chick-a-dee call change with context (Smith 1972; Gaddis 1985; Ficken et al. 1994; Freeberg and Lucas 2002), and new call compositions are often observed both in the field and during recording sessions in the laboratory.

Individual calls and note types within the chick-a-dee call have been shown to convey specific information. For instance, black-capped chickadees are capable of discriminating between their own and foreign flocks' chick-a-dee calls, and adapting their behaviour in response to playback of unfamiliar calls (Mammen and Nowicki 1981). This is thought to be mediated, in large part, by D notes. These notes have been shown to be subject to acoustic modification in adulthood, allowing flocks to produce D notes with flock-specific acoustic signatures (Nowicki 1989). Adding to the evidence for coding in chick-a-dee calls in the genus *Poecile*, Freeberg and Lucas (2002) showed that C notes from the chick-a-dee call of the closely related Carolina chickadee, *Poecile carolinensis* (Audubon, 1834), appear to be used to indicate the location or availability of food sources. Finally, black-capped chickadees perceive their chick-a-dee calls as well as their constituent note types as natural, open-ended categories (i.e., open-ended categorization is the ability to perceive similarities between novel and familiar category exemplars); thus, providing a perceptual mechanism capable of quickly handling the large volumes of acoustic processing required by this species in nature (Bloomfield et al. 2003; Sturdy et al. 2000). Although the chick-a-dee call has the potential to code significant amounts of information, the mechanisms by which the information is decoded remain either unclear or unknown altogether. For instance, what are the particular acoustic parameters in call notes used in note-type discrimination and in individual recognition? Our first hypothesis is that birds may use acoustic features that are variable between note types and invariable within note types. This assumption relies on the fact that each note type has been defined with regards to their structural differences between and within types (Ficken et al. 1978; Nowicki and Nelson 1990). Moreover, black-capped chickadees are able to discriminate among these four note categories, but they sometimes confuse adjacent note types (A with B or B with C; Sturdy et al. 2000). This supports the notion that sources of acoustic divergence between note types may allow birds to discriminate between note categories, and that sources of acoustic similarity between note types may sometimes induce confusion. A previous bioacoustic analysis of the chick-a-dee call of the black-capped chickadee has demonstrated through a principal component analysis (PCA) that different acoustic components allow the classification between note types, and that some overlap occurs between adjacent note types (Nowicki and Nelson 1990). The most parsimonious hypothesis is that birds may use one or several acoustic features that vary between note types to perceive

Fig. 1. Spectrogram of the different kinds of syntax in chick-a-dee calls from black-capped chickadees, *Poceile atricapillus*, (window size = 512 points, frequency precision = 86.1 Hz) showing the highly variable composition of note types. (A) Call with the four note types: ABCCDDD. (B) Call with two note types (A and D): AAAADDDDD. (C) Call with two other note types (C and D): CCCCDDDDDD.



the four note categories. Thus, it is necessary to quantify the potential of each acoustic feature to encode the note category by conducting a detailed bioacoustic analysis of the chick-a-dee call of the black-capped chickadee on a large sample of notes. Although several analyses of this call have been conducted in the past, such descriptive data have not yet been published.

The second question, i.e., what are the acoustic features used in individual recognition, is relevant because the black-capped chickadee is a highly social bird species. As such, each bird needs to be able to discriminate between members of its own flock from birds of other flocks, but also to discriminate among individuals of its own flock. Previous studies have shown that D notes display acoustic convergence within members of the same flock. In other words, D notes contain a flock-specific acoustic signature (Nowicki 1989). In a similar manner, the individual acoustic signature may also be found in one or all note types. Since chick-a-dee calls are not always composed of the four note types, individual identity information may be encoded in each note type, and by one acoustic feature alone or several acoustic features in combination. The prerequisite for individual recognition is individual variation (Falls 1982) so that an acoustic parameter encoding individual identity has to show a high individual stereotypy to be effective (i.e., a weak intra-individual variability combined with a high interindividual variability) (in birds: Beer 1979; Jouventin et al. 1979; Jouventin 1982; Robisson et al. 1993; Lambrechts and Dhondt 1995; Mathevon 1996; Lengagne et al. 1998; Mathevon et al. 2003; in mammals: Stirling and Warneke 1971; Trillmich 1981; Insley 1992; Phillips and Stirling 2000; Charrier et al. 2001*a*, 2002, 2003). Therefore, the second aspect of our bioacoustic analysis is to identify the acoustic features in each note type that could be potentially used in the individual recognition process. Taken together, we created a bioacoustic foundation for future perceptual studies of chick-a-dee call-note category perception and individual recognition.

Materials and methods

Animals

Ten adult (after 2nd year) black-capped chickadees were captured during the winters of 2002 and 2003 from two locations in Alberta: six from the Barrier Lake Field Station (51°02′N, 115°03′W) and four from the Forest Reserve, adjacent to the campus of the University of Alberta in Edmonton (Alberta, Canada). Age was assessed using the shape and coloration of the outer retrices (Pyle 1997), with adults having broad, white-fringed outer tail feathers. Of the 10 birds, 6 were males and 4 were females as assessed either by visually inspecting their gonads via laparotomy or by DNA analyses conducted on blood samples (see Griffiths 2000). Birds were housed in individual cages (38.5 cm wide × 26 cm deep × 41 cm high) and had ad libidum access to food, water, cuttle bone, and grit mixture (Rolf C. Hagen Inc., Montreal, Quebec, Canada). To ensure good health, liquid vitamin was added to the water three times per week (Rolf C. Hagen Inc., Montreal, Quebec, Canada). Supplemental food such as ground hard-boiled egg and spinach was given once per week and mealworms were provided three times per week. Animals were maintained on natural day–night cycle for the season in Edmonton and at approximately 20 °C.

Recording procedure and signal acquisition

Birds were recorded in a 1.83 m × 1.83 m × 1.83 m “walk-in” sound attenuating chamber (Industrial Acoustics Corporation, Bronx, New York, USA) using an AKG C 1000S microphone (frequency response: 20 – 20 000 Hz; AKG, Vienna, Austria) connected to an Applied Research Technology (ART) original microphone preamplifier (frequency response: 10 – 20 000 Hz; ART, Rochester, New York, USA) and a Sony SME Modified TCM-5000EV Bird Version tape recorder (frequency response: 90 – 12 000 Hz; Sony, Tokyo, Japan). On occasion, a mirror was attached to the cage or one human observer was present for a few minutes in the acoustic chamber to induce vocalizations. Each bird was recorded until we had a sample of at least 20 calls for each bird.

Recordings were digitized at 44 100 Hz, 16-bit samples/s using a 16-bit DartDisk Direct-to-Disk recorder (Engineering Design, Belmont, Massachusetts, USA). Calls were analyzed using SIGNAL version 4.0 sound analysis software (Engineering Design 2003).

Acoustic analysis

We measured a total sample of 100 calls, selected using the following method: for each bird recorded, we randomly chose the first 5 calls containing either a B or a C note. This was done to ensure more equal representation of low-probability B and C notes. Our method was an adaptation of Nowicki and Nelson’s (1990) selection procedure and was aimed at ameliorating a similar problem that they had in their sample. Once the B- and C-containing calls were selected, we randomly chose five additional calls, irrespective of their note-type composition, for each bird in our sample. To standardize our analyses, each individual call note was saved as a separate file with a duration set to 300 ms, which was accomplished by adding leading and trailing silence of equal duration to each individual note file.

For non-D notes (i.e., A, B, and C notes), we measured 10 acoustic features based on the methods described in Nowicki and Nelson (1990). These measurements included: start frequency (SF in Hertz), peak frequency (PF in Hertz), end frequency (EF in Hertz), and note peak frequency (i.e., loudest frequency in the highest harmonic when additional harmonics occur; NPF in Hertz); all of which were measured on a digital spectrogram (window size = 1024 points, frequency precision = 43 Hz; Fig. 2A). Measurements on A and B notes were made on the main (i.e., highest amplitude) harmonic, whereas measurements of SF, PF, and EF were made on the first visible harmonic for C notes. All measurements on spectrograms were performed by using a cutoff amplitude of –35 dB relative to the peak amplitude in the note. We also measured the loudest frequency (F_{max} in Hertz) using a power spectrum (average window size = 4096 points, frequency precision = 11 Hz; Fig. 2C).

The duration measurements included were ascending duration (AD in milliseconds), descending duration (DD in milliseconds), and total duration (TD in milliseconds), and were measured on a digital spectrogram (window size = 256

Fig. 2. Analysis of acoustic features of chick-a-dee call notes. (A) Spectrogram of non-D notes resolved at high frequency to assess the variables start (SF), peak (PF), and end frequencies (EF), and the note peak frequency (NPF) when it occurs (window size = 1024 points, frequency precision = 43.1 Hz). (B) Spectrogram of non-D notes resolved at high time to assess the variables total (TD), ascending (AD), and descending durations (DD) (window size = 256 points, time resolution = 5.8 ms). (C) Power spectrum of non-D notes used to measure the loudest frequency in the note (F_{max}). The window size used for this analysis depends on the duration of the note (the A note of the call shown: window size = 4096 points, frequency precision = 10.8 Hz). (D) Spectrogram of D notes resolved at high time to assess TD (window size = 256 points, time resolution = 5.8 ms). (E) Power spectrum on D notes used to measure the first visible harmonic (f_0), F_{max}, and the highest NPF (window size = 16 384 points, frequency precision = 2.7 Hz) with a cutoff amplitude of –35 dB relative to the peak amplitude in the note.

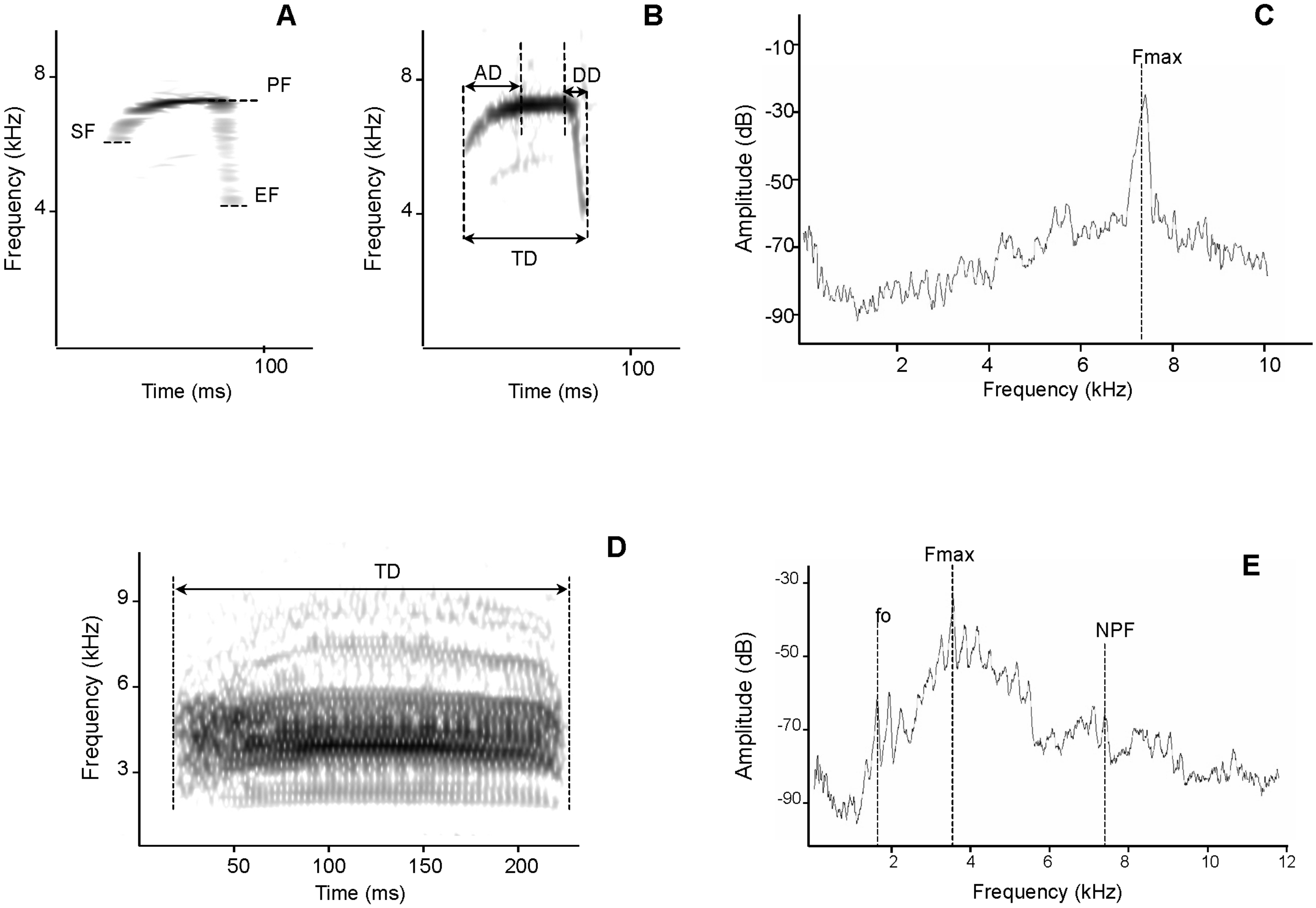


Table 1. Syntax of calls of black-capped chickadees, *Poecile atricapillus.*

	AD	BD	CD	ABC	ABD	ACD	BCD	ABCD
Percentage of calls	15	4	2	2	63	1	1	12
Number of birds	8	2	1	2	9	1	1	2

points, temporal precision = 5.8 ms; Fig. 2B). Two other measurements of frequency modulation were also made: the slope of the ascending frequency modulation (FM_{asc} in Hertz per milliseconds following the formula (PF – SF)/AD) and the slope of the descending frequency modulation (FM_{desc} in Hertz per milliseconds following the formula (EF – PF)/DD).

For D notes, we measured four acoustic features: total duration (TD in milliseconds; Fig. 2D), frequency of the first visible harmonic (f_0 in Hertz), loudest frequency (F_{max} in Hertz), and NPF. These three frequency parameters were obtained using a power spectrum with a fast Fourier transform window size of 16 384 points and a frequency precision of 2.7 Hz (smoothing width = 88.2 Hz; Fig. 2E).

Statistical analysis

All statistical analyses were performed using STATISTICA version 6 (StatSoft Inc. 2002) and SPSS version 11.5 (SPSS Inc. 2002).

For the analysis of note-specific acoustic features in non-D notes (i.e., A, B, C), we analyzed the potential for note-type coding (PNTC), which indicates whether an acoustic feature can be used in the note-type discrimination process. The PNTC is the ratio between the coefficient of variation between note types (CV_b) and the mean of the coefficients of variation within note types (mean CV_w). Note that PNTC is an adaptation of the method for the potential for individual identity coding (PIC) in animal vocalizations; see below for details. A high PNTC value for a given acoustic feature suggests that this feature is specific to a particular note type and may therefore provide birds with a cue to discriminate between the three note types (A, B, and C). For each acoustic feature, we performed univariate analyses of variance (ANOVA) to statistically assess the difference between non-D notes (A, B, and C). Since a significant difference between note types was found, we performed the post hoc Games–Howell test, which is designed for unequal variances and unequal sample sizes (Toothaker 1993), to determine which means differed.

Following current statistical recommendations (e.g., Moser et al. 1989; Moser and Stevens 1992), we employed corrections for unequal variances (Welch's correction; Welch 1938) for all *t* tests and ANOVAs, regardless of the results of the heteroscedasticity diagnostic tests. As we measured several acoustic features for each note type and performed multiple tests on the same data set, we adjusted the level of significance using a Bonferroni adjustment (i.e., we measured 9 for non-D notes and 3 for D notes, so the adjusted significance levels were $p' = 0.05/9 = 0.006$ and $p' = 0.05/3 = 0.017$, respectively; Keppel 1991). For the post hoc analysis, we also adjusted the level of significance for the Games–Howell test as a function of the number of performed comparisons (i.e., for the comparison between the A, B, and C notes, $p' = 0.017$).

To support individual recognition, calls have to show a highly individualized vocal signature; thus, allowing birds to discriminate their mates or the members of their winter flocks from other birds. Therefore, an acoustic parameter encoding individual identity has to show a high individual stereotypy (i.e., a weak intraindividual variability combined with a high interindividual variability). To identify the acoustic parameters that may encode individual identity in each note type, we assessed the intraindividual and interindividual variability of each parameter and calculated the ratio between the two to define a PIC. Acoustic cues showing PIC > 1 are generally regarded as parameters that may be used for individual recognition, since their intraindividual variability is smaller than their interindividual variability (Robisson et al. 1993; Lengagne et al. 1998; Charrier et al. 2001*a*, 2002, 2003; Mathevon et al. 2003).

We measured the intra- and inter-individual variations of each parameter by calculating the CV (Robisson et al. 1993; Lengagne et al. 1998; Charrier et al. 2001*a*, 2002, 2003; Mathevon et al. 2003). More precisely, we calculated CV_w (CV within individuals according to the formula for small samples: $CV_w = (SD/X_{mean})(1 + 1/4n) \times 100$ where SD is the standard deviation, X_{mean} is the mean of the sample, and n is the sample size for one individual) and CV_b (CV between individuals according to the formula: $CV_b = (SD/X_{mean}) \times 100$ where the SD and X_{mean} are calculated for the total sample) (Sokal and Rohlf 1995). To assess the PIC value for each parameter, we calculated the ratio CV_b/mean CV_w where the mean CV_w is the mean value of the CV_w for all individuals (Robisson et al. 1993). For each acoustic feature and each note type, we performed ANOVAs to statistically assess the difference between individuals.

Results

A total of 712 notes were analyzed: 205 A notes, 134 B notes, 31 C notes, and 342 D notes. After our initial call selection, we had only 16 C notes from three birds. In an effort to increase the number of C notes in our sample and the number of birds contributing C notes to our analysis, we chose to search our sample for additional C notes. For two birds, we randomly replaced one call without C notes with one containing C notes. We also replaced one bird that did not produce C notes with another that did produce C notes. By adopting this secondary strategy, we increased our C-note sample size to 32 notes from six birds.

Individual chick-a-dee calls of black-capped chickadees were composed of 3–21 notes (7 ± 3 notes). The mean call duration was 1147 ± 423 ms, ranging from 616 ms (3 notes) to 2423 ms (21 notes). In our sample, 63% of calls were composed of a combination of A, B, and D notes (e.g., AABDDD, AAAABDDDD; Fig. 2A–2E).

Location and sex differences

To test if the source of variability in our sample may come from the particular location where birds were caught or (and) from their gender, we performed Welch's *t* test on each acoustic feature and for each note type. No significant differences were found between the two locations (for non-D notes, all *t*s < 2.98, $p' = 0.006$, and all found p values ranged between 0.007 and 0.865; for D notes, $t < 0.571$, $p' = 0.017$, and p values ranged between 0.515 and 0.827). We also found no sex effect in non-D notes for each parameter (all *t*s < 1.59, $p' = 0.006$, and all found p values ranged between 0.204 and 0.895). For D notes, only F_{max} seems to differ between males and females (Welch's *t* test, $t_{[6.127]} = -4.221$, $p = 0.005$ and $p' = 0.017$). This does not implicate a general rule that differences in chick-a-dee call characteristics do not occur with geographic sites or sex, but that we did not detect such a source of variability in our sample.

Note-type acoustic features

Results obtained for the different acoustic measurements on non-D notes are summarized in Table 2. The three non-D note types differed significantly in all acoustic features, except for DD (ANOVA with Welch's correction, $F_{[2,145.9]} = 2.417$, $p = 0.093$; Table 2). However, for some features such as PF, FM_{desc}, and F_{max}, the PNTC values observed were close to 1; therefore, these features were unlikely to be used in note-type discrimination. In contrast, some other features such as TD, AD, SF, EF, and FM_{asc} showed PNTC > 1; therefore, these features were likely to be used in the note-type perception process.

By performing post hoc analyses for all acoustic measurements in non-D notes, we found no significant differences between B and C notes for the slopes of the ascending part (FM_{asc}: Games–Howell test, difference = 17.6, $p' = 0.017$ and $p = 0.280$) and descending part (FM_{desc}: Games–Howell

Table 2. Potential for note-type coding (PNTC) for the 10 acoustic parameters measured on A, B, and C notes.

	TD	AD	DD	SF	PF	EF	FM_{asc}	FM_{desc}	F_{max}
CV_b	25.7	38.2	42.9	35.1	11.8	19.9	66.4	32.3	11.7
Mean CV_w	16.5	26.2	34.2	12.8	11.2	12.7	42.1	31.4	11.4
PNTC	1.6	1.5	1.3	2.7	1.06	1.6	1.6	1.03	1.03
ANOVA	59.7*	77.7*	2.4^{ns}	2194*	135.4*	249.9*	264.7*	13.2*	133.3*
Games–Howell test	**	**	ns	**	**	**	**, except between B and C where $p = 0.28$	**, except between B and C where $p = 0.257$	**, except between B and C where $p = 0.041$

Note: TD, total duration; AD, ascending duration; DD, descending duration; SF, start frequency; PF, peak frequency; EF, end frequency; FM_{asc}, ascending frequency modulation; FM_{desc}, descending frequency modulation; F_{max}, loudest frequency in the note; CV_b, coefficient of variation between note types; CV_w, mean of the coefficients of variation within note types; ns, not significant.

*All parameters differed significantly between the three non-D notes (adjusted significance level $p < 0.0056$), except the DD parameter ($p = 0.093$).

**For multiple comparison tests (the Games–Howell test), we found that FM_{asc}, FM_{desc}, and F_{max} were not significantly different between the B and C notes (adjusted significant level $p < 0.0167$).

test, difference = 23.8, $p' = 0.017$ and $p = 0.257$), and for F_{max} (Games–Howell test, difference = 490, $p' = 0.017$ and $p = 0.04$). This could explain why the PNTC values found for these three features were lower than the others. Taken together, several features can potentially be used by birds to discriminate among the note types of a chick-a-dee call (Table 2).

Individual identity in note types

For each note type and for each acoustic feature examined, the ANOVA revealed significant differences between individual birds. The CV_b was larger than the mean CV_w, with the exception of the slope of FM_{desc} in A notes and the SF in B notes (see Table 3). We obtained PIC > 1 for all acoustic features except for both these parameters (0.96 and 0.98, respectively). The highest PIC values (PIC > 2; see Table 3) were obtained for three parameters in the C notes: PF, FM_{asc}, and F_{max}. However, in the C notes, we also found that there were no significant differences between individuals for four of the parameters, these same features having PIC values close to 1 (TD, DD, SF, and EF). For D notes, PIC values were >1 and all features were significantly different between individuals (Table 4). For F_{max}, we performed a separate analysis for males and females because a significant difference had been previously found between the sexes, and there was still a difference between individuals for both males ($F_{[5,66.96]} = 3.7$, $p = 0.005$) and females ($F_{[3,76.125]} = 8.0$, $p = 0.000$). To summarize, for each note type, several acoustic features were highly individualized, which may be used in the individual recognition process (PIC > 1).

Discussion

Acoustic features potentially involved in note-type perception

Our note-type analyses of the bioacoustic data revealed that the non-D notes differed significantly in all acoustic parameters, except for DD (Table 2). In other words, the only parameter that did not distinguish note types was the duration from the peak of the note to the end of the note (DD). What this analysis indicates is that each note type has several distinguishing acoustic features that are note-type unique, and from a communication standpoint, means that there are redundant cues for identifying notes by their type. This would significantly aid in ensuring correct note-type discrimination in the face of signal transmission problems or environmental interference such as wind, movement of leaves and branches, or the sounds of other animals' acoustic communication (Wiley and Richards 1978, 1982).

Although it is true that almost all acoustic features differ significantly among non-D note types, are all of these features used in note-type discrimination or only a few? Which ones are the most reliable? When the acoustic features of non-D notes were subjected to a PNTC analysis, all but the DD were significantly different among note types. However, when the PNTC was assessed, we saw some clear differences emerging that were not evident in our initial analyses. For instance, PF, FM_{desc}, and F_{max} had PNTC values close to 1. Therefore, although the mean values of these features differed significantly among note types, according to the PNTC analyses, they were not likely candidates for note-type dis-

Table 3. Analysis of the 10 acoustic features measured on non-D notes showing potential for individual identity coding (PIC).

Note type	TD	AD	DD	SF	PF	EF	FM_{asc}	FM_{desc}	F_{max}	NPF
A										
Mean ± SD	67.9±17.4 ms	37.4±13.1 ms	12.6±6.3 ms	5728±824 Hz	7241±381 Hz	3877±631 Hz	46.0±25.7 Hz/ms	–298.5±84.6 Hz/ms	7150.5±397.6 Hz	9476±895 Hz
CV_b	25.6	35.0	50.3	14.4	5.3	16.3	55.8	–28.4	5.6	9.4
Mean CV_w	21.2	31.3	30.0	13.0	4.8	15.5	47.2	–29.5	5.0	—
PIC	1.2	1.1	1.7	1.1	1.1	1.0	1.2	0.96	1.1	—
ANOVA	11.5*	4.1*	9.1*	4.8*	5.5*	3.7*	7.2*	9.2*	5.8*	—
B										
Mean ± SD	52.3±8.5 ms	24.4±5.7 ms	13.7±4.8 ms	3304±518 Hz	6337±660 Hz	3153±451 Hz	131.8±40.6 Hz/ms	–261.2±96.5 Hz/ms	6214.1±647.3 Hz	8867±1722 Hz
CV_b	16.2	23.5	35.1	15.7	10.4	14.3	30.8	–36.9	10.4	19.4
Mean CV_w	10.1	20.1	19.8	15.9	8.6	13.3	26.0	–29.2	8.6	—
PIC	1.6	1.2	1.8	0.98	1.2	1.1	1.2	1.3	1.2	—
ANOVA	16.1*	9.9*	19.3*	2.7^{ns}	9.3*	4.7*	12.1*	21.2*	9.9*	—
C										
Mean ± SD	56.7±4.4 ms	27.0±5.1 ms	12.6±2.2 ms	1713±144 Hz	5644±938 Hz	2634±126 Hz	154.0±57.6 Hz/ms	–239.3±67.0 Hz/ms	5737±1009 Hz	12085±1009 Hz
CV_b	7.0	19	17.3	8.4	16.6	4.8	37.4	–28.0	17.6	8.3
Mean CV_w	6.0	11.4	13.2	6.6	6.2	3.2	16.9	–17.0	8.8	—
PIC	1.2	1.7	1.3	1.3	2.7	1.5	2.2	1.6	2.0	—
ANOVA	6.8^{ns}	15.6*	4.7^{ns}	6.5^{ns}	51.4*	5.9^{ns}	16.2*	12.0*	20.2*	—

Note: We chose 100 calls from 10 individuals and analysed 205 A notes, 134 B notes, and 32 C notes. NPF, note peak frequency; mean CV_w, average of the coefficients of variation within individual birds; CV_b, coefficient of variation between birds; ns, not significant. For other abbrevations refer to Table 2.

*The difference between individuals was assessed by performing an ANOVA (adjusted significance level $p < 0.0056$).

Table 4. Analysis of the four acoustic features measured on D notes showing potential for individual identity coding (PIC).

	TD	f_0	F_{max}	NPF
Mean ± SD	199±17 ms	1638±336 Hz	3563±257 Hz	8485±336 Hz
CV_b	8.3	20.5	7.2	4.0
Mean CV_w	5.5	11.5	6.2	—
PIC	1.5	1.8	1.2	—
ANOVA	57.2*	24.8*	13.1* (male: 3.7*; female: 8.0*)	—

Note: We analysed 342 D notes from 100 calls. f_0, frequency of the first visible harmonic; CV_b, coefficient of variation between birds; mean CV_w, mean of the coefficients of variation within individual birds.

*The difference between individuals was assessed by performing an ANOVA (adjusted significant level $p <$ 0.0167). For F_{max}, a separate ANOVA was performed on males and females, as this parameter was found significantly different with sex.

crimination. However, TD, AD, DD, SF, EF, and FM_{asc} returned high PNTC values and were likely to be critical to note-type perception.

Sex differences in call production

Another interesting aspect of our analysis is the non-detection of sex differences for all features of all note types except F_{max} in D notes. However, this result must not be considered a general rule, as our sample is probably too small to detect a sex difference in acoustic features. The only sex difference that we found was the F_{max} in D notes, which was higher pitched in females than in males. This is not surprising because male chickadees are usually larger than females (Smith 1991), and frequency features are linked to the anatomy of the vocal tract (Kelemen 1963; Suthers 1994) and body size (Fitch 1999), although this remains to be confirmed in black-capped chickadees. Regardless of the possible differences in morphology, this frequency characteristic may be used by birds for sex identification.

Comparisons among the A and B notes and the B and C notes

In addition to our overall analysis, we also conducted post hoc analyses to assess differences between A and B notes and between B and C notes. Our rationale here was to compare acoustic parameters among notes that were adjacent on the production (A→B→C) and perceptual (A notes were more similar to B notes than to C notes; C notes were more similar to B notes than to A notes) continua, in an effort to elucidate the features that may be contributing to the perception of these particular note types. Consistent with our previous analysis (see above), DD was not significantly different between A and B notes nor was it significantly different between B notes and C notes. This parameter is therefore an unlikely candidate in the note-type perception process. Three other parameters (FM_{desc}, FM_{asc}, and F_{max}) also appeared not to differ significantly between B notes or C notes. The other parameters related to duration, frequency, and maybe FM were likely to be used in the adjacent note-type discrimination.

These parameters are likely candidates used by black-capped chickadees to discriminate among note types in the chick-a-dee call. This begs the question of which features are used, if any, and which features are the most reliable? Our analyses showed that duration parameters such as TD and AD were significantly different among the three non-D note types. However, it seems unlikely that these acoustic features could be used reliably to discriminate among note types, because although there are significant differences between note types in these parameters, some A notes are as short as B notes and some B notes are as long as A notes. Because of this overlap, these parameters could not be used reliably as note-type cues. Moreover, by using these duration parameters, birds would be forced to compare notes on the basis of duration at the very limits of their ability to do so (birds can accurately detect 10%–20% changes in duration; Dooling 1982).

Unlike duration parameters, frequency parameters (i.e., SF and EF) are likely candidates for note-type perception. For instance, SF would allow accurate note-type discrimination because, on average, A notes start at 5700 Hz, B notes start at 3300 Hz, and C notes start at 1700 Hz. Considering that birds can discriminate as little as a 1% change in frequency, and that the average SF is non-overlapping between note types, then both of these features should facilitate discrimination between note types. Moreover, this would fall in line with studies suggesting that pitch is the single most important feature for song recognition in songbird vocalizations (Falls 1963; Brémond 1986; Lohr et al. 1994; Weisman et al. 1998). However, discrimination on the basis of pitch alone, especially high frequencies, has some drawbacks. At long ranges, pitch perception may be less accurate because high frequencies are greatly degraded through propagation, especially through obstacles such as vegetation (Wiley and Richards 1982). With that said, the chick-a-dee call is most often used at relatively short distances, so this pitfall may not prove insurmountable. Moreover, degraded signals can provide birds with important distance cues (Naguib 1995), and it has been shown that black-capped chickadees are able to recognize songs and calls despite these degradations (Phillmore et al. 2002).

Another feature that holds promise as a cue for note-type discrimination is FM. This feature has been shown to support several types of information in other species, such as individual identity and alarm (Becker 1982; Aubin 1989; Mathevon and Aubin 2001; Aubin and Jouventin 2002; Charrier et al. 2001*b*, 2002, 2003). Moreover, FM is know to be resistant to degradation, and thus has little or none of the propagation issues associated with pitch perception over distance, and songbirds are also very sensitive to variations in

FM as well as pitch (Becker 1982; Aubin 1989; Mathevon and Aubin 2001). It could be the case, then, that chick-a-dee call notes have two redundant frequency-based acoustic features which can be used either alone or in combination to discriminate among note types. The ability to reliably discriminate among note types in any environmental condition is crucial to chickadees' fitness, especially since information relative to locomotion and alarm, for example, is encoded in the syntax (i.e., occurrence of note types) of chick-a-dee calls (Ficken 1981; Hailman et al. 1985; Freeberg and Lucas 2002). Determining which of these two features are used by chickadees will be the subject of future operant conditioning and field playback experiments.

Acoustic features potentially involved in individual recognition

One critical issue in communication research in general is whether information is encoded in the signals that animals emit. The chick-a-dee call is no exception. Nowicki (1983, 1989) showed that flock-specific information is indeed encoded in the relative spacing of the frequencies in D notes, and that this parameter exhibits a high degree of plasticity. Other note types may also encode information specific to the flock or to the individual bird. Rather than starting with an experiment to determine whether any of the acoustic parameters are controlling behaviour, we instead conducted a PIC analysis on the acoustic features measured.

Similar to our PNTC analyses, our PIC analyses revealed that each note type had several acoustic features which may be used for individual recognition. Indeed, for all note types and all acoustic features, PIC values were all >1 except for FM_{desc} in A notes and SF in B notes. However, even if highly individualized, we can suppose that some acoustic cues are unlikely to be used in the individual recognition process. For example, cues related to duration are unlikely to be used because birds cannot discriminate less than a 10%–20% change in duration (Dooling 1982), and we found that the variability of note duration between birds was within this range (A notes = 68 ± 17 ms, B notes = 52 ± 8 ms, C notes = 57 ± 4 ms). Moreover, duration features can be highly degraded during propagation and are therefore not reliable to support accurate information. In fact, it has been shown experimentally that winter wrens, *Troglodytes troglodytes* (L., 1758), did not use this song feature to elicit territorial response (Holland et al. 2000). Frequency features are highly individualized, which is not surprising because their characteristics are linked to anatomical structures of the vocal tract (Kelemen 1963). As previously demonstrated, frequency features are often used in the individual recognition process (Charrier et al. 2001*b*; for review see Aubin and Jouventin 2002). In the case of the black-capped chickadee, even if the frequencies are high pitched and degraded during propagation, it seems likely that they may use these features at short ranges. Finally, FM, especially that occurring in the initial part of the note (FM_{asc}), seems to be a reliable feature that may be used in individual recognition. Indeed, as previously argued, FM is highly adapted to environmental constraints and is used in individual recognition in several other species (Becker 1982; Jouventin et al. 1999; Aubin and Jouventin 2002; Charrier et al. 2001*b*, 2002, 2003).

On the basis of these detailed analyses, we propose the following three hypotheses: (1) for note-type discrimination, birds may use the TD of the note, SF and FM of the initial part; (2) for individual recognition, they may use the FM of the initial part and frequency characteristics of the note; and (3) black-capped chickadees may use a combination of acoustic cues in both types of discrimination (note type and individual), and some features such as FM may be used in both processes.

Another important aspect will be to determine if all note types are involved in the individual recognition process. Indeed, although all note types have the potential to code for individual identity, the sum of PIC values for each non-D note type reveals that some note types have a greater capacity for information coding than others. In particular, the sum of the PIC values for A and B notes are 10.46 and 11.58, respectively, whereas C notes have a total PIC of 17. In this sense then, although all of the non-D note types have the ability to carry information, C notes potentially have the most information coded within their acoustic parameters. This is also in agreement with evidence showing that C notes have a special role for both black-capped chickadees (Ficken 1981) and Carolina chickadees (Freeberg and Lucas 2002). With that said, C notes are relatively rare; therefore, it seems logical that A and B notes should also be used to provide information.

A related question is whether one note alone can be sufficient for recognition of an individual or a flock. For instance, Mammen and Nowicki (1981) showed that black-capped chickadees responded more vigorously to foreign than to local chick-a-dee calls, and speculated that this was mediated by acoustic features contained within D notes. Nowicki (1989) later showed that, indeed, the acoustic structure of D notes in black-capped chickadee calls converged on a common mean when he housed birds in artificial flocks. Therefore, although not tested, it is possible that a single D note could be enough to lead to flock recognition and also to individual recognition. Additionally, Phillmore et al. (2003) showed that black-capped chickadees could recognize individual black-capped chickadees on the basis of their fee-bee songs or individual female zebra finches, *Taeniopygia guttata* (Vieillot, 1817), on the basis of their distance calls; the latter composed of only a single note. Therefore, the possibility exists that individual recognition could in fact be mediated by single call notes. This could be important for highly social birds like chickadees, as individuals may need to be identified in conditions of high environmental noise (e.g., in a large winter flock or a family group). In this manner, the acoustic worlds of chickadees and the obstacles in communication encountered by chickadees are highly analogous to those seen in colonial birds and mammals. Whether or not individual recognition can be accomplished using notes of all types remains to be determined.

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