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Information Theoretical Approaches to Chick-a-dee Calls of Carolina Chickadees (*Poecile carolinensis*)

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One aim of this study was to apply information theoretical analyses to understanding the structural complexity of chick-a-dee calls of Carolina chickadees, *Poecile carolinensis*. A second aim of this study was to compare this structural complexity to that of the calls of black-capped chickadees, *P. atricapillus*, described in an earlier published report (Hailman, Ficken, & Ficken, 1985). Chick-a-dee calls were recorded from Carolina chickadees in a naturalistic observation study in eastern Tennessee. Calls were analyzed using approaches from information theory, including transition probability matrices, Zipf's rules, entropies, and information coding capacities of calls and notes of calls. As described for black-capped chickadees, calls of Carolina chickadees exhibited considerable structural complexity. Most results suggested that the call of Carolina chickadees is more structurally complex than that of black-capped chickadees. These findings add support to the growing literature on the complexity of this call system in *Paridae* species. Furthermore, these results point to the feasibility of detailed cross-species comparative analyses that may allow strong testing of hypotheses regarding signal evolution.

Keywords: call, chickadee, entropy, information, Parid, vocalization, Zipf

Information theoretical approaches to communication have a long history in ethology and comparative psychology (overviews in Bradbury & Vehrencamp, 1998; Hailman, 1977, 2009; Losey, 1978; Miller, 1951; Wiener, 1961; Wilson, 1975). Although these "information" views of communication have their critics (Burghardt, 1970; Dawkins & Krebs, 1978; Owings & Morton, 1998; Rendall, Owren, & Ryan, 2009), they have greatly advanced our understanding of the structural complexity of communicative events, as well as the organization of sequences of communicative behavior (e.g., Carazo & Font, 2010; Hailman, 2009; Halliday, 1983; Seyfarth et al., 2010; Smith, 1977; Wiley, 1983; Gleick, 2011). There are two general views of information that have been used by researchers in communication—one is the idea that if communication is one individual signaling "about something" to another individual, then that "about something" is what is meant by information. The other view—the information theory view—stems from engineering problems and is based in mathematics, and defines information not in the terminology of meaning, but as a reduction in uncertainty, "a measure of one's freedom of choice when one selects a message" (Shannon & Weaver, 1949, p. 9).

A series of studies on the black-capped chickadee, *Poecile atricapillus*, took such information theoretical approaches in attempting to understand the acoustic complexity of the chick-a-dee call of that species. This call system is used in black-capped chickadees (and in other *Paridae* species that possess the call) for, at minimum, social cohesion when it functions to keep members of a flock spatially organized as individuals move through their territory (Hailman & Ficken, 1996; Lucas & Freeberg, 2007; Smith, 1991). In a seminal study, Hailman, Ficken, and Ficken (1985, 1987) used several mathematical approaches from information theory to explain how the four different note types of black-capped chickadee chick-a-dee vocalizations were organized into calls, and to compare the structural complexity of these calls and notes to that of written English language. Hailman et al. found that this call with its limited number of distinct note types was nonetheless enormously complex—it possessed rules of note ordering, it was largely open-ended (one of the few nonhuman signaling systems that has been demonstrated as such), and variation in note compositions could potentially convey a wide variety of different messages to receivers. Subsequent experimental studies with black-capped chickadees and other chickadee species has started to support this last point on the function of variation in call structure (Baker & Becker, 2002; Bartmess-LeVasseur, Branch, Browning, Owens, & Freeberg, 2010; Ficken, Hailman, & Hailman, 1994; Freeberg & Lucas, 2002; Mahurin & Freeberg, 2009; Nolen & Lucas, 2009; Soard & Ritchison, 2009; Templeton, Greene, & Davis, 2005; review in Lucas & Freeberg, 2007; Sturdy, Bloomfield, Charrier, & Lee, 2007).

Many recent studies have begun to address the organization and note compositional characteristics of calls of different North American chickadee (black-capped: Charrier, Bloomfield, & Sturdy, 2004; Carolina, *P. carolinensis*: Bloomfield, Phillmore, Weisman, & Sturdy, 2005; Freeberg, Lucas, & Clucas, 2003; Smith, 1972; chestnut-backed, *P. rufuscens*: Hoeschele, Gammon, Moscicki, & Sturdy, 2009; Mexican, *P. sclateri*: Ficken et al., 1994; mountain, *P. gambeli*: Bloomfield, Charrier, & Sturdy,

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2004; Gaddis, 1985), Eurasian tit (black-lored, *P. xanthogenys*: Hailman, 1994; Siberian, *P. cinctus*: Haftorn & Hailman, 1997; willow, *P. montanus*: Haftorn, 1993, 2000), and North American titmouse (tufted, *Baeolophus bicolor*: Gaddis, 1979; Owens & Freeberg, 2007) species. However, only a few of these studies have taken the sort of detailed information theory approaches utilized by Hailman, Ficken, and colleagues in their early black-capped chickadee work (Hailman, Ficken, & Ficken, 1985, 1987; Hailman & Ficken, 1986). These previous articles provided an in-depth analysis of the information content and note compositional properties of black-capped chickadees. Indeed, the articles provide the most comprehensive analysis of any chick-a-dee system published to date, and therefore provide an ideal comparison for the chick-a-dee calls of Carolina chickadees undertaken by us. Here, we take several information theoretical approaches to a large set of chick-a-dee calls of an eastern Tennessee population of Carolina chickadees. Our two aims were to gain a greater understanding of the structural complexity of the call of this population and to make direct comparisons to the call organization of black-capped chickadees. Our call set for Carolina chickadees was taken from a naturalistic observation study of Freeberg (2008), in which over 5,000 calls of chickadees from 40 different flocks were analyzed and variation in note composition was linked to contextual factors such as the presence of an avian predator or flight behavior.

Hailman et al. (1985, 1987) used results from their information theoretical analyses to suggest that the four note types in black-capped chickadee chick-a-dee calls encode qualitatively different information and that the number of notes of each type encodes signal intensity (e.g., Templeton et al., 2005). Moreover, very short calls (1–5 notes) were underrepresented suggesting that the calls do not convey simple, one-dimensional meaning (such as the single-note contact calls of many species). Finally, the chick-a-dee call system was found to be generative, meaning that new call types will be found with ever increasing sample size. These syntactical properties derived from information theory should be seen as a first step in understanding the call system, but it is an important step nonetheless. Here we test whether the syntactic generalities derived by Hailman et al. (1985, 1987) fit the chick-a-dee call system of the congeneric Carolina chickadee.

A comparison of Carolina chickadees and black-capped chickadees allows an interesting test of predictions of the Social Complexity Hypothesis for communication (Dunbar, 1996, 1998; Freeberg, 2006). The Social Complexity Hypothesis argues that greater social complexity in groups of animals selects for greater complexity in their systems of (vocal) communication. Greater communicative complexity is needed to meet the demands of assessing and managing the behavior of group members. Social complexity is measured in a number of different ways by researchers, but two of the major methods involve group size (e.g., Freeberg, 2006) and the diversity of social relationships within groups (e.g., Blumstein & Armitage, 1997). These two major means of assessing social complexity lead to different predictions when comparing these two species of chickadees. Black-capped chickadees tend to have larger flock sizes than Carolina chickadees (reviews in Smith, 1993; Mostrom, Curry, & Lohr, 2002). Thus, if group size is the primary driver of vocal complexity in this genus, black-capped chickadees should have a more complex chick-a-dee call. However, dominance hierarchies in black-capped chickadees are known to be linear and rigid (summarized in Smith, 1991), whereas those in Carolina chickadees are known to be more ambiguous (Mostrom, 1993). A higher likelihood of “reversals” of dominance status is associated with more egalitarian and less despotic social structure in animals, and egalitarian social structures result in richer social relationships within groups. Richer social relationships within groups may serve as a social selection pressure for increased communicative complexity (e.g., Blumstein & Armitage, 1997; Dunbar, 1998). Thus, if greater diversity of social relationships within groups is the primary driver of vocal complexity in this genus, Carolina chickadees should have a more complex chick-a-dee call than black-capped chickadees.

There are two additional reasons why Carolina chickadees would have a more complex chick-a-dee call (e.g., more diversity in note compositions of calls) in comparison to black-capped chickadees. First, as Bloomfield et al. (2005) and Freeberg (2008) documented, there appear to be more distinct note types in Carolina chickadee calls as opposed to black-capped chickadee calls. Although this is no guarantee of greater structural complexity of a signaling system (especially if many of the note types are fairly rare, which is the case for Carolina chickadees), it seems logical that a greater diversity of basic units in a combinatorial communicative system can lead to a greater diversity of combinations of those units in generating calls. Second, the range of Carolina chickadees is further south than the range of black-capped chickadees in the United States. This suggests that the diversity of competitors for food resources and the diversity of predators (i.e., avian, or mammalian predators on nests, juveniles, and adults) may be greater for Carolina chickadees throughout the year in comparison to black-capped chickadees. A recent experimental study, for example, found that predation risk on artificial nests decreased with increasing latitude along a roughly 30° north-south Arctic gradient (McKinnon et al., 2010). Predation pressure has been suggested as a major force influencing complexity of vocal communication in nonhuman primates (see Clarke, Reichard, & Zuberbühler, 2006; Zuberbühler, 2002; Schel, Candiotti, & Zuberbühler, 2010).

We include an analysis of the English language described by Hailman et al. (1985, 1987). Hailman et al. (1985) laid out the rationale for the relevance of a comparison between English and the chick-a-dee system. They argued that the comparison is meaningful because each variant of the chick-a-dee call encodes different information, as with English. In addition, word-level syntax provides information at a level that is analogous with the chick-a-dee call (which is typically produced in bouts), and because a large-enough sample provides a robust description of both English and the chick-a-dee system, despite that fact that both are generative. We offer an additional rationale: the chick-a-dee call system is unique among call systems described to date. While some song systems have syntactical organization (e.g., primates: Clarke, Reichard, & Zuberbühler, 2006; birds: Ficken, Rusch, Taylor, & Powers, 2000; Berwick et al., 2011), no other previously described call (i.e., nonsong) system has this property (Hailman & Ficken, 1986). Furthermore, birdsong in many species, while highly structurally or syntactically complex, is also highly stereotyped (review in Cachpole & Slater, 2008). This is in stark contrast to the largely open-ended nature of the call system of chickadees and related species. In addition, chick-a-dee calls are given under an incredibly broad range of contexts (Smith, 1972; Lucas & Freeberg, 2007), making English as reasonable a comparison as any other communicative system.

Method

Call Sample and Note Types

Chick-a-dee calls of Carolina chickadees were recorded under nonmanipulated conditions at 40 different sites across three locations in eastern Tennessee (described in greater detail in Freeberg, 2008). Calls were recorded using Sennheiser ME-62 and ME-66 microphones with a Marantz PMD-222 cassette recorder and Maxell XL-II high-bias audiotape. Calls were digitized at a sample rate of 22,050 and 16-bit resolution in Microsoft Windows XP, using CoolEdit Pro, Version 2 (Syntrillium Software, Scottsdale, AZ).

Following Freeberg (2008; see also Bloomfield et al., 2005), we identified six note types in these chick-a-dee calls: A, E, B, C, D_h and D (Figure 1). Two of these are introductory whistles (A and E), with the A note generally having a longer duration and less frequency modulation than the E note. The B note is a whistle with relatively symmetric "arms"—the beginning frequency of the upsweep is typically the same frequency as the end of the downsweep. The C note is the noisiest note of the series, with a general increase in frequency over the course of the note. The D note is a series of stacked overtones, with a characteristic ladder-like structure when viewed in spectrogram form. The D_h note is a hybrid note resulting from the concatenation of an A (or B) note preceding a D note. Although these note type categories are arbitrarily defined, there is high interrater reliability in coding them (Bloomfield et al., 2005; Freeberg, 2008), and similar note type categories in black-capped chickadees are reliably categorized by individual chickadees in perceptual discrimination tests (Sturdy, Phillmore, & Weisman, 2000). The note types do not appear to be used randomly in calls by chickadee signalers (Freeberg, Lucas & Clucas, 2003). Freeberg (2008) suggested there was an $A \rightarrow E \rightarrow B \rightarrow C \rightarrow D_h \rightarrow D$ note ordering rule in this eastern TN population, whereby if, for example, 5 D notes, 3 C notes, 2 E notes and 1 A note occurred in a particular call, the note composition of that call would virtually always be AEECCCDDDDD.

We analyzed note composition of 5,591 calls recorded from flocks of Carolina chickadees in eastern Tennessee. These calls were composed of a total of 34,247 notes. Our analyses follow those of Hailman et al. (1985, 1987). We note that our analyses of Carolina chickadee chick-a-dee calls include two note types not considered by Hailman et al. (1985, 1987), the E and D_h note types. The D_h note types were treated as two notes (an A followed by a D note) in the original papers. Given that these notes can be extraordinarily common in some species (e.g., mountain chickadees, Bloomfield et al., 2004), we felt that they should be treated as a true note type (also see Lucas & Freeberg, 2007). The E note type represents a distinct note type that may represent a more complex chick-a-dee system in the Carolina chickadee compared to the black-capped chickadee. We note also that Hailman et al. (1985, 1987) deleted single A-note calls from their sample because they felt that the calls were too weak and therefore underrepresented in the sample. We have included these single-note calls of Carolina chickadees here because they are potentially an important component of the chick-a-dee call system. (We also note that we have run all the analyses discussed in this paper without single-A note calls and none of our conclusions would be altered if they were deleted.)

Call Analyses

Our analyses cover two aspects of the chick-a-dee call system, information content and note composition properties. We distinguish call-specific and note-specific components of each aspect.

Information content: Call-specific encoding capacity. Hailman et al. (1985) used Shannon's (Shannon & Weaver, 1949) equation for entropy (E) to describe the ability of a call to encode information:

$$E = \sum_{i=1}^{n} p_i \, (-\log_2 p_i)$$

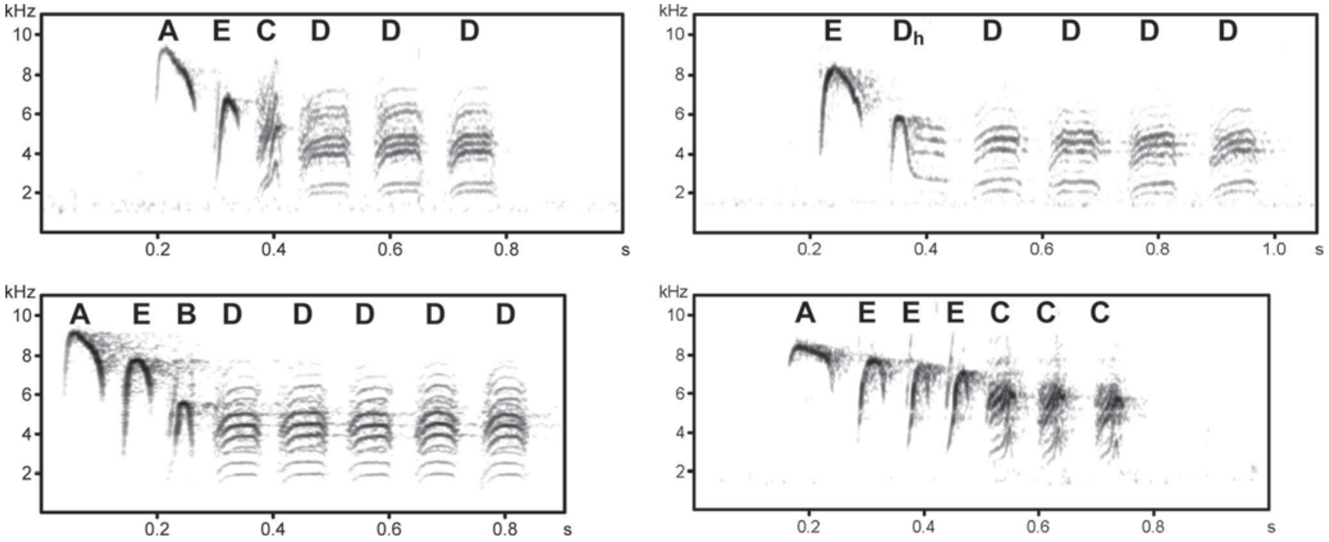

Figure 1. Spectrograms of chick-a-dee calls of Carolina chickadees from eastern TN, illustrating the different note types in the calls. Spectrograms were generated using Avisoft SASLab Pro (Raimund Specht, Berlin) with an FFT length of 512 and Blackman window. Note type designations are written above each note.

where p_i = the proportion of calls that have a unique sequence of note types, given a total of n different call types. Hailman et al. (1985) included several levels of entropy, three of which are used here. Each of these call-level entropy measures provides an estimate of the diversity of call structures across large samples of recorded calls—larger entropy measures relate to a greater variety of call material in the recording sample. E_{avg} is the entropy in a call, fixing call length at the modal value of call lengths in the sample and assuming that each note in the call is equally likely to be any of the species-specific note types. This measure of entropy gives an index of the encoding capacity in the call system if chickadees were unconstrained in their capacity to vary the syntax of notes within a call. E_0 is entropy based on the actual set of unique call types used in the repertoire of the birds, but it assumes that each unique call type is equally likely. This measure of entropy gives an index of encoding capacity within the observed note ordering constraints that are in place in the chick-a-dee system. However, this is a maximal encoding capacity for the chick-a-dee syntax because, for example, if some calls are more common than others (as is the case), then the actual encoding capacity is reduced because of the unequal distribution of call types in the call system. Finally, E_1 takes into account the observed frequency of each call type in our sample. This measure of entropy gives an index of encoding capacity both within the observed syntactical constraints in the system and within the observed distribution of call types. Using an analogy from English, E_0 assumes that each word in the language is equally represented, and E_1 accounts for the fact that some words (e.g., "the") are more commonly used than others (e.g., "chickadee"). These three estimates of call entropy can, in turn, be compared with the entropy of English words (Pierce, 1980; Shannon & Weaver, 1949).

Information content: Note-encoding capacity. Following Hailman et al. (1985), we can estimate the encoding capacity of note-to-note transitions within a call, using Shannon's (Shannon & Weaver, 1949) entropy:

$$U = \sum_{i=1}^{n} p_i(-\log_2 p_i)$$

where p_i is the probability of occurrence of the ith chickadee note, given n note types (including a null note indicating the end of the call). U can be thought of as the ability of a note (or series of notes) to encode information. As with call-specific encoding capacity, note encoding capacity can be calculated at several levels. Each of these note-level entropy measures provides an estimate of the diversity of note compositions across large samples of recorded calls—larger entropy measures relate to a greater variety of combinations of notes within calls. As with call-level entropy, entropy measured for chick-a-dee note syntax can be compared to entropy derived from letter syntax in English words.

U_0 assumes that all note types are equiprobable. Given six note types designated for Carolina chickadee chick-a-dee calls, this generates $p_i = 1/7$ for all note types (using the silent end-of-call as the seventh type). Black-capped chickadees have $p_i = 1/5$, and English words have $p_i = 1/27$. U_1 uses the observed frequency of occurrence of each note type, essentially measuring the potential information content of any given note in the call. U_2 measures the serial correlation between adjacent notes, providing an estimate of the potential additional information content of a second note, given that a first note exists in a call. For example, if A notes are always given in strings, then the information content of the first note might be high, but for the second (and subsequent) note it would be lower, because the first A note would be a strong predictor of the second. Thus,

$$U_2 = \Sigma_{ij}\, p_{ij}(-\log_2 p_{j|i})$$

where p_{ij} is the joint probability of the jth note following the ith note, and $p_{j|i}$ is the conditional probability of the jth note, given i. Similarly, U_3 is the additional potential information content of the third note in a string, conditional on any given pair of notes preceding it.

Note Composition and Ordering Rules

Hailman et al. (1985) explored several rules of language laid out by Zipf (1935, 1949) that are relevant to understanding the properties of the chick-a-dee system at the level of the call. We consider two here: Zipf's second rule and Zipf's Law.

Zipf's second rule (Zipf, 1935) posits that the diversity of unique call types should increase with call length. This is tested by plotting the number of unique call types per call as a function of call length. If the call system follows Zipf's second rule, the function will be monotonic increasing. More important, the shape of the function will provide information on the relative use of calls of different length. For example, Hailman et al. (1985) showed that the diversity of call types in black-capped chickadees did not increase for calls less than 8–9 notes. This mismatch to Zipf's second rule implies a deficit of call diversity for calls of intermediate length (e.g., 5–8 notes).

Arguably, the most important result reported in Hailman et al. (1985) was that chick-a-dee calls represent a generative system in which the number of unique call types is expected to increase without limit with an increase in sample size. As posited by Zipf's Law, one result of this property in English is that a plot of the log of the probability of occurrence of the rth-rank word as a function of the log of frequency rank is approximately linear, with a slope of 45° (Pierce, 1980). Zipf (1942a) saw Zipf's law as representing the compromise between effort (resulting in few commonly used words) and economy (resulting in many rarely used words). Regardless of the basis of the relationship, large English texts do approximately follow the law (Zipf, 1942a, 1942b). Hailman et al. (1985) showed that black-capped chickadee calls fail to meet this criterion, but that they did match a less restrictive model proposed by Mandelbrot (1953):

$$p = i(r+k)^{-s}$$

where p = probability of occurrence of the rth ranked word; r = rank; and i, k and s are best-fit constants. We fit this equation using our Carolina chickadee data with nonlinear regression (Proc. NLIN, SAS Inst.).

Shifts in the compositional properties of notes in a call as notes are progressively produced by a signaler can be quantified using a semi-Markov analysis. This technique was first used by Hailman et al. (1987) in the study of black-capped chickadee chick-a-dee calls. The value of this approach is that it can indicate whether note repetition follows simple rules or whether the repetition rules change with the length of a string of same-note elements. A simple repetition rule might indicate that variation in note numbers is used to encode intensity information. A change in repetition rules implies that calls of different lengths convey qualitatively different information. For example, short C strings may indicate food while long C strings might be an aggressive signal. The analysis uses first-order transition probabilities of the repetition of a note (see Hailman, 1977). If note production within a call followed a simple first-order Markov process, then the probability of adding each additional note to a string of notes of the same type would be constant. Under these conditions, the cumulative frequency (f_S) of strings of at least S number of notes would be

$$\log f_S = (S-1)\log p + \log S$$

where p is the probability of adding another repetition to a string of same-type notes. Hailman et al. (1987) showed that A notes follow the expectation of this semi-Markov process closely while B and D notes diverge from this expectation.

Results

Information Content: Call-Specific Encoding Capacity

Chick-a-dee call lengths of Carolina chickadees varied from 1 to 45 notes in our sample. The frequency distribution of Carolina chickadee call lengths is significantly different from the black-capped chickadee calls reported in Hailman et al. (1985; Kolmogorov–Smirnov two-sample test: $KS_a = 1.68$; $p = .007$) with a flatter distribution and longer right tail. This property contributes to the higher encoding capacity in Carolina chickadee calls (Figure 2).

For Carolina chickadees, the modal call length is five notes (compared with a mode of six notes in black-capped chickadees). Thus, in terms of E_{avg}, with six note types, $p_i = 1/6^5$ for each call type. In terms of E_0, we have a total of 1,093 different call types (that is, calls with unique combinations of note types). If we assume that each call type is equally likely, $p_i = 1/1{,}093$ for each call type. Hailman et al. (1985) identified 362 different call types in a sample of 3479 calls for black-capped chickadees. Given that our sample includes two notes not considered by Hailman et al. (1985), the E and D_h notes, it is not surprising that call entropy in our sample is greater than that measured for black-capped chickadees (Figure 3). However, as we show below, there are additional note compositional factors that result in higher entropy for Carolina chickadees compared with black-capped chickadees. Moreover, our analyses suggest that chick-a-dee calls are surprisingly diverse, even when compared with English words (Figure 3).

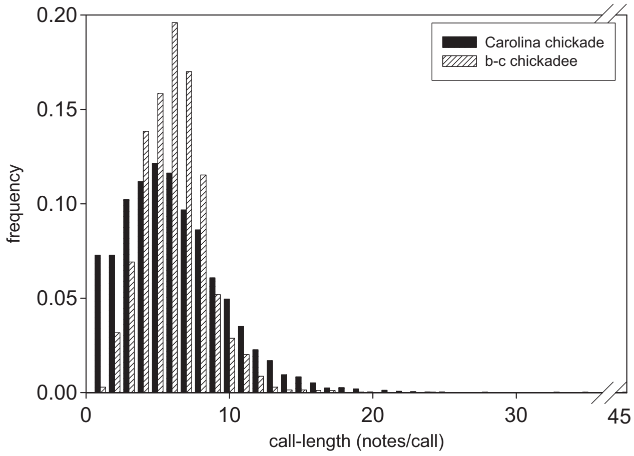

Figure 2. Frequency distribution of chick-a-dee call lengths of Carolina and black-capped chickadees (b–c chickadee data from Hailman et al., 1985).

Information Content: Note-Encoding Capacity

Our results suggest that the patterns identified for black-capped chickadees are mirrored in Carolina chickadees, except that note-encoding capacity is higher in Carolina chickadees than in black-capped chickadees for all levels of U (Figure 4). In both species, there is a drop-off in uncertainty from U_1 to U_2, reflecting a tendency for notes to be repeated in the call (unlike letters in a word). U_3 is similarly low for the same reason. However, in Carolina chickadees both U_2 and U_3 are nearly twice the value of black-capped chickadees. This, in part, reflects the increased number of notes in our Carolina chickadee sample and, in part, reflects a greater tendency in black-capped chickadees for note repetition.

Note Composition and Ordering Rules

Surprisingly, Zipf's second rule was not supported in black-capped chickadees for calls of less than eight notes, and call diversity in calls above eight notes increased rapidly to a threshold at about 14 notes per call (Hailman et al., 1985). In contrast, the distribution for Carolina chickadees matches Zipf's second rule more closely, with a gradual increase in call diversity as call length increases (Figure 5). The difference between species (as indicated by the lack of overlap in 95% confidence limits in Figure 5) is primarily caused by higher call diversity for Carolina chickadees relative to black-capped chickadees in intermediate-length calls (5–8 notes per call).

Turning to Zipf's law, Mandelbrot's modification fits the distribution of Carolina chickadee chick-a-dee calls quite well (Figure 6; $i = 0.27$, $s = 1.07$, $k = 5.50$; $R^2 = 0.994$). In addition, the function is flatter than the curve fit through the black-capped chickadee data (Figure 6), suggesting that Carolina chickadee chick-a-dee calls represent a generative system that is more diverse than the black-capped chickadee sample studied by Hailman et al. (1985).

A detailed description of the note compositional and ordering properties of the chick-a-dee call can give us insight into how chickadees use different note types to construct the call. In Carolina chickadee chick-a-dee calls, the transition of notes follows the pattern suggested by Freeberg (2008): [A] [E] [B] [C] [D_h] [D] (where brackets represent any number of repetitions of a note type; Table 1). Only 0.37% of calls failed to meet this sequence, and 90% of these exceptional calls resulted from a transposition of A and E notes, or of B and E notes (Table 1).

Based on call types (Table 1), the two species appear to use the B note differently, in that [B][C] and [B][C][D] calls are rare in Carolina chickadees but quite common in black-capped chickadees. Similarly, [A][D] calls are more common in black-capped chickadees. In contrast, [B][D] calls are common in Carolina chickadees but rare in black-capped chickadees. These species

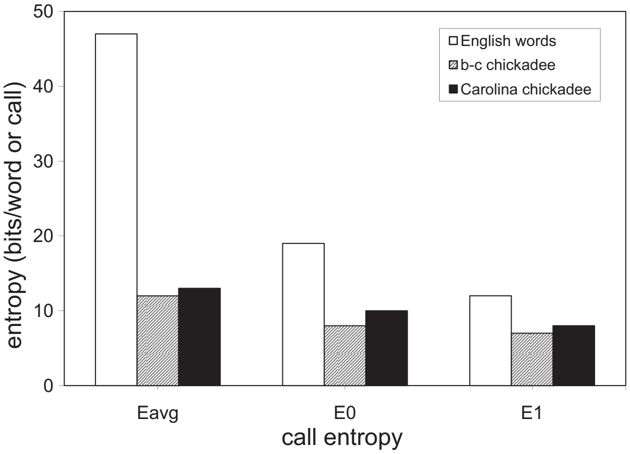

Figure 3. Encoding capacity of the chick-a-dee call of Carolina chickadees, black-capped chickadees, and of English words.

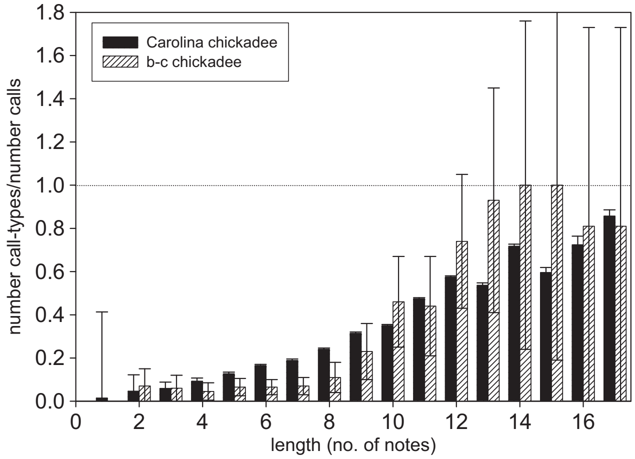

Figure 5. Number of unique call types per number of calls as a function of call length for Carolina and black-capped chickadees. Error bars are 95% confidence limits on the proportions. Data for black-capped chickadees are from Hailman et al. (1985).

differences can also be illustrated using a flow diagram that describes the conditional probability of the transition from each note type (or the silence preceding a call) to the next note type (or the silence ending a call). We provide flow diagrams here for both species that include all transitions with a probability of 0.05 and greater. In Carolina chickadees, calls tend to start with introductory A or E notes (Figure 7a). In black-capped chickadees, calls tend to start with A notes (Figure 7b). Carolina chickadee calls have few B notes, are less likely to start with a B note, and B notes almost always transition to D notes. In black-capped chickadees, B notes almost always transition to C notes.

The two introductory notes (A and E) are used in different ways in Carolina chickadees. Whereas both can begin a call, A notes primarily transition to E notes (or end the call), whereas E notes are most likely to transition to each of the other note types (B, C and D). D_h notes were not included in the flow diagrams because none of the transitions exceeded the 5% threshold. This note type was almost always preceded by an A (53%) or E (44%) note, and virtually always (96%) transitioned to a D note. There was only 1 (of 257) instance of a D_h note being repeated.

As the number of repetitions of each note type increases in a call, substantial constraints emerge for the note types to follow (Table 2). This was first reported in Hailman et al. (1987) for black-capped chickadees and is true of our Carolina chickadee call samples as well. For example, short strings of A notes are most likely to transition to E notes, but longer A-note strings are more likely to end the call (Table 2). The same is true of A notes given by black-capped chickadees, except that A notes are less likely to end the note in this species and much more likely to transition to D notes (Table 2). E notes of Carolina chickadees are most likely

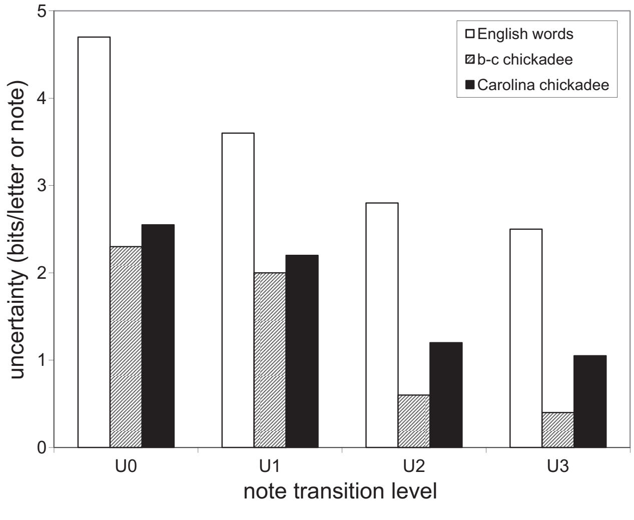

Figure 4. Encoding capacity of the notes in chick-a-dee calls of Carolina chickadees, black-capped chickadees, and of English words.

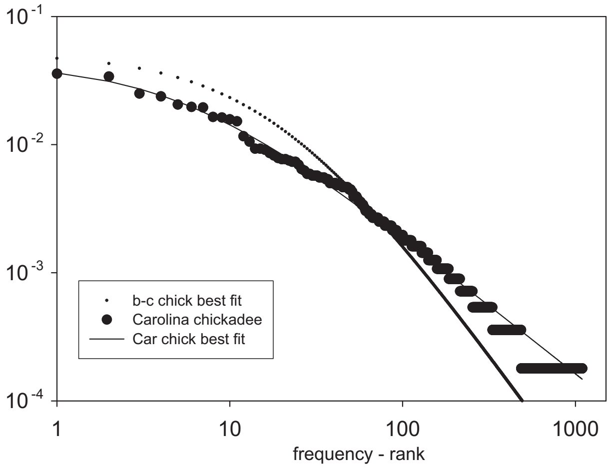

Figure 6. Best-fit function of Mandelbrot's modification of Zipf's Law for Carolina and black-capped chickadees (see text). Symbols represent raw data for Carolina chickadees. The curves represent the functions for Carolina chickadees (solid line) and black-capped chickadees (dotted line). Black-capped chickadee function is from Hailman et al. (1985).

Table 1
Percentage Occurrence of Types of Chick-A-Dee Calls of Carolina and Black-Capped Chickadees Defined by Sequence Type

Sequence type	Carolina *N*	Carolina %	Black-capped %
[A]	650	11.63	4.51
[E]	445	8.00	
[B]	4	0.07	1.72
[C]	50	0.89	0.92
[D]	377	6.74	5.23
[A] [E]	179	3.20	
[A] [B]	4	0.07	0.40
[A] [C]	1	0.02	0.80
[A] [D]	132	2.36	48.63
[E] [B]	4	0.07	
[E] [C]	279	4.99	
[E] [D_h]	8	0.14	
[E] [D]	1,029	18.40	
[B] [C]	7	0.13	5.32
[B] [D]	345	6.17	0.72
[C] [D]	60	1.07	2.44
[D_h] [D]	84	1.50	
[A] [B] [C]	2	0.04	0.37
[A] [B] [D]	95	1.70	0.37
[A] [E] [C]	77	1.38	
[A] [E] [D]	98	1.75	
[A] [C] [D]	2	0.04	0.11
[A] [D_h] [D]	86	1.54	
[E] [B] [C]	9	0.16	
[E] [B] [D]	244	4.36	
[E] [C] [D]	660	11.80	
[E] [D_h][D]	53	0.95	
[B] [C] [D]	9	0.16	25.93
[B] [D_h] [D]	3	0.05	
[A] [B] [C] [D]	6	0.11	2.18
[A] [E] [B] [C]	5	0.09	
[A] [E] [B] [D]	98	1.75	
[A] [E] [C] [D]	194	3.47	
[A] [E] [D_h] [D]	13	0.23	
[E] [B] [C] [D]	28	0.50	
[A] [E] [B] [C] [D]	18	0.32	
Exceptional sequences total	205	0.37	0.32
[E] [A] transpose	133		
[B] [E] transpose	54		

Note. Brackets indicate notes can be repeated any number of times. Only sequence types found more than twice or provided in Hailman et al. (1985) are listed. Sample size is given for Carolina chickadees and percentage occurrence for both species. Black-capped chickadee data are from Hailman et al. (1985).

to transition to C notes after short strings (2–4) but are most likely to end the call after longer strings (Table 2).

Finally, we test whether chick-a-dee calls of Carolina chickadees obey a semi-Markov process. Our analysis of Carolina chickadee calls is strikingly similar to the black-capped chickadee results. A notes show a fairly strong fit to the expected semi-Markov expectation (Figure 8a). In contrast to A notes, E notes (which were not identified in Hailman et al., 1985, 1987) showed a change in transition probability above four notes (Figure 8b). As shown in Table 2, E notes in strings of more than 4 are more likely to end the call, as opposed to transitioning to C notes after shorter strings. Even though the transition probability of B notes in Carolina chickadees (0.12) is lower than in black-capped chickadees (0.35), both show semi-Markov behavior up to about strings of four notes, then show a higher same-note transition probability for strings of four or greater B notes (Figure 8c). C notes in both species match expectations of a fixed transition probability (Figure 8d). D_h notes typically are only found once in a call (if they are present), so the semi-Markov analysis is not relevant for this note type. D notes are the most enigmatic of the note types, with patterns similar in both Carolina and black-capped chickadees: There are too many short strings (<9) and too few long strings (>10). Hailman et al. (1987) showed that black-capped chickadee D notes approximately fit a Poisson distribution for strings less than eight notes and fit a Gaussian distribution for strings less than 15. However, neither the Poisson (Figure 8e) nor the Gaussian distribution (Figure 9) provides an adequate fit for the cumulative distribution of D notes in Carolina chickadees.

Discussion

We had two main aims in this study. Our first aim was to apply several information theoretical approaches to the structural analysis of chick-a-dee calls of Carolina chickadees. Our second aim was to compare the call complexity of Carolina chickadees to that of black-capped chickadees, as a first species-level test of predictions of the Social Complexity Hypothesis for communication. We address these two main aims in turn.

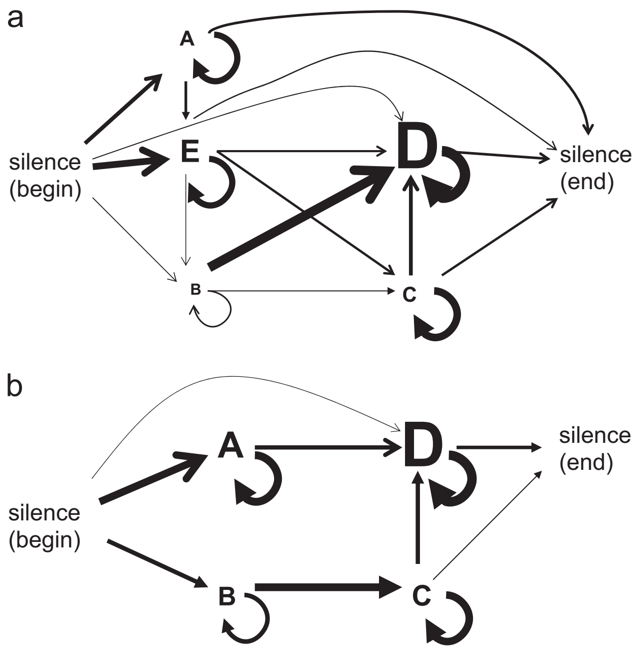

Figure 7. a) Transition probabilities across note types for Carolina chickadee chick-a-dee calls. Only transitions with a probability >5% are shown. The size of the note represents the overall proportion of each note type. Arrow width is linearly proportional to the transition probability. b) Transition probabilities across note types for black-capped chickadee chick-a-dee calls. Only transitions with a probability >5% are shown. Note size represents the overall proportion of each note type. Arrow width is linearly proportional to the transition probability. Data from Hailman et al. (1985).

Table 2
Transition Probabilities From Each Note Type to Each Other Note Type or End of the Call After Strings of Varying Length

No. A notes in sequence	*N*	Cc to E	Cc to B	b-c to B	Cc to C	b-c to C	Cc to D_h	Cc to D	b-c to D	Cc to end	b-c to end
1	967	0.48	0.09		0.00		0.08	0.13		0.22	
2	397	0.42	0.07	0.03	0.00	0.01	0.02	0.09	0.95	0.39	0.02
3	248	0.32	0.06	0.02	0.00	0.01	0.00	0.02	0.92	0.59	0.05
4	141	0.24	0.01	0.07	0.00	0.13	0.00	0.01	0.59	0.73	0.22
5	57	0.19	0.02	0.03	0.00	0.01	0.00	0.00	0.72	0.79	0.24
6	24	0.04	0.00	0.07	0.00	0.00	0.00	0.00	0.50	0.96	0.43
7	23	0.17	0.00	0.07	0.00	0.00	0.00	0.04	0.59	0.78	0.33
8	5	0.20	0.00	0.03	0.00	0.00	0.00	0.00	0.35	0.80	0.63
9	7	0.14	0.00		0.00		0.00	0.00		0.85	
10–13	5	0.20	0.00		0.00		0.00	0.00		0.80	

No. E notes in sequence	*N*	Cc to A	Cc to B	Cc to C	Cc to D	Cc to D_h	Cc to end
1	1,904	0.03	0.16	0.26	0.39	0.03	0.13
2	1,010	0.04	0.08	0.42	0.29	0.01	0.16
3	404	0.05	0.05	0.51	0.15	0.01	0.22
4	165	0.05	0.02	0.49	0.11	0.00	0.32
5	91	0.03	0.12	0.33	0.10	0.00	0.41
6	60	0.07	0.15	0.23	0.13	0.00	0.42
7	32	0.06	0.13	0.16	0.13	0.00	0.53
8	19	0.16	0.05	0.32	0.05	0.00	0.42
9	9	0.11	0.00	0.33	0.00	0.00	0.56
10	11	0.09	0.00	0.27	0.09	0.00	0.55
11	6	0.00	0.17	0.17	0.00	0.00	0.67
12	5	0.00	0.00	0.00	0.20	0.00	0.80
13	3	0.00	0.00	0.00	0.00	0.00	1.00
14	2	0.00	0.00	0.00	0.00	0.00	1.00
15–20	4	0.75	0.00	0.25	0.00	0.00	0.00

No. B notes in sequence	*N*	Cc to A	b-c to A	Cc to E	Cc to C	b-c to C	Cc to D_h	Cc to D	b-c to D	Cc to end	b-c to end
1	861	0.00	0.00	0.05	0.07	0.98	0.01		0.01	0.01	
2	80	0.00	0.00	0.14	0.24	0.96	0.00	0.61	0.01	0.01	0.03
3	8	0.00	0.00	0.63	0.25	0.57	0.00	0.13	0.10	0.00	0.33
4	3	0.00	0.00	0.33	0.33	0.36	0.00	0.33	0.15	0.00	0.49
5	1	0.00	0.02	0.00	0.00	0.11	0.00	0.00	0.19	1.00	0.68
6	3	0.00		0.00	0.00		0.33	0.67		0.00	
7–10	1	0.00		0.00	0.00		1.00	0.00		0.00	

No. C notes in sequence	*N*	Cc to A	b-c to A	Cc to E	Cc to B	b-c to B	Cc to D_h	Cc to D	b-c to D	Cc to end	b-c to end
1	682	0.00		0.00	0.00	0.03	0.00	0.87	0.75	0.13	0.22
2	301	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.89	0.33	0.11
3	186	0.00	0.00	0.01	0.00	0.00	0.00	0.54	0.83	0.45	0.17
4	127	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.66	0.61	0.34
5	71	0.00	0.00	0.01	0.00	0.00	0.01	0.37	0.74	0.61	0.26
6	44	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.50	0.59	0.50
7	31	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.16	0.74	0.84
8	17	0.00		0.00	0.00		0.00	0.59		0.41	
9	4	0.00		0.00	0.00		0.00	0.25		0.75	
10	5	0.00		0.20	0.00		0.00	0.40		0.40	
11–24	3	0.00		0.00	0.00		0.00	0.33		0.67	

No. D notes in sequence	*N*	Cc to A	Cc to E	Cc to B	Cc to C	Cc to D_h	Cc to end
1	385	0.00	0.01	0.00	0.00	0.00	0.99
2	543	0.00	0.00	0.00	0.00	0.00	1.00
3	564	0.00	0.01	0.00	0.00	0.00	1.00
4	490	0.00	0.00	0.00	0.00	0.00	1.00
5	382	0.00	0.00	0.00	0.00	0.00	1.00

(table continues)

Table 2 (*continued*)

No. D notes in sequence	*N*	Cc to A	Cc to E	Cc to B	Cc to C	Cc to D_h	Cc to end
6	380	0.00	0.00	0.00	0.00	0.00	1.00
7	301	0.00	0.00	0.00	0.00	0.00	1.00
9	229	0.00	0.00	0.00	0.00	0.00	1.00
10	142	0.00	0.00	0.00	0.00	0.00	1.00
11	106	0.00	0.00	0.00	0.01	0.00	0.99
12	59	0.00	0.00	0.00	0.00	0.00	1.00
13	50	0.00	0.00	0.00	0.00	0.00	1.00
14	31	0.00	0.00	0.00	0.00	0.00	1.00
15	22	0.00	0.00	0.00	0.00	0.00	1.00
16	20	0.00	0.00	0.00	0.00	0.00	1.00
17	14	0.00	0.00	0.00	0.00	0.00	1.00
18	7	0.00	0.00	0.00	0.00	0.00	1.00
19	5	0.00	0.00	0.00	0.00	0.00	1.00
20	3	0.00	0.00	0.00	0.00	0.00	1.00
21–44	15	0.00	0.00	0.00	0.00	0.00	1.00

Note. Cc = Carolina chickadee; b-c = Black-capped chickadee. Missing cells were not reported or strings of that length did not occur. Data on black-Capped chickadees from Hailman et al. (1987). Unfilled cells represent cases not seen or reported in that species.

Information Theoretical Approaches to Carolina Chickadee Chick-a-dee Calls

Chick-a-dee calls of this eastern population of Carolina chickadees contain a mode of 5 notes and a mean of roughly 6 notes per call. The number of notes per call ranged from 1 to 45 in our sample and, combined with the combinatorial nature of the call (Figure 7), this suggests a very large number of calls with unique note compositions. In terms of entropy measures related to whole calls, chick-a-dee calls in this species are somewhat comparable to English words. Application of Zipf's law suggests that the chick-a-dee call of Carolina chickadees is an open-ended communicative system. This means that increased sampling of individuals will continue to add new calls (calls with unique note compositions) to the sample. Such an open-ended system is quite rare in nonhuman animal vocal systems. Despite the generative, open-ended nature of the chick-a-dee call system, there are fairly rigid rules that govern how notes are produced by a signaler to build a call, and receivers respond differently to playbacks of calls that violate these note ordering rules (Clucas, Freeberg, & Lucas, 2004).

Hailman et al. (1985, 1987) hypothesized that the four note types used by black-capped chickadees each encode qualitatively different information and that note number encodes signal intensity. The latter hypothesis is derived from the close fit of the distribution of note numbers to a semi-Markov distribution: for A and C introductory notes, the probability that a given note is followed by the same note type is independent of call length. Hailman et al. (1985, 1987) also suggested that the number of introductory notes was constrained because long strings of introductory notes tend to end the call instead of transitioning to another note type. Carolina chickadee chick-a-dee calls show some of these same properties. A and C notes are distributed as expected of a semi-Markovian system. However, the probability that a B or an E note follows another note of the same type is not constant. Instead, the probability of occurrence of a following B note changes at 3 B notes and the probability of occurrence of a following E note changes at 5 E notes. Moreover, Carolina chickadee B notes rarely end calls, irrespective of the number of B notes in a call. Finally, the syntactical properties of D notes in both Carolina chickadees and black-capped chickadees are quite different from those of the other notes in the call. Hailman et al. (1985, 1987) suggested that the notes hold a special meaning, in part related to individual recognition (see Mammen & Nowicki, 1981; Nowicki, 1983, 1989).

Our results suggest that two conclusions of Hailman et al. (1985, 1987) need to be reevaluated if one wishes to extend these ideas in more comparative ways beyond black-capped chickadees. First, they suggested that there is some constraint on call length, as indicated by the tendency of calls to end after long strings of any single note instead of transitioning to another note type. However, Carolina chickadee calls with long strings of E notes (which are spectrally similar to the black-capped A notes) are more likely to end than are black-capped A stings. However, Carolina B strings are much less likely to end calls than are black-capped B strings. More generally, the patterns are not quantitatively similar in the two species. Indeed, constraints on call length are difficult to argue when Carolina chickadee chick-a-dee calls can be 45 notes long.

The second generality is that note types encode qualitatively different information and that note number encodes intensity. This hypothesis is derived, in part, by the semi-Markov property of the introductory notes. Yet two of the four Carolina chickadee introductory notes (E and B) do not show semi-Markov dynamics. Instead, the distribution of E and B notes is semi-Markov to some threshold where the probability of continuing the string of notes changes. One possible hypothesis that would explain this pattern is that long strings of E or B notes carry qualitatively different information than short strings of these same note types. For example, short D-note strings (which also diverge significantly from semi-Markov dynamics) are given under a wide variety of conditions whereas long D-note strings are typically produced when the birds are faced with threats (Templeton et al., 2005; Nolen, 2010).

As the number of notes in a call increases, there is an increasing likelihood that the call will be unique in its note composition (Figure 5), obeying Zipf's second rule. Given this finding, how-

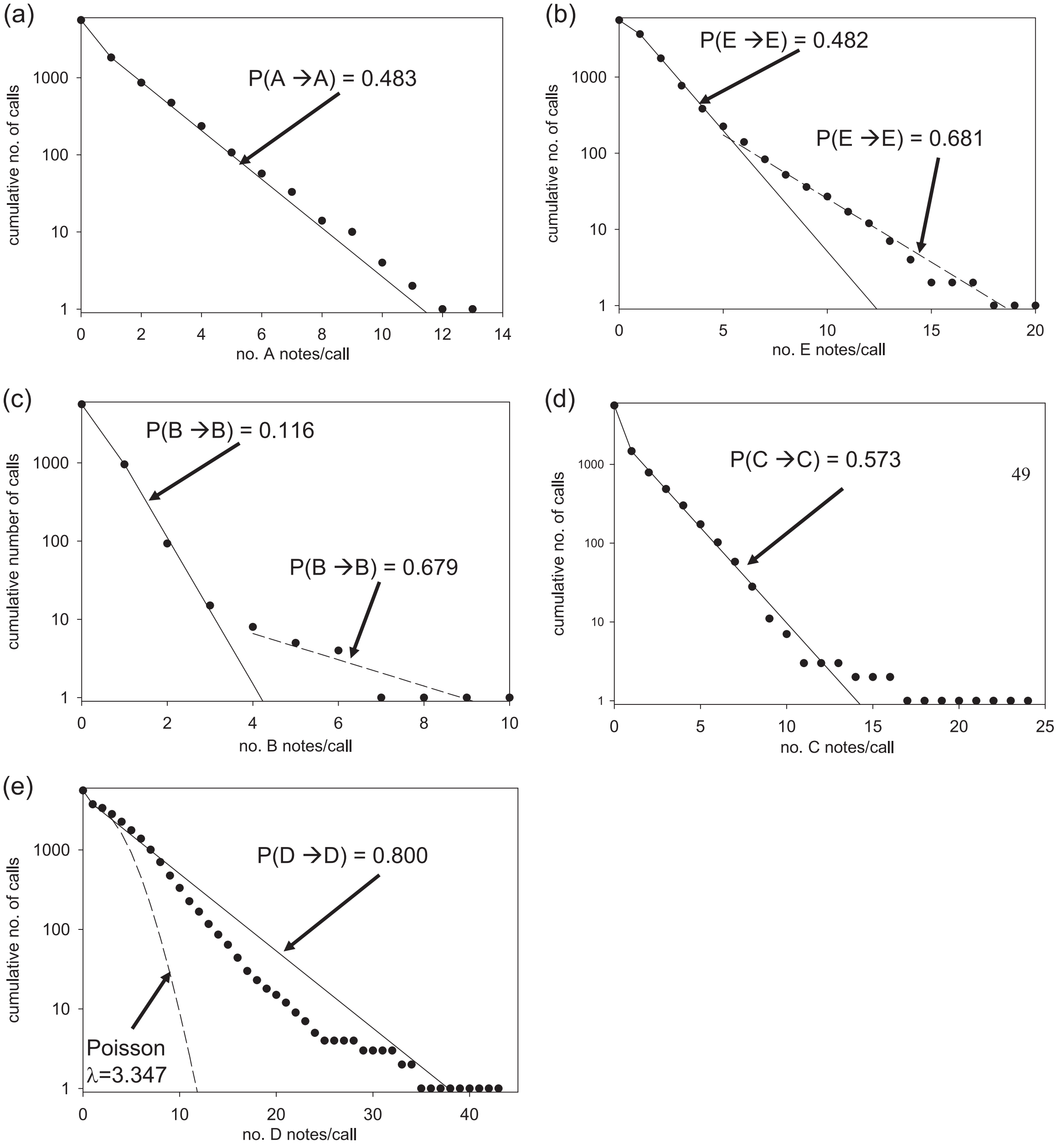

Figure 8. Survivorship curves (cumulative number of notes with at least x number of notes per call) for note types in Carolina chickadees: (a) A, (b) E, (c) B, (d) C and (e) D. Symbols = raw data. Straight line = semi-Markov expectation given the average transition probability of a note following another note of the same type. In (b) and (c), a separate regression line is fit through the portion of the raw data that does not fit semi-Markov expectations. In (e), an expected line based on a Poisson distribution is also included.

ever, there were interesting internal constraints influencing how notes were used in calls with a large number of notes. When a call contained a large number of A notes, for example, it was much more likely to end with an A note, as opposed to transitioning to an E note if the call contained a small number of A notes. This general trend of long strings of a given note tending to lead to that particular note ending the call was found for E and C notes as well, and also, unsurprisingly, for D notes. Two note types clearly violated this trend, which might be related to their relatively low frequency of use in chick-a-dee calls of this eastern Tennessee population. B and D_h notes, when they occurred in calls, were rarely repeated. Taking these findings on differential note usage in calls together, some note types may influence the message of a call primarily by their presence or absence (B and D_h notes), whereas other note types may influence the message by whether a small or large number of the note occurs (A, E, C, and D notes). Another possibility that future research should address is whether the proportion of a certain note type in a call is more relevant to

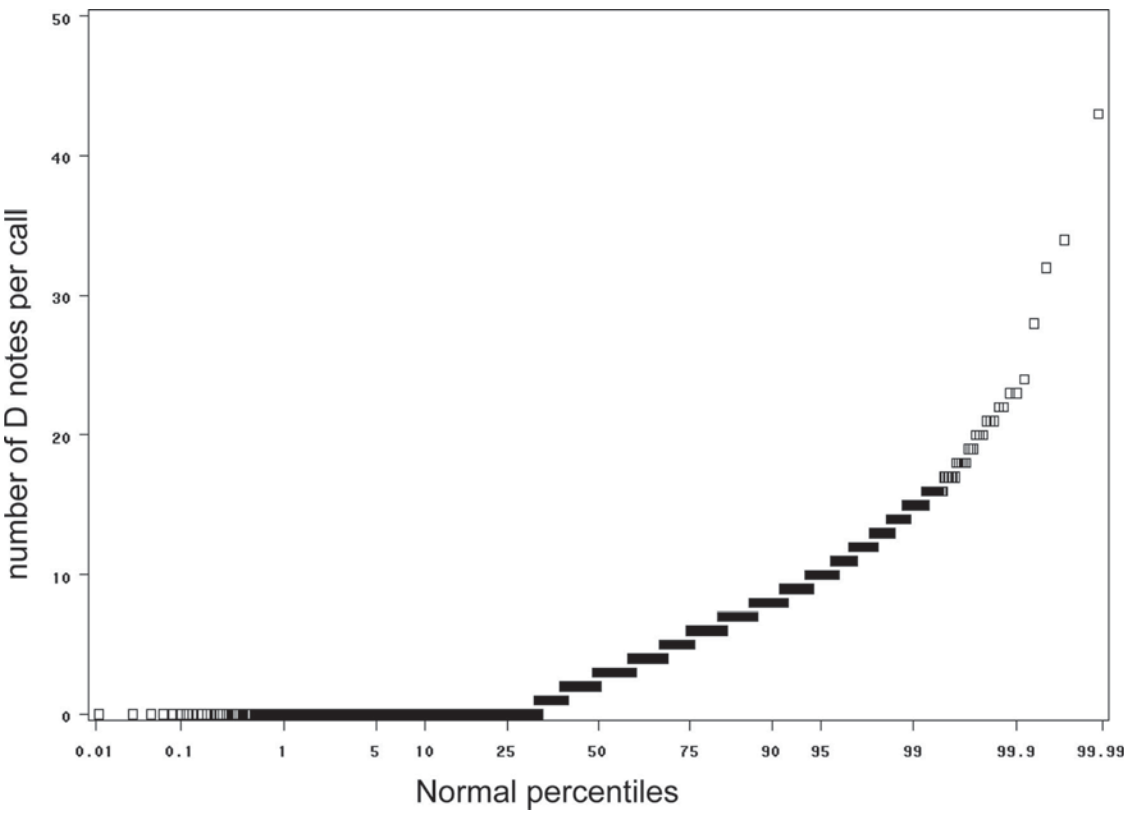

Figure 9. qq-plot for D notes. If D notes are normally distributed, the function should be linear.

receivers than the absolute number, a point raised by Hailman et al. (1985). For example, is the message of an "EECDDDDD" call different from the message of an "EEECCCDDDDD" call not because of the increase in E and C notes in the latter, but rather because of the decrease in the proportion of D notes in the latter, relative to the former?

Testing the Social Complexity Hypothesis With Chick-a-dee Calls

Our second aim was to compare these information-theory measures in Carolina chickadees to those previously published for the closely related black-capped chickadees (Hailman et al., 1985, 1987). The calls of Carolina chickadees are quite comparable to those of black-capped chickadees. Whole call analyses suggest greater diversity of calls with unique note compositions in Carolina chickadees compared to black-capped chickadees (Figures 2, 3, and 6). Much of this species-level difference appears to emerge from calls of intermediate note number—calls with greater than the modal number of notes, but calls that are not extremely long—in which Carolina chickadees have a larger number of calls with unique note compositions when compared with black-capped chickadees (Figure 5). In terms of analyses of uncertainty as measured on note type usage in calls, both Carolina and black-capped chickadees show a sharp drop in information at U_0 and U_1, when compared with $U_{\max}$ and letters in English words (Figure 4). At higher levels of uncertainty, U_2 and U_3, black-capped chickadees exhibit another rapid drop in information, whereas the drop is much less steep in Carolina chickadees. This indicates that transitions between note types at higher levels of note ordering (e.g., a new note type following an ordered pair or triad of notes) are relatively diverse in Carolina chickadees, whereas there is more note repetition in black-capped calls. Thus, although both species very often exhibit repeating of notes, receivers may need to attend more to complete calls in Carolina chickadees to gain the meaning, rather than just to a subset of a call.

Taking the results from these information theoretical approaches together, then, it appears that the calls of Carolina chickadees are more complex than the calls of black-capped chickadees. This outcome lends support to the argument from the Social Complexity Hypothesis that the diversity of social relationships within groups/species in chickadees may be a stronger driver of vocal communicative complexity than simple group size. We remain cautious in this interpretation, however, for two main reasons. First, the data sets on black-capped chickadees and Carolina chickadees, while enormous, come from essentially only one population for each species. Greater population sampling within each species is needed before stronger claims can be made about differences in call complexity between the two species. Second, this interpretation begs the question that the structure of social relationships is richer in Carolina chickadees compared to black-capped chickadees. Whereas data on reversals of dominance hierarchies do speak to the question raised here, stronger data sets on the linearity and steepness of dominance hierarchies (de Vries, Stevens, & Vervaecke, 2006) in the two species—and how these relate to call and note type diversity—are needed to answer this question more directly. Furthermore, it would be highly informative to increase sampling effort of potential competitors and predators in the environments where calls of black-capped and Carolina chickadee populations would be recorded.

Chickadee Complexity and Chick-a-dee Complexity

For decades in animal communication, there has been a general view of species possessing distinct vocal signals that serve rather distinct functions. In studies of calls of birds and mammals, in particular, this view has prevailed (e.g., Marler, 2004; Owings, Beecher, & Thompson, 1997). Recently, researchers are beginning to uncover the greater complexity of communication that individuals can achieve by combining different call elements to produce call "clusters" that convey different meanings to receivers. For example, Ouattara, Lemasson, and Zuberbühler (2009a) show that Campbell's monkeys, *Cercopithecus campbelli*, follow certain call types with different call types in ways that predict the context of the signaler, and individuals can modify the meaning of particular alarm calls that they use by adding suffix-like call elements to the initial vocalization (Ouattara, Lemasson, & Zuberbühler, 2009b). Recent studies in Carolina chickadees and related species (see reviews by Lucas & Freeberg, 2007; Sturdy et al., 2007) suggest that the variation in note usage and note combinations may allow this single chick-a-dee call system to convey a similar wide range of messages observed by call combinations in nonhuman primates.

It is important to stress that the measures we used here from information theory largely assess the *hypothetical* information that can be transmitted with this chick-a-dee call system. What are needed in parallel with these information theoretical approaches are functional tests of variation in call production in different contexts and of responses to playbacks of calls that differ in note composition or in other aspects of acoustic structure. The last decade has seen a great increase in studies of this kind, indicating that for various species the structure of the chick-a-dee call can vary in different contexts related to predator detection, distance of predator from signaler, size of avian predator, flight or perched state of avian predator, immediate flock size, presence or absence of heterospecifics in mixed-species flocks, flight behavior and height off ground of the signaler, and detection of food. Clearly chickadees can convey a wide variety of distinct messages with this single call system. However, how the diversity of functional messages maps onto the measures we assessed from information theory is still a rather open question. Furthermore, we and other authors have largely neglected the substantial variation within note types, and evidence suggests that marked changes to acoustic parameters of notes can occur in different contexts (e.g., Bartmess-LeVasseur et al., 2010; Templeton et al., 2005).

Carolina chickadees, like many of the other members of the Paridae, possess an atypical and complex social structure, in that they form stable multiindividual flocks during the overwintering months (Mostrom, Curry, & Lohr, 2002). They also are commonly found in mixed-species flocks, often as a nuclear species (Morse, 1970). This sort of complex social dynamic has been argued to be a selective pressure leading to increased communicative complexity (e.g., Dunbar, 1996, 1998; Freeberg, 2006; McComb & Semple, 2005). Carolina chickadees, like other parid species whose vocalizations have been described, have a wide range of distinct songs and calls in their vocal repertoires (Hailman, 1989; Hailman & Ficken, 1996). One of the key vocal signals in their vocal repertoire is the chick-a-dee call, used year-round and by both females and males, and functioning in social cohesion (Hailman, 1989; Lucas & Freeberg, 2007). In their seminal study of the chick-a-dee call of black-capped chickadees, Hailman et al. (1985) described a call that was among the most complex in terms of its structure and potential information encoded, outside of human language. Here, we describe the chick-a-dee call of the related Carolina chickadee, and have found that this call system is at least as structurally complex as that of black-capped chickadees. Like the call of black-capped chickadees, the chick-a-dee call of Carolina chickadees is largely open-ended, and so represents one of the few nonhuman animal generative vocal systems that has been documented. Our structural analyses of the call suggest some potential hypotheses regarding signal use and function that await future testing. We hope that these information theoretical approaches will be applied to this call system in other parid species, with the aim of testing comparative hypotheses regarding the roles of phylogeny, natural selection (e.g., related to predation), and social selection pressures on signal complexity.

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