CHAPTER 13

"Information" and the *chick-a-dee* call: Communicating with a complex vocal system

Jeffrey R. Lucas and Todd M. Freeberg

13.1 Introduction

The *chick-a-dee* call is one of the most commonly used, and complex, vocal signals of chickadees and is given by all members of the genus *Poecile*. The complexity of the *chick-a-dee* call arises not just from its structural characteristics, but also from its potential functions in social organization. Earlier work demonstrated that the call is unusual because it has a computable syntax that can generate an open-ended number of unique call types (e.g. Hailman *et al*. 1985, 1987; Hailman and Ficken 1986; Ficken *et al*. 1994). Hypothetically, this means the call could convey an enormous amount of information. However, despite two decades since the generative properties of the call were described, we know little about how much information is actually conveyed by this call. In this sense, Hailman *et al*. (1987, p. 63) were prescient in suggesting that the information encoded in these calls "presents a difficult challenge in decoding". Nevertheless, some progress has been made in the study of this fascinating system, as we demonstrate below.

The review is broken into three sections. First, we describe some general characteristics of chickadee vocal behavior and some of the major arguments regarding definitions of "communication" and "information", as these ideas are important for interpreting the notions of complexity in the *chick-a-dee* call. Second, we review work of the Hailmans and Fickens on the structural complexity of *chick-a-dee* calls in black-capped and Mexican chickadees. We also review some of our own studies on the *chick-a-dee* call of Carolina chickadees, as well as studies from others on various chickadee species, all of which are beginning to address exactly what chickadees might be communicating when the birds vary the structure of their calls. Third, we draw some conclusions about *chick-a-dee* call complexity and raise the need for comparative research to elucidate *chick-a-dee* call evolution and function.

Most of the work on North American Paridae vocal behavior has concentrated on chickadee species. One reason for this concentration is the large repertoires of diverse vocalizations possessed by these species (e.g. Hailman 1989; Hailman and Ficken 1996). The different vocal signals used by chickadees and related species are believed to represent different communicative entities—for example, an individual producing *fee-bees* is presumably communicating something different than if it were producing *chick-a-dee* calls. Even within the *chick-a-dee* call itself, structurally different *chick-a-dee* variants (e.g. calls differing in note composition) likely hold different meanings to receivers. This raises the question of what is being communicated about the signaler or the signaler's immediate environmental context. Indeed what, exactly, is "communication"?

Most definitions of "communication" (e.g. Burghardt 1970, p. 16; Wilson 1975, p. 176; Hailman 1977, p. 52) focus on three parts of communication—a feature (often a signal) of one individual (the signaler) affects the behavior of another individual (the receiver). However, two major arguments have arisen over the definition. The first argument relates to whether the signaler primarily benefits, or the signaler and receiver both benefit, from the communicative interaction (e.g. Dawkins and Krebs 1978; Owings and Morton 1998; Bradbury and Vehrencamp 1998). One can argue that the "target of selection" argument is tangential to the question of how and whether communication occurs, although clearly it is important to determining the types of communicative events that occur (e.g. distinctions between signals and cues as discussed in Maynard Smith and Harper 2003). The second argument revolves around the usefulness of the notion of "information" or "information transfer".

A precise definition of "information" has proven difficult to pin down, despite a general understanding of the concept. There are two major views—one is the view that if communication involves one individual signaling "about something" to another individual, then that "about something" is the information. The other view defines information not in the terminology of meaning, but mathematically as "a measure of one's freedom of choice when one selects a message … in the simplest cases, to be measured by the logarithm of the number of available choices" (Shannon and Weaver 1949, p. 9). Smith (1977, p. 193) bridges these two ideas nicely by defining information as "an abstract property of entities and events that makes their characteristics predictable to individuals with suitable sensory equipment for receiving the information. Information thus enables such individuals to make choices … " (see also Halliday 1983). In the next section, we attempt to place these ideas of "information" in the context of the *chick-a-dee* call by discussing the seminal work on black-capped chickadees by the Hailmans and Fickens and our work on Carolina chickadees.

13.2 "Information" and the *chick-a-dee* call

13.2.1 Basic note types of *chick-a-dee* calls

The first detailed investigation of the *chick-a-dee* call from the mathematically-based information perspective was carried out on black-capped chickadees. Hailman *et al*. (1985) recorded roughly 3500 calls from at least 20 individuals. The call was described as being composed of four note types (see Fig. 13.1 for Carolina chickadee examples). Two note types—A and B—are relatively pure tones and span a considerable frequency range. A notes tend to have a higher peak frequency, with a short ascending arm followed by an abrupt and long descending arm (in Carolina chickadees, the ascending arm is typically much longer than the descending arm in terms of frequency span). B notes tend to be relatively lower in frequency and shorter in duration, and both the ascending and descending arms are relatively similar in the frequencies they span.[1] C notes are harsh sounding notes with a fairly complex and noisy structure, with a relatively lower pitch than A or B notes. D notes have a longer duration that the other three note types, and are relatively unmodulated in terms of frequency, with a characteristic harmonic-like structure when seen in sonagram form.

Hailman *et al*.'s (1985) sample of nearly 3500 calls resulted in 362 calls that were distinct in note composition. This large number of unique calls illustrates one component of *chick-a-dee* call complexity—the number of distinct calls (in terms of note composition) increases with sample size. This is very different from, for example, the songs of many songbird species, in which the sampling of dozens or a few hundred songs will often completely capture the song repertoire of an individual—the *chick-a-dee* call possesses the language-like feature of being open-ended.

13.2.2 Variability in note types

One aspect of the *chick-a-dee* complex that needs more attention is how many notes any one species actually uses in its calls—we can't understand the call complex completely without understanding its

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[1] Note that Bloomfield *et al*. (2003) redefined Carolina chickadee A notes in a series as A, B_1, and B_2 notes. Given the precedence in the literature, we will define their B_1 and B_2 notes as A notes and suggest that only their B_3 notes be called true B notes. Of course, the only way to resolve this issue is to evaluate whether the birds themselves distinguish these notes as we have defined them—see also Chapter 10.

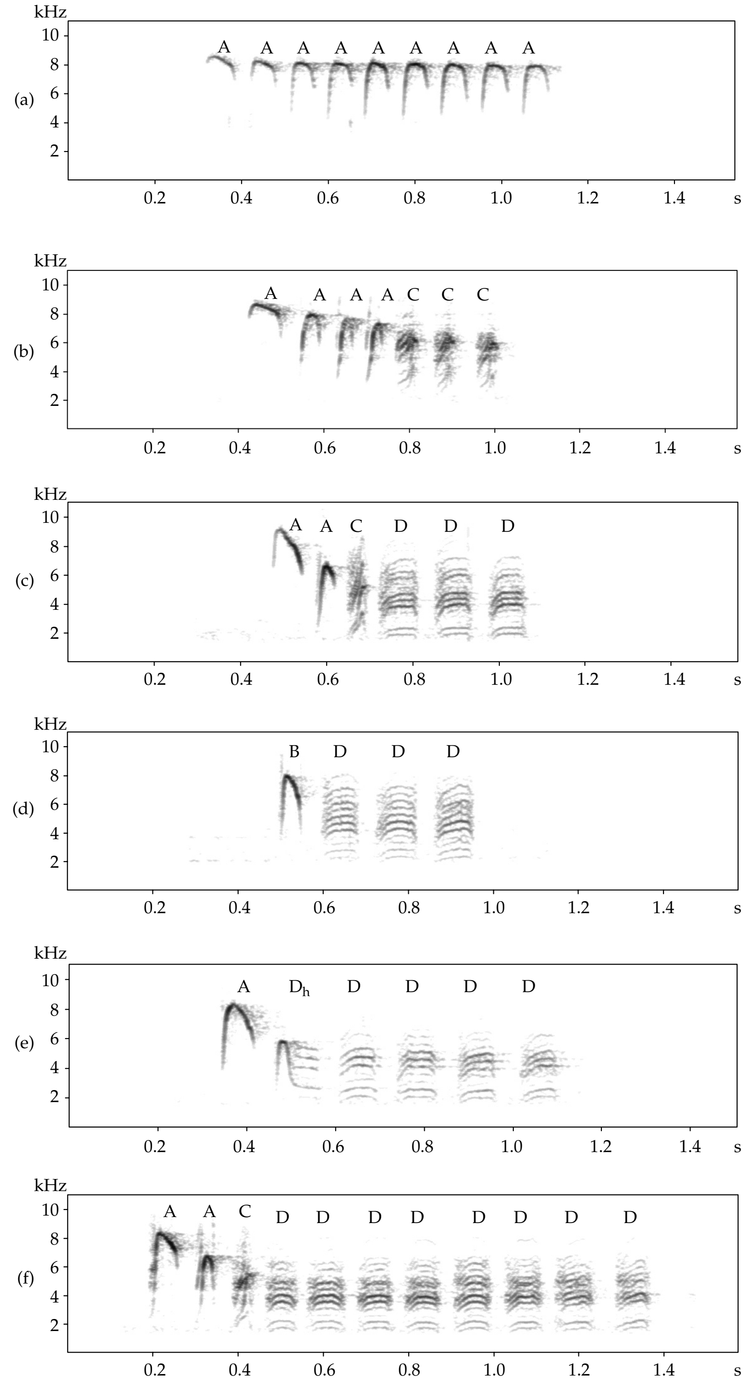

Figure 13.1 Sonagrams of Carolina chickadee calls that vary in syntax using **A**, **B**, **C**, and **D** note classifications. (a) String of **A** notes. (b) Four **A** notes, three **C** notes. (c) Two **A** notes, one **C** note, three **D** notes. (d) One **B** note, three **D** notes. (e) One **A** note, one "hybrid" **D** note, four **D** notes. (f) Two **A** notes, one **C** note, eight **D** notes. Sonagrams were generated using Avisoft SASLab Pro with an FFT length of 512, frame 75%, and Blackman window.

elements. Clearly, virtually all chickadees have some variant of the A, B, C, D series of primary note types (Hailman 1989). However, there are some intriguing species differences. Mountain chickadees (Bloomfield *et al*. 2004) and Mexican chickadees (Ficken *et al*. 1994) have a common hybrid note described by Ficken *et al*. (1994) as an A running into a D note. We found these notes in Carolina chickadees (e.g. Fig. 13.1e), but they were rare enough that we concluded that they were anomalies. Given that this note occurs in 94% of mountain chickadee calls analyzed by Bloomfield *et al*. (2004), our notion of "anomalous" notes needs to be revisited. Interestingly, Mexican chickadees (Ficken *et al*. 1994) have, for the most part, lost one of the four primary notes from their repertoire—B notes are quite rare in their *chick-a-dee* calls. Also, in mountain chickadees (Gaddis 1985) C notes and D notes appear to be a single graded series (see also Hailman *et al*. 1985). Thus, for most chickadee species, it is arguably an open question as to how many distinct note types occur in the call.

New or hybrid notes notwithstanding, it is clear that in many species the A, C, and D notes have several subtypes (Fig. 13.2). The A note in particular is quite varied. A spectral analysis by Nowicki and Nelson (1990) showed that A and B notes in black-capped chickadees grade into each other. A note variants should therefore grade into each other as well, but these variants are sufficiently distinct that Smith (1972) defined at least four different A-like notes in Carolina chickadees (high see, high tee, loud tee, lisping tee), and our own analyses of Carolina chickadee calls (T. M. Freeberg and J. R. Lucas, unpublished data) support this conclusion (Fig. 13.2).

C notes also vary. Smith (1972) described at least two, the *chip* and *chick* notes, that were elicited in different situations: the *chip* is an aggressive call usually given in a string without D notes, and the *chick* note is a component of the more standard *chick-a-dee* call given in a variety of circumstances. Similarly, Haftorn (1993) suggested that willow tits have two C-like notes, one used in mobbing calls and the other in more standard *chick-a-dee* calls. We have sonagrams of a third C-like note in Carolina chickadees that Arch McCallum (personal communication) called a "*begging* C", which appears structurally similar to the *soft dee* described by Smith (1972).

Smith (1972) defined four different D notes in Carolina chickadees: *dee*, *broken dee*, *harsh dee*, and *soft dee*. Ficken *et al*. (1994) indicated that D notes in Mexican chickadees varied from banded (Smith's *dee* note) to uniformly noisy (Smith's *harsh dee*). Similarly, mobbing black-capped chickadees employ a noisy variant of the D note (Ficken and Popp 1996), and female black-capped chickadees use a *broken dee* when they solicit food from their mates (Ficken *et al*. 1978).

In some cases, there are species differences in the structure of notes. Introductory notes of most chickadees are pure tones (Carolina chickadees, Smith 1972; black-capped chickadees, Ficken *et al*. 1978; mountain chickadees, Gaddis 1985; willow tits, Haftorn 1993). However, the A note is a frequency-modulated trill in Mexican chickadees (Ficken 1990; Ficken *et al*. 1994). The D note of Mexican chickadees is also noisier than its North American counterparts (Ficken 1990), although as noted above, noisy D notes are found in a number of other species as well.

A critical question related to our perception of note types is whether the birds themselves share this perception. An acoustical analysis of black-capped chickadee note types by Nowicki and Nelson (1990) suggested that they should: A and B notes are statistically distinguishable from one another, although they tend to be a part of a graded series, and C and D notes are quite distinct. Sturdy *et al*. (2000) showed that black-capped chickadees can learn to discriminate between note types more rapidly than within variants of the same note type, suggesting that the birds do indeed discriminate among note types and generalize within note types. Moreover, the birds' behavior was consistent with the suggestion of Nowicki and Nelson (1990) that A and B notes are more similar to one another than to the other note types. This is good news for the field, although Sturdy *et al*.'s (2000) important contribution needs to be extended to other chickadee species.

Arguably the most interesting aspect of the *chick-a-dee* call complex is that it shares some similarities to human language (Hailman *et al*. 1985, 1987; Hailman and Ficken 1986). As we will discuss

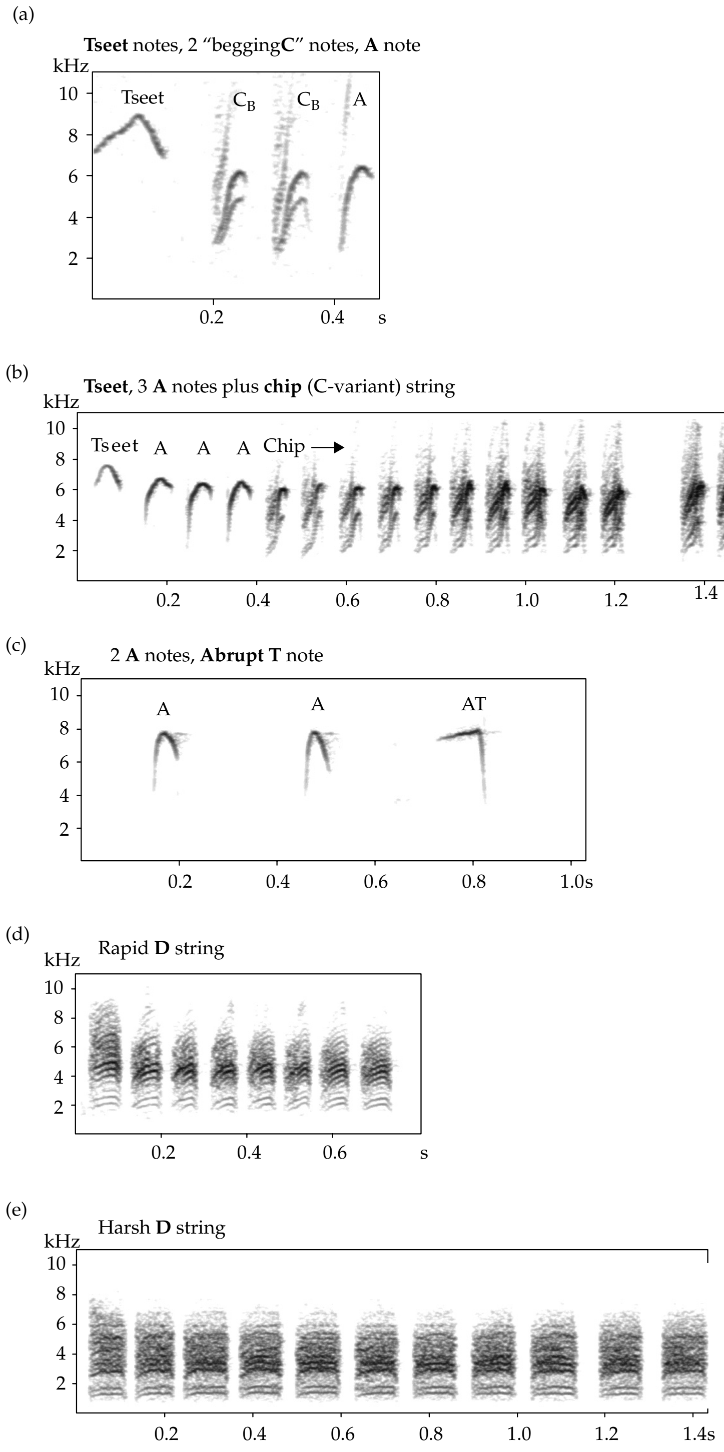

Figure 13.2 Sonagrams of Carolina chickadee calls illustrating note type diversity (partly based on Smith 1972). Sonagrams generated as in Fig. 13.1.

below, the call system has a rudimentary "syntax"—notes that occur in any given call follow simple rules of note ordering. In addition to syntax, the literature on *chick-a-dee* calls has addressed a number of other non-syntactical components of information. We will address these alternative sources of information first, in part because they may influence how we think about syntax, or at least about constraints on syntax.

13.2.3 Signal redundancy

The first component of information we will address is "internal" information, or the redundancy in a signal. Redundancy results from multiple signals, or multiple components of a signal, encoding similar information. Theoretically, redundancy increases the probability that receivers correctly perceive the information embodied in the signal, although redundancy also reduces the total amount of information that can be encoded in the signal (Bradbury and Vehrencamp 1998). A more practical aspect of redundancy is that we can potentially over-interpret experimental results if we ignore redundant cues.

Freeberg *et al*. (2003) showed that, in Carolina chickadees, the spectral structure of the first A, C, and D notes in a string of similar notes is significantly correlated with the note composition in that call. This suggests that a chickadee might be able to predict the syntax of the rest of the call even if it were able to hear only a fraction of that call, although this statement must be tested. Nowicki and Nelson (1990) offer a complementary viewpoint: single A and B notes in a string of notes tend to decline in frequency and amplitude (black-capped chickadees: Hailman *et al*. 1985; Carolina chickadees: Freeberg *et al*. 2003). Chickadees may be able to use the change in frequency and amplitude as an index of syntax, again without hearing the entire call.

The statistical analysis of Freeberg *et al*. (2003) suggested that we can expect note properties to change if syntax changes. We need to be careful about reading anything more complex into the call. As such, conclusions about *chick-a-dee* calls could be premature if spectral analyses fail to correct for syntax (e.g. Nowicki 1989; Mammen and Nowicki 1981; Templeton *et al*. 2005).

13.2.4 Identity

One kind of information a signal can communicate is identity. Identity can range from individual to group to species, although we will limit our discussion to the population level and below.

Signals communicating individual identity are well established (Bradbury and Vehrencamp 1998), at least in relatively stable social groups (Slater *et al*. 2000). In black-capped chickadees, Nowicki (1989) suggested that the D note plays a special role in encoding identity and Hailman *et al*. (1987) suggested that this may be why *chick-a-dee* calls tend to be more likely than chance to have at least one D note in them—the trailing D essentially acts as an identification flag. More recent work by Charrier *et al*. (2004) and Bloomfield *et al*. (2004) has made this viewpoint even more intricate. These studies showed that both mountain chickadees and black-capped chickadees (and, by extension, other species) have individually specific introductory notes in addition to individually specific D notes, although both studies concluded that the D note has the highest potential for identity coding. The implication is that identity coding need not reside only in the D note, but playback experiments are needed to resolve this issue.

Mammen and Nowicki (1981) were the first authors to suggest that flock-level call properties develop in black-capped chickadees. This possibility was strengthened by a playback experiment showing that birds played foreign calls were less likely to visit a feeder than those played calls of flock members (Nowicki 1983). Nowicki (1989) then put five birds together in an aviary flock and demonstrated convergence in one component of the D note of the call. However, a potential confound of the Mammen and Nowicki (1981) study is that syntax was not controlled for in the spectral analysis; indeed, their data suggest that birds from different flocks tended to have calls with different syntax. Given that syntax itself affects note structure (Freeberg *et al*. 2003), Mammen and Nowicki's (1981) results may have had artifacts of flock-specific differences in note composition. It is also possible that the putative flock-level recognition detected in these studies was actually due to individual recognition. Nowicki (1989) found a single trait converging in a single flock in the laboratory; this is not, however, unequivocal evidence for convergence among flock members of a *chick-a-dee* call structure that marks flock membership.

There is stronger evidence for population-level variation in the structure of *chick-a-dee* calls. For example, Baker and Logue (2003) were able to identify the population of origin of 100% of black-capped chickadees calls based on multitaper spectral analysis (see Tchernichovski *et al*. 2000). Spectrogram cross-correlation was nearly as effective. Similarly, Freeberg *et al*. (2003) demonstrated population-level differences in Carolina chickadees in both A and D notes. These results mirror the demonstration of population-specific dialects in the gargle call of black-capped chickadees (Ficken *et al*. 1985; Miyasato and Baker 1999).

13.2.5 Syntactical information

There are at least three ways that we can begin to understand the "meaning" of the *chick-a-dee* call from the perspective of syntactical information. The first, pioneered by Hailman *et al*. (1985), is a structural analysis of syntax *per se* to determine the hypothetical information that may reside in a signaling system. The second is a natural-history approach, documenting calls produced in natural settings and what behavioral or other contextual correlates exist (e.g. Smith 1972). The third is an experimental analysis, using playbacks to test predicted information content in the calls (e.g. Freeberg and Lucas 2002; Clucas *et al*. 2004; Templeton *et al*. 2005).

13.2.5.1 Syntax

Hailman *et al*. (1985) measured the amount of information that might be conveyed by the *chick-a-dee* call system of black-capped chickadees. From Shannon and Weaver's (1949) theory of communication, a communicative system with four distinct units (note types) has a maximum uncertainty of two bits of information ($U_M = \log_2 N$, where N = number of units). The maximum information in a communicative system occurs when all of the system's units are used with equal probability. As is the case with letters in the English language (e.g. relative use of "e" vs. "x"), however, note types in *chick-a-dee* calls are not used equally—D notes are far more common. This means that the actual information in terms of note use in *chick-a-dee* calls is lower than the maximum possible information. The uncertainty measured for actual use of the different units of a communication system is referred to as the zero-order uncertainty, and is calculated as:

$$U_0 = \Sigma P_i\,(-\log_2 P_i)$$

where P_i is the probability of each of the i units occurring in the system. In the case of the *chick-a-dee* call of black-capped chickadees, there is indeed a drop-off from U_M to U_0. However, a much greater drop-off in uncertainty occurs when one assesses the transition probabilities between pairs of notes. This measure of first-order uncertainty, U_1, represents the uncertainty of a given unit to occur in a sequence when a previous unit has already occurred. It is calculated as:

$$U_1 = \Sigma\Sigma P_{ij}\,(-\log_2 P_{j|i})$$

where P_{ij} is the probability of the i and j note occurring in the ijth sequence, and $P_{j|i}$ is the conditional probability of the j unit occurring given that the i unit has occurred. For the chickadee call this analysis would address the ability to predict that, for example, a D note will follow if a C note occurs in a call. Hailman *et al*. (1985) found that there is a considerable drop-off in information at this level of uncertainty—if a researcher (and, presumably, a chickadee receiver) detects one note type in a call, there is a good probability of predicting what the next note type will be in the call.

The preceding discussion leads into one of the other major structural features of the *chick-a-dee* call. Notes and pairs of notes do not occur with equal probability. Instead, the *chick-a-dee* call obeys rules of note ordering, a simple form of syntax. In black-capped chickadees, the two most common call structures are [A][D] and [B][C][D], with brackets indicating that the particular note type can occur more than once. In other words, if the following notes occurred in a nine-note call, BBCCCDDDD, they would virtually always (e.g. over 99% of the time) occur in the order [B][C][D]. Taken together, the *chick-a-dee* call represents an interesting case of an open-ended communicative system that is nonetheless constrained by its note ordering rules.

In addition to the constraints upon the call imposed by the note ordering rules, other constraints appear to limit the diversity of potential call structures (Hailman *et al*. 1987). For example, as the number of A, B, and C notes increase in a call, the number of D notes that might occur decreases. Therefore, there seems to be a constraint on the overall number of notes that can occur in an average call. However, calls with extremely large numbers of D notes are more common than expected by chance, suggesting that the constraints on introductory notes are relaxed when calls contain many D notes (Hailman *et al*. 1987).

This mathematic approach to the question of information in the *chick-a-dee* call was extended to another species, Mexican chickadees (*P. sclateri*; Ficken *et al*. 1994), and interesting comparative results emerge. The Mexican chickadee *chick-a-dee* call system is open-ended, the C note is more common than the D note, and the B note is extremely rare. Notes follow the A-B-C-D note-ordering rule shared by black-capped chickadees. The most common call structures were [A][D], [C], and [A], and calls tended to be shorter in note number than black-capped chickadee calls. Ficken *et al*. (1994, p. 80) indicate that, relative to the *chick-a-dee* call of black-capped chickadees, the "rarity of B notes and the shorter note length of calls means that the Mexican chickadee's utterances tend to be syntactically simpler, although not necessarily semantically simpler … " This quote nicely captures the two approaches to information discussed earlier. For information as a mathematically-defined measure, Mexican chickadee calls appear to convey less information than black-capped chickadee calls. Mountain chickadee calls also appear to convey less information than black-capped or Carolina chickadees because their calls are substantially shorter (three–four notes/call vs. six–eight notes/call, respectively; Bloomfield *et al*. 2004). For information as meaning, however, it is an open question in these species as to which call system conveys more information.

Hailman *et al*. (1987) published an additional method of evaluating the syntactical properties of black-capped chickadees' calls. They compared the cumulative number of calls containing at least some number of A, B, C, and D notes (a "survivorship" plot) with the expected cumulative number of notes based on a semi-Markovian model. A departure from the simple semi-Markovian expectation implies some meaning in the note composition of the call beyond a simple repetition of notes. They found that A notes fit expectations almost exactly. B notes did not: calls with three or fewer notes fit expectations whereas those with four or more B notes were too common. As with A notes, the probability of repeating a C note was constant, albeit somewhat less than expected by chance. The survivorship curve for D notes departed completely from semi-Markovian expectations, with too many short-D calls, too few intermediate-D calls, and too many long-D calls. Hailman *et al*. (1987) suggested that this distribution represented a compound of two or more separate processes, and potentially separate syntactical functions.

We repeated Hailman *et al*.'s (1987) analysis with a preliminary data set of 2153 Carolina chickadee calls recorded in non-manipulated field settings in eastern Tennessee (nine sites) and central Indiana (six sites). The uncertainty measures for Carolina chickadees for this sample of the field recordings showed a similar pattern to those reported for black-capped chickadees (Hailman *et al*. 1985) and Mexican chickadees (Ficken *et al*. 1994), with a marked reduction between zero-order and first-order uncertainty ($U_M = 2$, $U_0 = 1.49$, $U_1 = 0.63$). A and D notes did not meet semi-Markovian expectations (Fig. 13.3). Long strings of A notes (>six A notes/calls) were more common than expected by chance. The survivorship curve for D notes was qualitatively similar to that of black-capped chickadees: too many calls with a few notes, too few with a large number of notes (10–25), and too many with a very large number of notes.

We asked whether our *chick-a-dee* calls met expectations of Mandlebrot's modification of Zipf's Law (see Hailman *et al*. 1985). Stated simply, Zipf's law argues that the frequency of utterances should be reciprocally related to their frequency rank—the tenth most common utterance (word in a human language, call syntax in the *chick-a-dee* call) should occur with 1/10th the frequency of the most common utterance. Human language meets this criterion, but black-capped *chick-a-dee* calls do not.

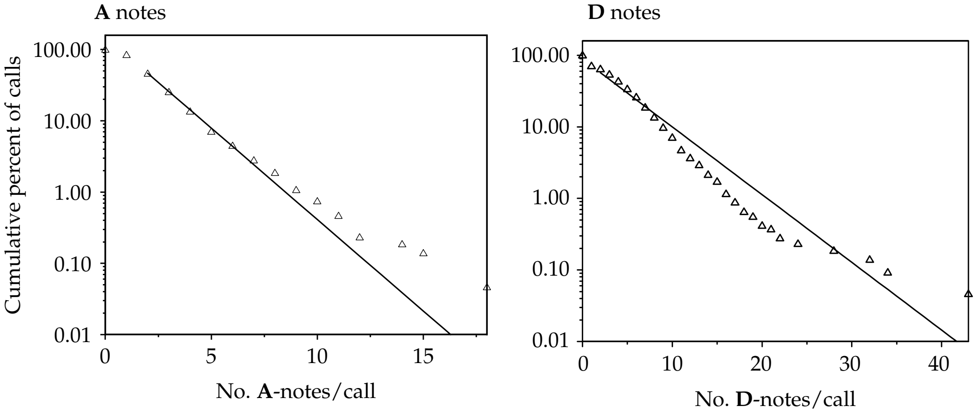

Figure 13.3 Survivorship plots of **A** notes and **D** notes of the Carolina chickadees. These are based on a sample of 2153 calls. The triangles represent calls in the sample, the line is the predicted survivorship from a semi-Markovian model, based on the transitions between same-type notes (e.g. in the left panel, the transition probability from **A** to another **A** note).

However, black-capped calls do fit a broader form suggested by Mandelbrot (Hailman *et al.* 1985). Interestingly, our Carolina chickadees do not fit Mandelbrot's function (Fig. 13.4), at least based on a least-squares best fit of the data. Nonetheless, the general increase in cumulative call types with an increase in the number of calls sampled indicates that the call system is generative, or open-ended.

As Hailman *et al.* (1987) showed in black-capped chickadees, the probability that a call ends (instead of continuing with a new note) increases with an increase in the number of A and C notes (Table 13.1). In Carolina chickadees, longer strings of A notes (eight–ten) are more likely to transition to C notes whereas shorter strings (one–five) are as likely to transition to B or D notes. B notes almost always transition into D notes or end the call.

We need to add a caveat that the differences between black-capped and Carolina chickadees could result from differences in the field recording contexts. Assuming that this caveat does not generate a bias in our data sets, the results suggest that Carolina chickadees use long strings of introductory notes in different ways (with different meanings?) than black-capped chickadees. It would be instructive to perform this analysis on mountain and Mexican chickadees, given the species differences reported earlier. It would also be instructive to see this analysis done on European tits, particularly the marsh and willow tits, which are closely related to the North American chickadees (Gill *et al.* 2005).

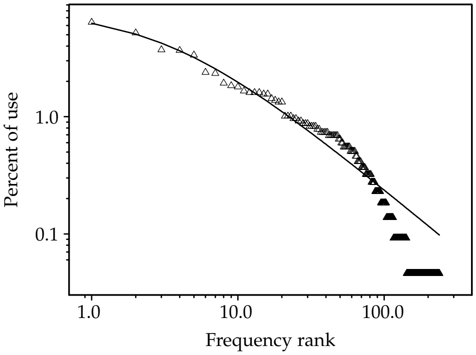

Figure 13.4 Percent use of *chick-a-dee* variants as a function the frequency rank (1 = most common). Triangles are data from our set of 2153 calls of Carolina chickadees. Line represents the best fit line: $p = i(r+k)^{-s}$, where p = percent use, r = rank, and i, k, and s are fit constants (see Hailman *et al.* 1985).

13.2.5.2 Context

Studies of correlations between *chick-a-dee* variants and behavior are critical because they give us some insight into the potential for syntactically-mediated information transfer. Results to date clearly

Table 13.1 Transition probabilities for strings of **A**, **B** and **C** notes in *chick-a-dee* calls of Carolina chickadees; in each case, the number of elements in a string of same-type notes is given, followed by the probability that the string ends in another note type or silence (A0, B0, or C0)

AA	AB	AC	AD	A0	BB	BC	BD	B0	CC	CD	C0
1	0.11	0.32	0.36	0.21	1	0.06	0.82	0.12	1	0.81	0.19
2	0.20	0.20	0.29	0.31	2	0.5	0	0.5	2	0.77	0.23
3	0.10	0.22	0.29	0.39	3	0	0.5	0.5	3	0.48	0.52
4	0.08	0.26	0.08	0.58					4	0.33	0.67
5	0.06	0.14	0.28	0.52					5	0.63	0.37
6	0	0.11	0.05	0.84					6	0.36	0.64
7	0	0.11	0.35	0.54					7	0.43	0.57
8	0	0.14	0	0.86					8	0.50	0.50
9	0	0.17	0	0.83							
10	0	0.20	0	0.80							
11	0	0	1.0	0							
13–17	0	0	0	1.0							

demonstrate that different *chick-a-dee* variants are given under different conditions.

The first extensive, though qualitative, study of this type was published by Smith (1972) on Carolina chickadees. Smith suggested that different note types had different meanings. For example, *chip* (a C-variant) notes are aggressive calls whereas *chick* notes (another C variant) are non-aggressive, often heard around feeding stations. Haftorn's (1993) study of willow tits demonstrated similar meaning in the C note, with one variant characteristic of alarm calls and another typically embedded in less aggressive calls.

Ficken *et al*. (1994) suggested that A notes are given by Mexican chickadees moving in space, whereas C notes are given in response to a disturbing stimulus (e.g. when mobbing a screech owl tape) or when birds change directions. D notes tend to be given by perched birds. These trends for A and D notes are similar to those reported by Smith (1972) for Carolina chickadees. Gaddis (1985) found that *chick-a-dee* variants were context specific in mountain chickadees. For example B notes are given when birds leave food; A notes are given when birds fly up, and [A][D] strings are given in flocks.

There are at least three studies of the syntactical cues given in black-capped chickadee mobbing calls. Hurd (1996) suggested that mobbing calls had more introductory notes than non-mobbing calls but the same number of C and D notes. Baker and Becker (2002) showed a similar pattern, with more B notes and fewer A notes given under more immediate risk (1 m vs. 6 m from a stuffed prairie falcon), but no difference in the number of C or D notes. In contrast, Templeton *et al*. (2005) showed that the number of D notes correlated strongly with the intensity of risk represented by different species of predators. It is not clear why these results are so different, although there were considerable methodological differences across the three studies.

In addition to syntactical cues, some cues may be given by call rate itself, with higher rates indicating more intense conditions. Black-capped chickadee mobbing calls, for example, tend to be given at higher rates under more immediate risk (Baker and Becker 2002). Carolina chickadee *chick-a-dee* call rates are higher when the birds are light-weight and hungry than when they are heavy or sated (Lucas *et al*. 1999)—*chick-a-dee* calls may encode information about signaler physiological condition. We (K. Bledsoe and J. Lucas, unpublished data) have limited data on two Carolina chickadees that indicate just this: D note fundamental frequency and duration correlated strongly with changes in corticosterone levels. These results are consistent with Owings and Morton's (1998) assessment/management model of communication, although clearly we need more extensive studies of this aspect of the *chick-a-dee* complex.

13.2.5.3 Playback studies

We can use playback experiments to test implications about syntactical information derived from field (or laboratory) observational studies. Here we focus on recent field-based playback studies (Sturdy *et al.* review laboratory-based studies of perception in Chapter 10). Freeberg and Lucas (2002) proposed that the C-note (*chick* variant) was food related, based on preliminary field observations. They tested this by broadcasting either C-rich or D-rich *chick-a-dee* calls at a temporary seed stand. Consistent with the hypothesis, birds tended to come to the stand and take seeds in response to C-rich calls but never took a seed in response to D-rich calls. Moreover, the rate of *chick-a-dee* calling was significantly higher in playbacks with C-rich calls than those with D-rich calls. There are at least two alternative explanations for this result. One is that the C note is indeed a food-associated note. The second is that D-rich calls are aggressive calls that elicit an aggressive reaction by receivers (and, by comparison, C-rich calls are non-aggressive). While we cannot distinguish these alternatives with this experimental design, the results indicate that *chick-a-dee* variants vary in their meaning to receivers.

Templeton *et al.* (2005) tested the relative function of black-capped chickadee mobbing calls. They found that the number of D notes was negatively correlated with predator wingspan and body length (smaller, more dangerous, predators elicit more D notes). Smaller predators elicited D notes with a narrower band width and more narrowly spaced overtones. Templeton *et al.* (2005) used playbacks of the mobbing calls in the absence of predators as an important test of the proposed information embodied in the calls. The birds gave responses appropriate to the predator that was being mobbed when the calls were first recorded, suggesting the calls conveyed some quantitative index of predation risk.

Finally, Clucas *et al.* (2004) monitored Carolina chickadees' responses to artificially constructed calls that varied in both note composition (AAAACCCC, AAAADDDD, and CCCCDDDD) and note ordering (AAAACCCC vs. CACACACA, CCCCDDDD vs. DCDCDCDC). The playback was repeated in two seasons, spring and fall/winter, to test for the potential role of seasonal context on receiver's responses to the calls. The experiment tested whether chickadees respond to manipulation of the two components of syntactical organization, note composition and note order, but did not test any specific hypotheses about the meaning of *chick-a-dee* variants. The birds showed no differential response to calls with atypical note ordering that varied in note composition (CACACACA vs. DCDCDCDC). Birds did, however, distinguish between calls that varied in note composition if the note order followed the species-typical A-B-C-D ordering. Season and social context also affected the birds' response to the playbacks. The number of introductory notes in the responding birds' *chick-a-dee* calls was affected by note composition in the fall but not in the spring: AAAACCCC playback calls elicited A/B-rich responses, and D-rich playback calls elicited C-rich responses. But this latter response was evident only when white-breasted nuthatches and tufted titmice (two dominant heterospecifics) were present. In the fall, the number of D notes in the call was also positively correlated with the number of birds responding, but this relationship was positive only when heterospecifics were not present. Only the number of birds responding affected the number of D notes in the spring [note: Table 2 in Clucas *et al.* (2004) is correct, but the discussion of this pattern in the text of that paper and Figure 8 are not correct].

Our results suggest that both note ordering and note composition affect the information content of the *chick-a-dee* complex. In addition, context (season and presence of dominant heterospecifics) matters, as predicted by Hailman *et al.* 1985 (also see Leger 1993; Marler and Evans 1996).

13.3 Conclusions, concessions, and a call for comparative work

The *chick-a-dee* call is complex both structurally and functionally. The structure of *chick-a-dee* calls can depend upon numerous characteristics of the signaler or its context—energetic state, flock/local population, sex, feeding behavior, flight behavior, and presence of avian predators. Thus, the *chick-a-dee* call can potentially convey a great deal of information about the different states, behavioral probabilities, events, etc. relevant to the signal's sender. Furthermore, *chick-a-dee* calls of black-capped chickadees (Hailman *et al*.1985), Mexican chickadees (Ficken *et al*. 1994), and Carolina chickadees (Fig. 13.4) are generative and possess fairly high levels of uncertainty. Thus, in terms of "information" as a mathematical measure of binary choices, call structural rules result in an information-rich signaling system. In addition, the number of a particular note type seems to influence acoustic characteristics and numbers of other notes, which suggests an interesting form of redundancy in these calls. This redundancy may increase a signaler's ability to transmit, and a receiver's ability to exploit, a message of a call, while limiting the total number of different messages a single call might convey. As we noted earlier, our claim about *chick-a-dee* call complexity is by no means novel to us—Hailman *et al*. (1985) first raised it two decades ago in their work with black-capped chickadees. In this final section of the chapter, we draw some conclusions about this complexity and why it might exist, point out some gaps in our understanding of the call system, and suggest a need to make broader comparative analyses of the call system in other Paridae groups.

A possible driving force for such a complex call system in chickadees might be their complex and fairly atypical social structure (at least for temperate zone birds). In late summer and early fall, chickadee female–male pairs join other pairs (and often juveniles) to form a flock with a relatively stable membership (Ekman 1989; Smith 1991). Flocks remain together, generally defending their territory from other flocks or individual intruders, until the following early spring, when flocks break up into breeding pairs. Thus, chickadee social organization changes over the course of a year from female–male pairs in the breeding season to larger, stable social units in the fall and winter. Could it be that the demands of a complex social structure have driven the evolution of a complex communicative system (see Blumstein and Armitage 1997; Wilkinson 2003)? It is too early to answer this question definitively for chickadees (our first concession). And although we still cannot unequivocally state what structurally different calls mean to the birds themselves (our second concession), some interesting findings are emerging.

Playback studies in field settings are one of the strongest ways of testing whether structural variation in *chick-a-dee* calls conveys information (operant conditioning experiments offer an important complementary approach, see Chapter 10). Unfortunately, playback studies are relatively rare for this call system in the Paridae. Those that have been conducted, however, indicate that *chick-a-dee* calls that vary in their note composition and/or in the structural characteristics of their notes can influence receiver behavior dramatically. In Carolina chickadees, receivers respond differently in a feeding context to calls containing a large number of C notes relative to calls containing no C notes and a relatively large number of D notes (Freeberg and Lucas 2002). In black-capped chickadees, individuals respond differently to playbacks of *chick-a-dee* calls of flockmates relative to *chick-a-dee* calls of non-flockmates (Nowicki 1983), and acoustic variation in D note structure is thought to be the basis for this discrimination (Mammen and Nowicki 1981; although see our caveat about these studies described above). Playbacks of calls recorded in a "high threat" context of a northern pygmy owl, *Glaucidium gnoma*, resulted in more receivers approaching the playback speaker and also producing more *chick-a-dee* calls, relative to playbacks of calls recorded in a "low threat" context of a great horned owl, *Bubo virginianus* (Templeton *et al*. 2005). The results from these three playback studies in two chickadee species indicate that variation in *chick-a-dee* call structure can potentially convey information about a feeding context, identity, and degree of threat corresponding to predator size.

In terms of general structural characteristics of the note types and note ordering in *chick-a-dee* calls, all of the North American Paridae possess a *chick-a-dee*-like call (Hailman 1989), although work on *Baeolophus* (titmice) species is needed. Ficken (2000) indicates that *chick-a-dee* call note similarities extend beyond the chickadees and titmice in North America (even if the *chick-a-dee* call itself does not), to include some of the species that occur in mixed-species flocks with those Paridae species, including golden-crowned kinglets, *Regulus satrapa*, and brown creepers, *Certhia americana*.

Many of the European tit species possess a similar call system (Hailman 1989). Perhaps the most thoroughly studied European *chick-a-dee* call system is that of the willow tit. Haftorn (1993) describes a long-term study of the major vocalizations of willow tits in central Norway, including the "*si-tää*" call of this species that appears homologous with the *chick-a-dee* call. In adults, the call seems to be a medium range signal for flock members moving through their territory and often out of visual contact. The call system thus has a general function in social cohesion, similar to that of North American Paridae. It often occurs with two distinct note types, "alarm" ("*zi*") notes and "*spitt*" notes, in what are defined as mixed vocalizations, and its structure appears to vary with context (e.g. mixed calls containing alarm notes are produced more often in contexts of tits mobbing perched predators or in surprising or other potentially threatening situations—see also Haftorn 2000). The "*pjä*" call is produced primarily in agonistic contexts such as when two flocks interact, and is often combined with the pure-tone introductory notes and/or the D-like "*tää*" notes of the "*si-tää*" call into mixed calls.

Hailman (1989, p. 305) argued that Parid vocalizations represent "one of the most interesting and theoretically important communication systems known in the animal kingdom". We agree. We have to conclude, though, that it is still largely an open question as to how rich in information this system may be. Studies aimed at documenting whether different call structures are produced in different contexts have been conducted in only a handful of species. There is a more serious paucity of information from playback studies to determine experimentally what different call structures might mean to the birds themselves. In short, comparative studies are desperately needed—studies not just of other members of the Paridae but also of the penduline tits (Remizidae). We are not yet in a position to answer fundamental questions about the evolution of this call system. For example to what extent do phylogeny and ecology impact the structure, and perhaps function, of this call system in different groups of Paridae? Phylogenies are being established and clarified, but we don't have sufficient information about the *chick-a-dee* call system to provide a firm answer. We do hope, however, that our review has been of sufficient interest—and information—to generate more observational and experimental work to help elucidate the information-rich nature and evolution of this call system.

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