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Chapter 13

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

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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* (and *Parus* – see Preface). 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.

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

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

44 Most definitions of ‘communication’ (e.g. Burghardt 1970, pg. 16; Wilson 1975, pg. 176; Hailman
45 1977, pg. 52) focus on three parts of communication – a feature (often a signal) of one individual
46 (the signaler) affects the behavior of another individual (the receiver). However, two major
47 arguments have arisen over the definition. The first argument relates to whether the signaler

48 primarily benefits, or the signaler and receiver both benefit, from the communicative interaction
49 (e.g., Dawkins and Krebs 1978; Owings and Morton 1998; Bradbury and Vehrencamp 1998). One
50 can argue that the “target of selection” argument is tangential to the question of how and whether
51 communication occurs, although clearly it is important to determining the types of communicative
52 events that occur (e.g., distinctions between signals and cues as discussed in Maynard Smith and
53 Harper 2003). The second argument revolves around the usefulness of the notion of ‘information’
54 or ‘information transfer’.

55 A precise definition of ‘information’ has proven difficult to pin down, despite a general
56 understanding of the concept. There are two major views – one is the view that if communication
57 involves one individual signaling “about something” to another individual, then that “about
58 something” is the information. The other view defines information not in the terminology of
59 meaning, but mathematically as “a measure of one’s freedom of choice when one selects a
60 message... in the simplest cases, to be measured by the logarithm of the number of available
61 choices” (Shannon and Weaver 1949, pg. 9). Smith (1977, pg. 193) bridges these two ideas nicely
62 by defining information as “an abstract property of entities and events that makes their
63 characteristics predictable to individuals with suitable sensory equipment for receiving the
64 information. Information thus enables such individuals to make choices...” (see also Halliday
65 1983). In the next section, we attempt to place these ideas of ‘information’ in the context of the
66 *chick-a-dee* call by discussing the seminal work on black-capped chickadees by the Hailmans and
67 Fickens and our work on Carolina chickadees.

68

69 **13.2. “Information” and the *chick-a-dee* call**

70 **13.2.1. Basic note types of *chick-a-dee* calls**

71 The first detailed investigation of the *chick-a-dee* call from the mathematically-based information
72 perspective was carried out on black-capped chickadees. Hailman *et al.* (1985) recorded roughly
73 3500 calls from at least 20 individuals. The call was described as being composed of four note
74 types (see Figure 13.1 for Carolina chickadee examples). Two note types – **A** and **B** – are
75 relatively pure tones and span a considerable frequency range. **A** notes tend to have a higher peak
76 frequency, with a short ascending arm followed by an abrupt and long descending arm (in Carolina
77 chickadees, the ascending arm is typically much longer than the descending arm in terms of
78 frequency span). **B** notes tend to be relatively lower in frequency and shorter in duration, and both
79 the ascending and descending arms are relatively similar in the frequencies they span¹. **C** notes are
80 harsh sounding notes with a fairly complex and noisy structure, with a relatively lower pitch than
81 **A** or **B** notes. **D** notes have a longer duration than the other three note types, and are relatively
82 unmodulated in terms of frequency, with a characteristic harmonic-like structure when seen in
83 sonagram form.

84 Hailman *et al.*'s. (1985) sample of nearly 3500 calls resulted in 362 calls that were distinct in note
85 composition. This large number of unique calls illustrates one component of *chick-a-dee* call
86 complexity – the number of distinct calls (in terms of note composition) increases with sample
87 size. This is very different from, for example, the songs of many songbird species, in which the

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.

88 sampling of dozens or a few hundred songs will often completely capture the song repertoire of an
89 individual – the *chick-a-dee* call possesses the language-like feature of being open-ended.

90 [insert Figure 13.1 here]

91 **13.2.2. Variability in note types**

92 One aspect of the *chick-a-dee* complex that needs more attention is how many notes any one
93 species actually uses in its calls – we can't understand the call complex completely without
94 understanding its elements. Clearly, virtually all chickadees have some variant of the **A**, **B**, **C**, **D**
95 series of primary note types (Hailman 1989). However, there are some intriguing species
96 differences. Mountain chickadees (Bloomfield *et al.* 2004) and Mexican chickadees (Ficken *et al.*
97 1994) have a common hybrid note described by Ficken *et al.* (1994) as an **A** running into a **D** note.
98 We found these notes in Carolina chickadees (e.g., Fig. 13.1E), but they were rare enough that we
99 concluded that they were anomalies. Given that this note occurs in 94% of mountain chickadee
100 calls analyzed by Bloomfield *et al.* (2004), our notion of 'anomalous' notes needs to be revisited.
101 Interestingly, Mexican chickadees (Ficken *et al.* 1994) have, for the most part, lost one of the four
102 primary notes from their repertoire – **B** notes are quite rare in their *chick-a-dee* calls. Also, in
103 mountain chickadees (Gaddis 1985) **C** notes and **D** notes appear to be a single graded series (see
104 also Hailman *et al.* 1985). Thus, for most chickadee species, it is arguably an open question as to
105 how many distinct note types occur in the call.

106 New or hybrid notes notwithstanding, it is clear that in many species the **A**, **C**, and **D** notes have
107 several subtypes (Figure 13.2). The **A** note in particular is quite varied. A spectral analysis by
108 Nowicki and Nelson (1990) showed that **A** and **B** notes in black-capped chickadees grade into each
109 other. **A** note variants should therefore grade into each other as well, but these variants are
110 sufficiently distinct that Smith (1972) defined at least four different **A**-like notes in Carolina

111 chickadees (high see, high tee, loud tee, lisping tee), and our own analyses of Carolina chickadee
112 calls (T.M. Freeberg & J.R. Lucas, unpublished data) support this conclusion (Figure 13.2).

113 **[insert Figure 13.2 here]**

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

121 Smith (1972) defined four different **D** notes in Carolina chickadees: *dee*, *broken dee*, *harsh dee*,
122 and *soft dee*. Ficken *et al.* (1994) indicated that **D** notes in Mexican chickadees varied from
123 banded (Smith’s *dee* note) to uniformly noisy (Smith’s *harsh dee*). Similarly, mobbing black-
124 capped chickadees employ a noisy variant of the **D** note (Ficken and Popp 1996), and female
125 black-capped chickadees use a *broken dee* when they solicit food from their mates (Ficken *et al.*
126 1978).

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

133 A critical question related to our perception of note types is whether the birds themselves share this
134 perception. An acoustical analysis of black-capped chickadee note types by Nowicki and Nelson
135 (1990) suggested that they should: **A** and **B** notes are statistically distinguishable from one another,
136 although they tend to be a part of a graded series, and **C** and **D** notes are quite distinct. Sturdy *et*
137 *al.* (2000) showed that black-capped chickadees can learn to discriminate between note types more
138 rapidly than within variants of the same note type, suggesting that the birds do indeed discriminate
139 among note types and generalize within note types. Moreover, the birds' behavior was consistent
140 with the suggestion of Nowicki and Nelson (1990) that **A** and **B** notes are more similar to one
141 another than to the other note types. This is good news for the field, although Sturdy *et al.*'s
142 (2000) important contribution needs to be extended to other chickadee species.

143 Arguably the most interesting aspect of the *chick-a-dee* call complex is that it shares some
144 similarities to human language (Hailman *et al.* 1985, 1987; Hailman and Ficken 1986). As we will
145 discuss below, the call system has a rudimentary “syntax” – notes that occur in any given call
146 follow simple rules of note ordering. In addition to syntax, the literature on *chick-a-dee* calls has
147 addressed a number of other non-syntactical components of information. We will address these
148 alternative sources of information first, in part because they may influence how we think about
149 syntax, or at least about constraints on syntax.

150

151 **13.2.3. Signal redundancy**

152 The first component of information we will address is “internal” information, or the redundancy in
153 a signal. Redundancy results from multiple signals, or multiple components of a signal, encoding
154 similar information. Theoretically, redundancy increases the probability that receivers correctly
155 perceive the information embodied in the signal, although redundancy also reduces the total

156 amount of information that can be encoded in the signal (Bradbury and Vehrencamp 1998). A
157 more practical aspect of redundancy is that we can potentially over-interpret experimental results if
158 we ignore redundant cues.

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

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

171

172 **13.2.4. Identity**

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

175 Signals communicating individual identity are well established (Bradbury and Vehrencamp 1998),
176 at least in relatively stable social groups (Slater *et al.* 2000). In black-capped chickadees, Nowicki
177 (1989) suggested that the **D** note plays a special role in encoding identity and Hailman *et al.* (1987)

178 suggested that this may be why *chick-a-dee* calls tend to be more likely than chance to have at
179 least one **D** note in them – the trailing **D** essentially acts as an identification flag. More recent
180 work by Charrier *et al.* (2004) and Bloomfield *et al.* (2004) have made this viewpoint even more
181 intricate. These studies showed that both mountain chickadees and black-capped chickadees (and,
182 by extension, other species) have individually specific introductory notes in addition to
183 individually specific **D** notes, although both studies concluded that the **D** note has the highest
184 potential for identity coding. The implication is that identity coding need not reside only in the **D**
185 note, but playback experiments are needed to resolve this issue.

186 Mammen and Nowicki (1981) were the first authors to suggest that flock-level call properties
187 develop in black-capped chickadees. This possibility was strengthened by a playback experiment
188 showing that birds played foreign calls were less likely to visit a feeder than those played calls of
189 flock members (Nowicki 1983). Nowicki (1989) then put 5 birds together in an aviary flock and
190 demonstrated convergence in one component of the **D** note of the call. However, a potential
191 confound of the Mammen and Nowicki (1981) study is that syntax was not controlled for in the
192 spectral analysis; indeed, their data suggest that birds from different flocks tended to have calls
193 with different syntax. Given that syntax itself affects note structure (Freeberg *et al.* 2003),
194 Mammen and Nowicki's (1981) results may have had artifacts of flock-specific differences in note
195 composition. It is also possible that the putative flock-level recognition detected in these studies
196 was actually due to individual recognition. Nowicki (1989) found a single trait converging in a
197 single flock in the laboratory; this is not, however, unequivocal evidence for convergence among
198 flock members of a *chick-a-dee* call structure that marks flock membership.

199 There is stronger evidence for population-level variation in the structure of *chick-a-dee* calls. For
200 example, Baker and Logue (2003) were able to identify the population of origin of 100% of black-

201 capped chickadees calls based on multitaper spectral analysis (see Tchernichovski *et al.* 2000).
202 Spectrogram cross-correlation was nearly as effective. Similarly, Freeberg *et al.* (2003)
203 demonstrated population-level differences in Carolina chickadees in both **A** and **D** notes. These
204 results mirror the demonstration of population-specific dialects in the gargle call of black-capped
205 chickadees (Ficken *et al.* 1985; Miyasato and Baker 1999).

206

207 **13.2.5. Syntactical Information**

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

215 **13.2.5.1 Syntax**

216 Hailman *et al.* (1985) measured the amount of information that might be conveyed by the *chick-a-*
217 *dee* call system of black-capped chickadees. From Shannon and Weaver’s (1949) theory of
218 communication, a communicative system with four distinct units (note types) has a maximum
219 uncertainty of 2 bits of information ($U_M = \log_2 N$, where N = number of units). The maximum
220 information in a communicative system occurs when all of the system’s units are used with equal
221 probability. As is the case with letters in the English language (e.g., relative use of “e” vs. “x”),
222 however, note types in *chick-a-dee* calls are not used equally – **D** notes are far more common. This

223 means that the actual information in terms of note use in *chick-a-dee* calls is lower than the
 224 maximum possible information. The uncertainty measured for actual use of the different units of a
 225 communication system is referred to as the zero-order uncertainty, and is calculated as:

$$226 \quad U_0 = \sum P_i (-\log_2 P_i)$$

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

$$232 \quad U_1 = \sum \sum P_{ij} (-\log_2 P_{ji})$$

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

240 The preceding discussion leads into one of the other major structural features of the *chick-a-dee*
 241 call. Notes and pairs of notes do not occur with equal probability. Instead, the *chick-a-dee* call
 242 obeys rules of note ordering, a simple form of syntax. In black-capped chickadees, the two most
 243 common call structures are **[A][D]** and **[B][C][D]**, with brackets indicating that the particular note
 244 type can occur more than once. In other words, if the following notes occurred in a 9-note call,

245 **BBCCDDDD**, they would virtually always (e.g., over 99% of the time) occur in the order
246 **[B][C][D]**. Taken together, the *chick-a-dee* call represents an interesting case of an open-ended
247 communicative system that is nonetheless constrained by its note ordering rules.

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

255 This mathematic approach to the question of information in the *chick-a-dee* call was extended to
256 another species, Mexican chickadees (*P. sclateri*; Ficken *et al.* 1994), and interesting comparative
257 results emerge. The Mexican chickadee *chick-a-dee* call system is open-ended, the **C** note is more
258 common than the **D** note, and the **B** note is extremely rare. Notes follow the **A-B-C-D** note-
259 ordering rule shared by black-capped chickadees. The most common call structures were **[A][D]**,
260 **[C]**, and **[A]**, and calls tended to be shorter in note number than black-capped chickadee calls.
261 Ficken *et al.* (1994, pg. 80) indicate that, relative to the *chick-a-dee* call of black-capped
262 chickadees, the “rarity of **B** notes and the shorter note length of calls means that the Mexican
263 chickadee’s utterances tend to be syntactically simpler, although not necessarily semantically
264 simpler...” This quote nicely captures the two approaches to information discussed earlier. For
265 information as a mathematically-defined measure, Mexican chickadee calls appear to convey less
266 information than black-capped chickadee calls. Mountain chickadee calls also appear to convey
267 less information than black-capped or Carolina chickadees because their calls are substantially

268 shorter (3-4 notes/call vs. 6-8 notes/call, respectively; Bloomfield *et al.* 2004). For information as
269 meaning, however, it is an open question in these species as to which call system conveys more
270 information.

271 Hailman *et al.* (1987) published an additional method of evaluating the syntactical properties of
272 black-capped chickadees' calls. They compared the cumulative number of calls containing at least
273 some number of **A**, **B**, **C** and **D** notes (a "survivorship" plot) with the expected cumulative number
274 of notes based on a semi-Markovian model. A departure from the simple semi-Markovian
275 expectation implies some meaning in the note composition of the call beyond a simple repetition of
276 notes. They found that **A** notes fit expectations almost exactly. **B** notes did not: calls with 3 or
277 fewer notes fit expectations whereas those with 4 or more **B** notes were too common. As with **A**
278 notes, the probability of repeating a **C** note was constant, albeit somewhat less than expected by
279 chance. The survivorship curve for **D** notes departed completely from semi-Markovian
280 expectations, with too many short-**D** calls, too few intermediate-**D** calls and too many long-**D** calls.
281 Hailman *et al.* (1987) suggested that this distribution represented a compound of two or more
282 separate processes, and potentially separate syntactical functions.

283 We repeated Hailman *et al.*'s (1987) analysis with a preliminary data set of 2153 Carolina
284 chickadee calls recorded in non-manipulated field settings in eastern Tennessee (9 sites) and
285 central Indiana (6 sites). The uncertainty measures for Carolina chickadees for this sample of the
286 field recordings showed a similar pattern to those reported for black-capped chickadees (Hailman
287 *et al.* 1985) and Mexican chickadees (Ficken *et al.* 1994), with a marked reduction between zero-
288 order and first-order uncertainty ($U_M = 2$, $U_0 = 1.49$, $U_1 = 0.63$). **A** and **D** notes did not meet semi-
289 Markovian expectations (Figure 13.3). Long strings of **A** notes (>6 **A** notes/calls) were more
290 common than expected by chance. The survivorship curve for **D** notes was qualitatively similar to

291 that of black-capped chickadees: too many calls with a few notes, too few with a large number of
292 notes (10-25), and too many with a very large number of notes.

293 **[insert Figure 13.3. here]**

294 We asked whether our *chick-a-dee* calls met expectations of Mandelbrot's modification of Zipf's
295 Law (see Hailman *et al.* 1985). Stated simply, Zipf's law argues that the frequency of utterances
296 should be reciprocally related to their frequency rank – the tenth most common utterance (word in
297 a human language, call syntax in the *chick-a-dee* call) should occur with 1/10th the frequency of
298 the most common utterance. Human language meets this criterion, but black-capped *chick-a-dee*
299 calls do not. However, black-capped calls do fit a broader form suggested by Mandelbrot (Hailman
300 *et al.* 1985). Interestingly, our Carolina chickadees do not fit Mandelbrot's function (Figure 13.4),
301 at least based on a least-squares best fit of the data. Nonetheless, the general increase in
302 cumulative call types with an increase in the number of calls sampled indicates that the call system
303 is generative, or open-ended.

304 **[insert Figure 13.4 here]**

305 As Hailman *et al.* (1987) showed in black-capped chickadees, the probability that a call ends
306 (instead of continuing with a new note) increases with an increase in the number of **A** and **C** notes
307 (Table 13.1). In Carolina chickadees, longer strings of **A** notes (8-10) are more likely to transition
308 to **C** notes whereas shorter strings (1-5) are as likely to transition to **B** or **D** notes. **B** notes almost
309 always transition into **D** notes or end the call.

310 **[insert Table 13.1]**

311 We need to add a caveat that the differences between black-capped and Carolina chickadees could
312 result from differences in the field recording contexts. Assuming that this caveat does not generate
313 a bias in our data sets, the results suggest that Carolina chickadees use long strings of introductory

314 notes in different ways (with different meanings?) than black-capped chickadees. It would be
315 instructive to perform this analysis on mountain and Mexican chickadees, given the species
316 differences reported earlier. It would also be instructive to see this analysis done on European tits,
317 particularly the marsh and willow tits, which are closely related to the North American chickadees
318 (Gill *et al.* 2005).

319 13.2.5.2. Context

320 Studies of correlations between *chick-a-dee* variants and behavior are critical because they give us
321 some insight into the potential for syntactically-mediated information transfer. Results to date
322 clearly demonstrate that different *chick-a-dee* variants are given under different conditions.

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

329 Ficken *et al.* (1994) suggested that **A** notes are given by Mexican chickadees moving in space,
330 whereas **C** notes are given in response to a disturbing stimulus (e.g. when mobbing a screech owl
331 tape) or when birds change directions. **D** notes tend to be given by perched birds. These trends for
332 **A** and **D** notes are similar to those reported by Smith (1972) for Carolina chickadees. Gaddis
333 (1985) found that *chick-a-dee* variants were context specific in mountain chickadees. For
334 example, **B** notes are given when birds leave food; **A** notes are given when birds fly up and [**A**][**D**]
335 strings are given in flocks.

336 There are at least 3 studies of the syntactical cues given in black-capped chickadee mobbing calls.
337 Hurd (1996) suggested that mobbing calls had more introductory notes than non-mobbing calls but
338 the same number of **C** and **D** notes. Baker and Becker (2002) showed a similar pattern, with more
339 **B** notes and fewer **A** notes given under more immediate risk (1m vs. 6m from a stuffed prairie
340 falcon), but no difference in the number of **C** or **D** notes. In contrast, Templeton *et al.* (2005)
341 showed that the number of **D** notes correlated strongly with the intensity of risk represented by
342 different species of predators. It is not clear why these results are so different, although there were
343 considerable methodological differences across the three studies.

344 In addition to syntactical cues, some cues may be given by call rate itself, with higher rates
345 indicating more intense conditions. Black-capped chickadee mobbing calls, for example, tend to
346 be given at higher rates under more immediate risk (Baker and Becker 2002). Carolina chickadee
347 *chick-a-dee* call rates are higher when the birds are light-weight and hungry than when they are
348 heavy or sated (Lucas *et al.* 1999) – *chick-a-dee* calls may encode information about signaler
349 physiological condition. We (K. Bledsoe and J. Lucas, unpublished data) have limited data on 2
350 Carolina chickadees that indicate just this: **D** note fundamental frequency and duration correlate
351 strongly with changes in corticosterone levels. These results are consistent with Owings and
352 Morton's (1998) assessment/management model of communication, although clearly we need
353 more extensive studies of this aspect of the *chick-a-dee* complex.

354 13.2.5.3. Playback studies

355 We can use playback experiments to test implications about syntactical information derived from
356 field (or lab) observational studies. Here we focus on recent field-based playback studies (Sturdy
357 *et al.* review lab-based studies of perception in Chapter 10). Freeberg and Lucas (2002) proposed
358 that the **C**-note (chick variant) was food related, based on preliminary field observations. They

359 tested this by broadcasting either **C**-rich or **D**-rich *chick-a-dee* calls at a temporary seed stand.
360 Consistent with the hypothesis, birds tended to come to the stand and take seeds in response to **C**-
361 rich calls but never took a seed in response to **D**-rich calls. Moreover, the rate of *chick-a-dee*
362 calling was significantly higher in playbacks with **C**-rich calls than those with **D**-rich calls. There
363 are at least two alternative explanations for this result. One is that the **C** note is indeed a food-
364 associated note. The second is that **D**-rich calls are aggressive calls that elicit an aggressive
365 reaction by receivers (and, by comparison, **C**-rich calls are non-aggressive). While we cannot
366 distinguish these alternatives with this experimental design, the results indicate that *chick-a-dee*
367 variants vary in their meaning to receivers.

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

376 Finally, Clucas *et al.* (2004) monitored Carolina chickadees' responses to artificially constructed
377 calls that varied in both note composition (**AAAACCCC**, **AAAADDDD**, and **CCCCDDDD**) and
378 note ordering (**AAAACCCC** vs. **CACACACA**, **CCCCDDDD** vs. **DCDCDCDC**). The playback
379 was repeated in two seasons, spring and fall/winter, to test for the potential role of seasonal context
380 on receiver's responses to the calls. The experiment tested whether chickadees respond to
381 manipulation of the two components of syntactical organization, note composition and note order,

382 but did not test any specific hypotheses about the meaning of *chick-a-dee* variants. The birds
383 showed no differential response to calls with atypical note ordering that varied in note composition
384 (CACACACA vs. DCDCDCDC). Birds did, however, distinguish between calls that varied in
385 note composition if the note order followed the species-typical **A-B-C-D** ordering. Season and
386 social context also affected the birds' response to the playbacks. The number of introductory notes
387 in the responding birds' *chick-a-dee* calls was affected by note composition in the fall but not in
388 the spring: AAAACCCC playback calls elicited **A/B**-rich responses, and **D**-rich playback calls
389 elicited **C**-rich responses. But this latter response was evident only when white-breasted
390 nuthatches and tufted titmice (two dominant heterospecifics) were present. In the fall, the number
391 of **D** notes in the call was also positively correlated with the number of birds responding, but this
392 relationship was positive only when heterospecifics were not present. Only the number of birds
393 responding affected the number of **D** notes in the spring [note: Table 2 in Clucas *et al.* (2004) is
394 correct, but the discussion of this pattern in the text of that paper and Figure 8 are not correct].
395 Our results suggest that both note ordering and note composition affect the information content of
396 the *chick-a-dee* complex. In addition, context (season and presence of dominant heterospecifics)
397 matters, as predicted by Hailman *et al.* 1985 (also see Leger 1993; Marler and Evans 1996).

398

399 **13.3. Conclusions, concessions, and a call for comparative work**

400 The *chick-a-dee* call is complex both structurally and functionally. The structure of *chick-a-dee*
401 calls can depend upon numerous characteristics of the signaler or its context – energetic state,
402 flock/local population, sex, feeding behavior, flight behavior, and presence of avian predators.
403 Thus, the *chick-a-dee* call can potentially convey a great deal of information about the different

404 states, behavioral probabilities, events, etc. relevant to the signal's sender. Furthermore, *chick-a-*
405 *dee* calls of black-capped chickadees (Hailman *et al.* 1985), Mexican chickadees (Ficken *et al.*
406 1994), and Carolina chickadees (Figure 13.4) are generative and possess fairly high levels of
407 uncertainty. Thus, in terms of 'information' as a mathematical measure of binary choices, call
408 structural rules result in an information-rich signaling system. In addition, the number of a
409 particular note type seems to influence acoustic characteristics and numbers of other notes, which
410 suggests an interesting form of redundancy in these calls. This redundancy may increase a
411 signaler's ability to transmit, and a receiver's ability to exploit, a message of a call, while limiting
412 the total number of different messages a single call might convey. As we noted earlier, our claim
413 about *chick-a-dee* call complexity is by no means novel to us – Hailman *et al.* (1985) first raised it
414 two decades ago in their work with black-capped chickadees. In this final section of the chapter,
415 we draw some conclusions about this complexity and why it might exist, point out some gaps in
416 our understanding of the call system, and suggest a need to make broader comparative analyses of
417 the call system in other Paridae groups.

418 A possible driving force for such a complex call system in chickadees might be their complex and
419 fairly atypical social structure (at least for temperate zone birds). In late summer and early fall,
420 chickadee female-male pairs join other pairs (and often juveniles) to form a flock with a relatively
421 stable membership (Ekman 1989; Smith 1991). Flocks remain together, generally defending their
422 territory from other flocks or individual intruders, until the following early spring, when flocks
423 break up into breeding pairs. Thus, chickadee social organization changes over the course of a year
424 from female-male pairs in the breeding season to larger stable social units in the fall and winter.
425 Could it be that the demands of a complex social structure have driven the evolution of a complex
426 communicative system (see Blumstein and Armitage 1997; Wilkinson 2003)? It is too early to

427 answer this question definitively for chickadees (our first concession). And although we still
428 cannot unequivocally state what structurally different calls mean to the birds themselves (our
429 second concession), some interesting findings are emerging.

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

448 In terms of general structural characteristics of the note types and note ordering in *chick-a-dee*
449 calls, all of the North American Parid Subfamily Parinae (‘true’ tits) possess a *chick-a-dee*-like call

450 (Hailman 1989), although work on *Baeolophus* (titmice) species is needed. Ficken (2000) indicates
451 that *chick-a-dee* call note similarities extend beyond the chickadees and titmice in North America
452 (even if the *chick-a-dee* call itself does not), to include some of the species that occur in mixed-
453 species flocks with those Parinae species, including golden-crowned kinglets, *Regulus satrapa*,
454 and brown creepers, *Certhia americana*.

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

468 Hailman (1989, pg. 305) argued that Parid vocalizations represent “one of the most interesting and
469 theoretically important communication systems known in the animal kingdom”. We agree. We
470 have to conclude, though, that it is still largely an open question as to how rich in information this
471 system may be. Studies aimed at documenting whether different call structures are produced in
472 different contexts have been conducted in only a handful of species. There is a more serious

473 paucity of information from playback studies to determine experimentally what different call
474 structures might mean to the birds themselves. In short, comparative studies are desperately needed
475 – studies not just of other members of the Parinae subfamily, but also of the penduline tits
476 (Remizinae). We are not yet in a position to answer fundamental questions about the evolution of
477 this call system. For example, to what extent do phylogeny and ecology impact the structure and
478 perhaps function of this call system in different groups of Paridae? Phylogenies are being
479 established and clarified, but we don't have sufficient information about the *chick-a-dee* call
480 system to provide a firm answer. We do hope, however, that our review has been of sufficient
481 interest – and information – to generate more observational and experimental work to help
482 elucidate the information-rich nature and evolution of this call system.

483

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

612

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							

613

614 **Figure Legends**

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

621
622 **Figure. 13.2.** Sonagrams of Carolina chickadee calls illustrating note type diversity (partly based
623 on Smith 1972). Sonagrams generated as in Fig. 1.

624
625 **Figure 13.3.** Survivorship plots of **A** notes and **D** notes of the Carolina chickadees. These are
626 based on a sample of 2153 calls. The triangles represent calls in the sample, the line
627 is the predicted survivorship from a semi-Markovian model, based on the transitions
628 between same-type notes (e.g. in the left panel, the transition probability from **A** to
629 another **A** note).

630
631 **Figure13.4.** Percent use of *chick-a-dee* variants as a function the frequency rank (1 = most
632 common). Triangles are data from our set of 2153 calls of Carolina chickadees. Line
633 represents the best fit line: $p = i(r+k)^{-s}$, where p = percent use, r = rank, and i , k and s
634 are fit constants (see Hailman *et al.* 1985).

635

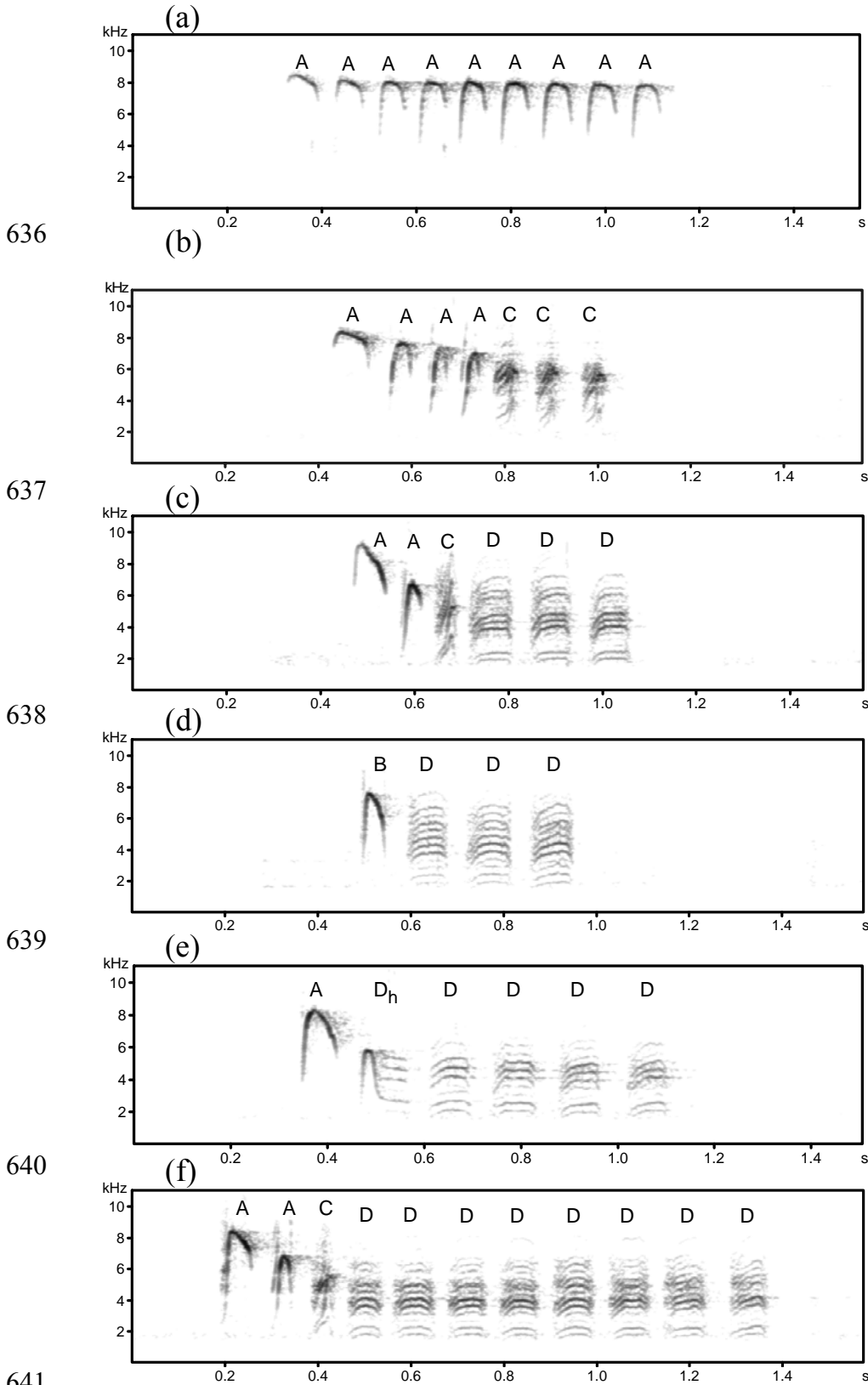
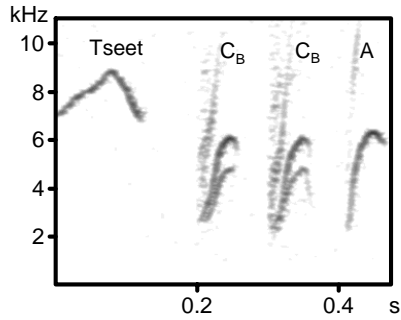


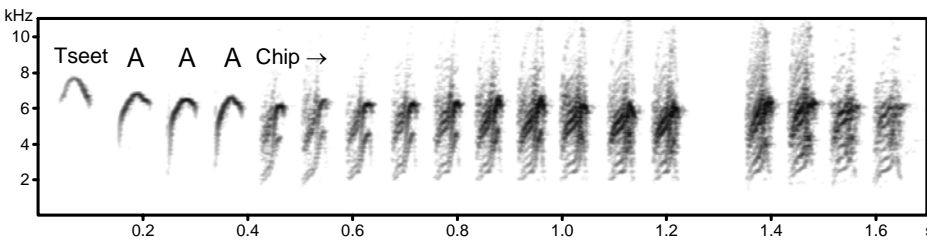
Figure 13.1

643

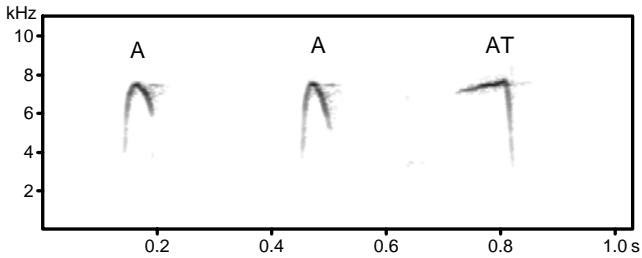
(a) Tseet notes, 2 'begging C' notes, A note



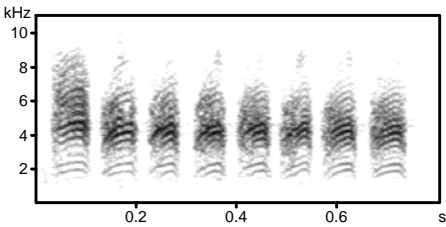
(b) Tseet, 3 A notes plus chip (C-variant) string



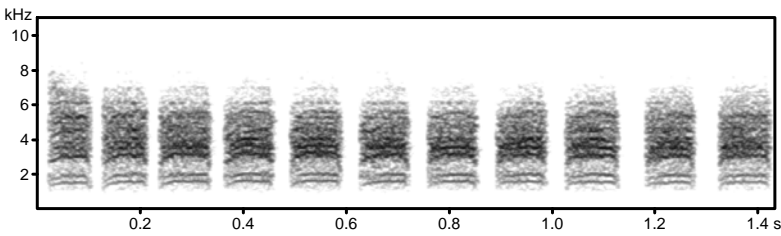
(c) 2 A notes, Abrupt T note



(d) Rapid D string



(e) Harsh D string



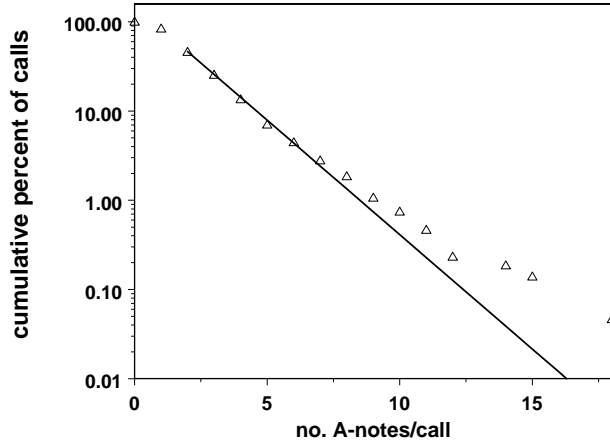
644

645 Figure 13.2

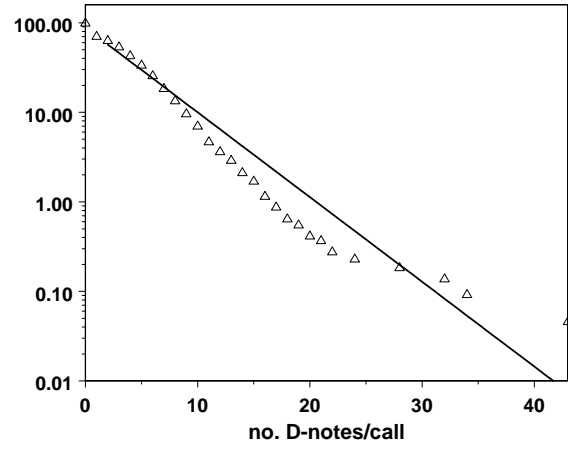
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A notes



D notes

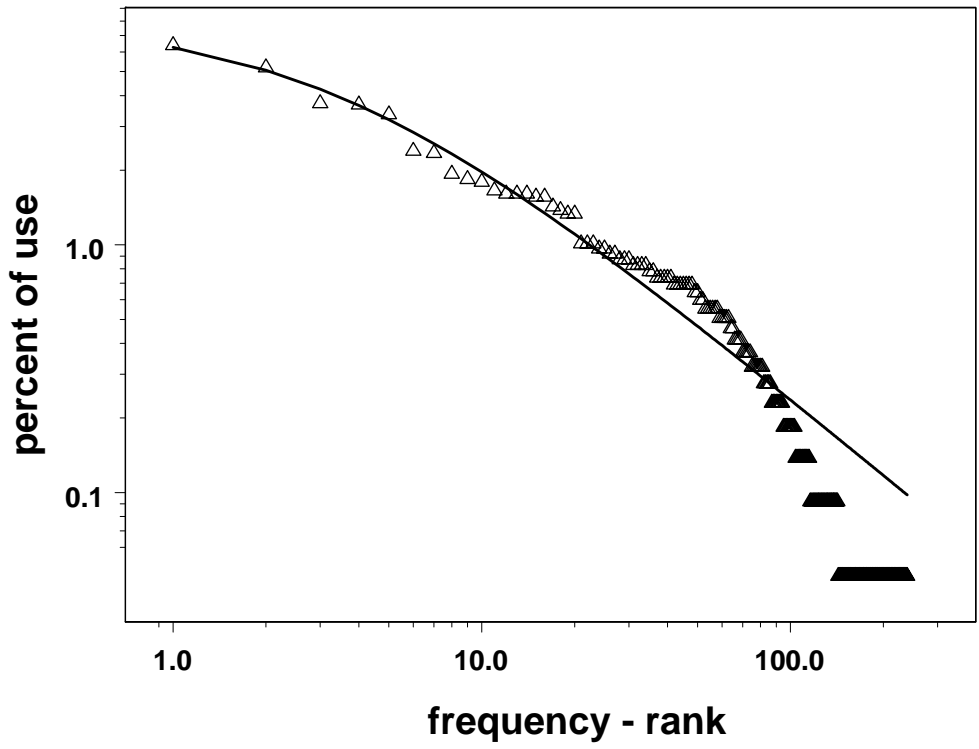


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650 Figure 13.3.

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654 Figure 13.4

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