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THE CHICK-A-DEE CALL SYSTEM OF THE MEXICAN CHICKADEE[1]

MILLICENT SIGLER FICKEN
Department of Biological Sciences, University of Wisconsin–Milwaukee, Milwaukee, WI 53211

ELIZABETH D. HAILMAN
Department of Dairy Science, University of Wisconsin–Madison, Madison, WI 53706

JACK P. HAILMAN
Department of Zoology, University of Wisconsin–Madison, Madison, WI 53706

Abstract. Chick-a-dee calls of the Mexican Chickadee (*Parus sclateri*) are composed of combinations of three common note types (A, C and D) and one very rare type (B). Calls have the invariant sequence of notes A-B-C-D, where any note type may be omitted, given once or repeated a variable number of times before transiting to the next type. The B and C notes are phonologically similar to the B and C notes of chick-a-dee calls of the Black-capped Chickadee (*P. atricapillus*), but the A note is markedly different and the D note somewhat different from equivalent notes of the congener. A total of 2,071 calls recorded yielded 60 different call types, and Zipf-Mandelbrot plots show that the call system is "open"; as the sample size is increased new call types will be found without demonstrable bound. In relatively undisturbed contexts (with mate on territory, in fall flocks, alone in fall) birds gave mainly [A][D] calls with lesser numbers of [A] and [C] calls, where brackets indicate variable repetition of note types. In disturbed contexts (mobbing plastic Great Horned Owl, mobbing speaker playing calls of the Northern Pygmy-Owl, observer sitting under the nest cavity) the birds gave more [C] calls with [A][C] as well. In the longest mobbing session to owl calls, birds gave mainly [A] calls when approaching, switched to [C] calls while flying about the speaker, and then resumed [A] calls and moved off when the playback was stopped. Outside of human language, this is the second truly combinatorial system of vocal communication found in animals, the first being chick-a-dee calls of the Black-capped Chickadee. This study provides the first data substantiating quantitative differences in calls from different contexts, an important step toward understanding what kinds of information combinatorial chick-a-dee calls encode.

Key words: Parus sclateri; *Mexican Chickadee; vocalizations; calls; syntax; mobbing; flocks.*

INTRODUCTION

All tit species of the subgenus *Poecile* (genus *Parus*) appear to give combinatorial "chick-a-dee" calls (Hailman 1989), but this complicated call system has heretofore been analyzed quantitatively only in the Black-capped Chickadee, *P. atricapillus* (Hailman et al. 1985, 1987; Hailman and Ficken 1986). Chick-a-dee calls of the Mexican Chickadee (*P. sclateri*) were first recorded by Dixon and Martin (1979), whose spectrograms (their figures 1a and b, p. 422) show two kinds of notes. Ficken (1990a) found that in a sample of over 1,000 recorded calls, four types of notes were given but one of them only rarely (see also Ficken and Nocedal 1992). The present study, based on further field work including mobbing experiments, (1) describes the acoustical features and analyzes the syntactical structure of the Mexican Chickadee's calls, (2) compares these results with those from Black-capped Chickadees, and (3) documents differences in calling in different contexts.

Chick-a-dee calls are of special interest because these compose the only presently documented combinatorial system of animal communication outside of human language. The Black-capped Chickadee uses four note types (Ficken et al. 1978) in combination to create hundreds of different call types (Hailman et al. 1985). The note types (designated A, B, C and D) occur in the fixed sequence A-B-C-D, where any note type may be omitted, given once, or repeated a variable number of times before transiting to the next note type within the call. This straightforward phonological syntax was shown to be logically explicit by writing a "characteristic function" (correctly working algorithm) for a Turing machine (Hailman and Ficken 1986). However, systematic departures from first-order Markov

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chains of transitions between note types show that far more complicated rules underlie the precise structure of calls (Hailman et al. 1987). Despite extensive analyses of syntactical structure, the communicative significance of chick-a-dee calls remains elusive. The present study of the Mexican Chickadee provides not only the first comparative data on syntax in another species but also an important first step toward understanding differences in calls in different behavioral contexts.

METHODS

All recordings were made at or in the vicinity of Rustler Park in the Chiricahua Mountains (Cochise County) in southeastern Arizona. Recordings were made by M.S.F. in October 1985, and May and October 1986 (Ficken 1990a); further field work by the three authors together was conducted in April 1990 and March 1991, by M.S.F. in May 1991, and by the three authors together in April 1992.

Calls were divided into four principal contexts of recording: (1) with mate on the breeding territory, (2) in mixed-species flocks in the fall, (3) when disturbed by the presence of an observer near the nest, and (4) when mobbing a speaker playing the call of a Northern Pygmy-Owl, *Glaucidium gnoma*. In addition, small samples of vocalizations were taped in two other contexts: (5) lone birds in the fall and (6) mobbing a plastic model of a Great Horned Owl, *Bubo virginianus*. The mobbing experiments using owl tapes were conducted at five different sites. The partially diurnal Northern Pygmy-Owl takes small birds and is common in the study site; during one experiment, an owl answered the playback from across a canyon. In two experiments tapes were played back from a Marantz PMD 430 Professional cassette recorder through a Realistic Minimus-0.6 amplified speaker near the ground on a log or stump. In the other three experiments, tapes were played back from a Sony Walkman Professional cassette recorder through a Sony SRS-27 amplified speaker. All playbacks attracted a number of small forest species besides Mexican Chickadees.

Most of the recordings were made on a Sony Walkman Professional cassette tape recorder (details in Ficken 1990a, 1990b), with further recordings of mobbing experiments made with a Sony 8 mm camcorder. Tapes were analyzed by M.S.F. with a Kay 7800 Digital Sona-Graph (150 Hz filter band width). Note types (described in the Results) were classified by eye and written on data sheets. In all, 2,045 calls were analyzed (a few occurred in other contexts with insufficient sample sizes for analysis). Data on the note composition and context of each call were read into a database and made accessible to mainframes and microcomputers for analyses. Analyses were basically a subset of those performed on calls of Black-capped Chickadees by Hailman et al. (1985), designed by J.P.H. and programmed by E.D.H. Most of the special analytical programs were written in PASCAL and run on microcomputers.

Contingency tables were analyzed statistically using "computer-intensive" methods of the publicly available software MONTE CARLO RXC written for the Apple Macintosh by W. R. Engels of the University of Wisconsin–Madison, Department of Genetics. Such analyses provide a more sensitive and accurate assessment than Chi-square methods often applied to such data (Engels 1988). At least 1,000 trials were run for a given test to create the distribution against which the data were compared. Sequential analysis by the method of Markov chains was done with UNCERT, publicly available software for DOS computers copyrighted by E.D.H. and J.P.H.

RESULTS

PHONOLOGY

Chick-a-dee call systems as a whole are doubtless homologous among species possessing them. Two of the Mexican Chickadee's note types differ somewhat in acoustical structure from those of the Black-capped Chickadee, so they might not be homologous. Unlike the basically chevron-shaped A note of the Black-capped Chickadee, the Mexican Chickadee's A note (Fig. 1) is frequency modulated at a high rate, giving it a buzzing aspect to the human ear. Buzzing notes characterize other vocalizations of the Mexican Chickadee as well (Dixon and Martin 1979; Ficken 1990a, 1990b). The A note usually sweeps downward in frequency during its duration (Fig. 1) but the magnitude of the decline is variable. Dixon and Martin (1979, Fig. 1a) showed a call with three A notes that lacked this frequency downsweep completely, and there seems to be a continuum in the slope of the downsweep. The A note was common (1965 notes recorded), comprising 28.4% of all notes.

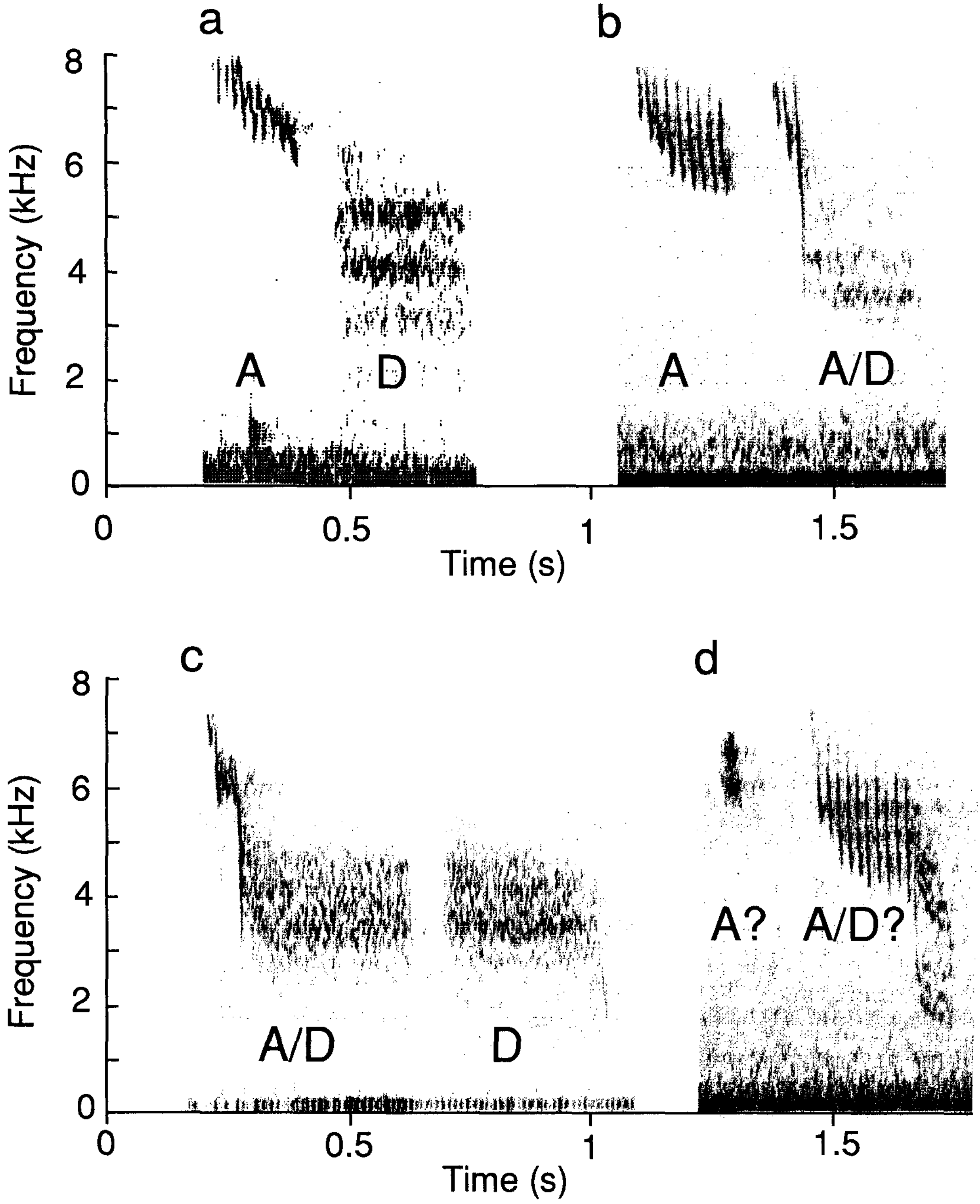

FIGURE 1. Sound spectrograms illustrating the A and D notes of chick-a-dee calls of the Mexican Chickadee, selected to illustrate some of the phonological variation found in notes. The frequency and time scales are the same for all spectra. (a) Commonest of all calls is the call type AD, with typical down-slurred A note. Notice the banded structure of the D note. (b) A call showing the typical A/D contraction of the final A and first D notes of calls containing both types. (c) The contracted A/D may begin a call; notice the noisy (unbanded) structure of the D notes. (d) Rare phonological structures occur, as in this call with an A-like introductory note followed by an A/D-like structure of long A component and short D component.

TABLE 1. Durations, highest frequencies, and lowest frequencies of note types in chick-a-dee calls of the Mexican Chickadee. Entries are mean ± standard deviation (sample size).

Call type: duration Note(s)	Fig. No. of call type	Duration (msec)	Lowest frequency (kHz)	Highest frequency (kHz)
Single A	—	151 ± 35 (13)	5.7 ± 0.7 (13)	8.0 ± 0.5 (13)
"Low frequency" A	2a	208 ± 28 (14)	3.4 ± 0.2 (14)	6.3 ± 0.6 (14)
AA: 331 ± 92 (16)	—			
First A		127 ± 53 (16)	5.5 ± 0.6 (16)	8.1 ± 0.6 (16)
Second A		120 ± 35 (16)	5.7 ± 0.8 (15)	7.3 ± 1.8 (16)
AA/D: 521 ± 118 (20)	1b			
First A		170 ± 32 (20)	5.8 ± 0.4 (20)	8.4 ± 0.2 (20)
Second A (of A/D)		50 ± 31 (20)	4.2 ± 0.7 (18)	8.2 ± 0.3 (20)
D (of A/D)		212 ± 67 (20)	3.2 ± 0.3 (19)	6.2 ± 0.5 (18)
A/D: 425 ± 107 (17)	—			
A (of A/D)		100 ± 76 (17)	4.4 ± 0.6 (16)	8.3 ± 0.2 (16)
D (of A/D)		319 ± 95 (17)	3.2 ± 0.2 (17)	6.4 ± 0.5 (12)
A/D D: 690 ± 181 (18)	1c			
A (of A/D)		87 ± 59 (18)	4.3 ± 0.7 (15)	8.2 ± 0.3 (16)
First D (of A/D)		245 ± 117 (18)	3.1 ± 0.3 (14)	5.6 ± 0.3 (15)
Second D		270 ± 85 (18)	2.9 ± 0.4 (14)	5.5 ± 0.3 (15)
[C] (First of a series)	2e	23 ± 2 (14)	2.8 ± 0.3 (14)	7.6 ± 0.1 (13)

The Mexican Chickadee's D note more closely resembles that of the Black-capped Chickadee, and is typically the longest note-type in duration (Fig. 1)—even longer than that of the Black-capped Chickadee. The D note varies from having a distinctly banded frequency structure (Fig. 1a) to being nearly uniformly noisy (Fig. 1c). The Mexican Chickadee's D note often has an onset "spike" of higher frequency (also evident in spectrograms of Dixon and Martin 1979, and Ficken 1990a). The 1,080 D notes recorded comprise 15.6% of the sample. When A and D notes occur in the same call (always in the order A–D), they may be independently uttered (Fig. 1a), or more typically the last A in a sequence merges with the first D note to form a sort of contracted note we designate by "A/D" (Figs. 1b, c). The A part of this contraction is variable in duration, but usually much shorter than a typical A. Rarely, peculiar phonations occur in recordings, as in Figure 1d where an A-like note occurs before an A/D-like contraction.

It might be that some variations in A notes are communicatively significant. Single A notes, not combined with other As or other note types, are particularly variable. Among the 6,918 notes recorded, 34 single A notes of unusually low acoustical frequency were found (Fig. 2a). These may represent a rare but distinct subtype of A notes, treated here as A notes but deserving of further study. The Mexican Chickadee also commonly utters high frequency notes that resemble brief A notes (Fig. 2b) but are much shorter and never combined with other notes into multi-note calls. These notes appear to be related to or variants of "tseets," of which Ficken (1990a) recorded only six examples. These A-like notes are not included in the analyses below.

The B note, which was very rare (3 occurrences in 6,918 notes), is chevron-shaped (Fig. 2d) and similar to the B note of the Black-capped Chickadee. The C note, which was the commonest type (3,870 recorded, comprising 55.9% of all notes), is a "noisy chevron" (Figs. 2c, d), again similar to the C note of the Black-capped Chickadee. The C notes were usually uttered in distinct couplets (Fig. 2e), another variation of phonology worthy of further study.

The duration of a given type of note varies, in some cases markedly (Table 1), depending upon the type of call and where the note falls within the call. Internote intervals vary from about 50 to 90 msec for various types, but the only systematic variation found was a bimodal distribution of C-C intervals (shorter intervals within than between couplets). The interval between the last note of one call and the first note of the next is one to two orders of magnitude longer than internote intervals within calls, thus defining the call as a natural unit of phonation.

Notes of the Mexican Chickadee (especially the A and D notes) are noticeably longer than those of the Black-capped Chickadee (Table 1) whereas the number of notes in a call is notice-

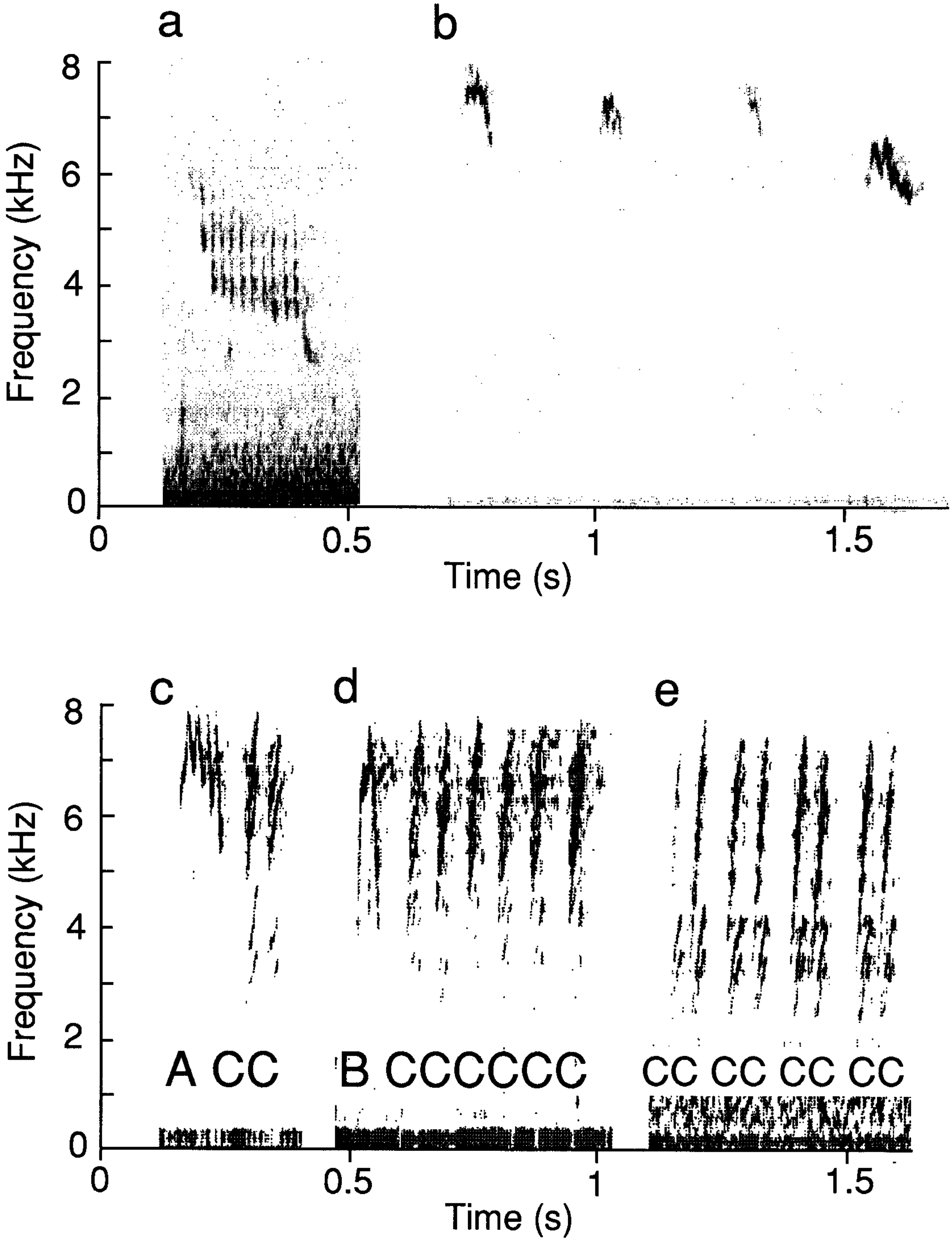

FIGURE 2. Spectrograms illustrating other notes of chick-a-dee calls (cf. Fig. 1). The frequency and time scales are the same for all spectra. (a) A low-frequency A note that may represent a special subtype. (b) High-frequency notes resembling abbreviated A notes, which appear to be "tseet" notes related to flight intention. (c) An A note with two C notes. (d) The rare B note followed by a series of C notes. (e) The couplet structure of C notes, found only in calls composed of this note type alone.

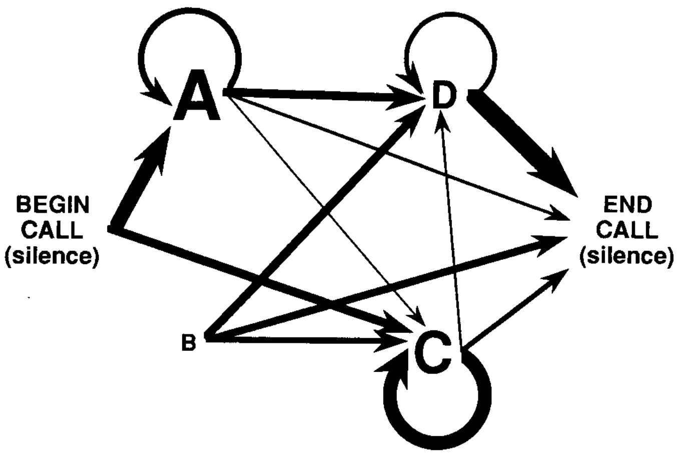

FIGURE 3. Kinematic graph of first-order transitions between notes within chick-a-dee calls. The sizes of the letters A, B, C and D are approximately proportional to the probabilities of occurrence of those note types (except that the rare B would not be visible if shown in correct proportion). The widths of the arrows are proportional to the probabilities of transition, such that outgoing arrows sum to unity. (Rare transitions that would have invisibly thin lines are omitted: B either begins a call or follows A.) Recurrent arrows represent repetitions of the same note type.

ably fewer than in the other species. The chick-a-dee calls of the Mexican Chickadee are from one to at least 14 notes in length, which is a smaller maximum note-length than in calls of the Black-capped Chickadee. The longest in Hailman et al. (1985) was 24 notes, and that sample did not include predator contexts, where calls are apparently often longer (Apel 1985).

Table 1 contains several examples of how the placement of a note affects its duration. For example, the A note of single-A calls is longer than either note of an AA call, but not as long as the first A that is followed by an A/D contraction to compose a call. Similarly the D part of an A/D contraction is shorter if the contraction is preceded by an A note than if the contraction is itself the entire call. The frequency characteristics of notes may also vary somewhat according to their placement within calls (Table 1).

SYNTAX

Markov chain analysis showed that the sequence of notes within a call follows the same rule as in the Black-capped Chickadee: note types always occur in the order A-B-C-D (no exceptions in 2,071 calls), where any note type may be omitted entirely, given once, or repeated a variable number of times. The first-order Markov chain (Fig. 3) reveals the principal syntactic structure. Calls begin with A or C (less than 1% begin with B or D). If beginning with A, that note-type repeats, transits to D, or ends the call; if transiting to D, that note repeats or ends the call. If the call begins with C, that note most commonly repeats, or ends the call.

From Figure 3 one may infer that calls will commonly have the structure [A], [C] or [A][D], where the enclosure of the note type in square brackets denotes possible repetition. Other call structures should be much rarer. Categories such as [A][D] are termed sequence types, and each may include many distinct call types such as AD, AAD, AAAAD, ADD, ADDDD, and so on. There are 15 such sequence types possible, but because of the rarity of B notes five of these did not occur in the record: [B], [B][D], [A][B][C], [B][C][D], and [A][B][C][D]. The commonest sequence types were: 735 [A][D] calls, 664 [C] and 517 [A], as expected from Figure 3. Two sequence types occurred with sufficient frequency to be of interest: 88 [A][C] and 30 [C][D]. The remaining types were very rare: 7 [D], 2 [A][C][D], and 1 each [A][B], [B][C], and [A][B][D].

The departure of Mexican Chickadee calls from a first-order Markov process was small. The maximum uncertainty possible with four note-types is $\log_2 4 = 2$ bits/note, but the unequal frequencies of note types yielded a zero-order Markov chain of only 1.21 bits/note. First-order analysis reveals a large drop to only 0.36 bit/note, which would be a true first-order Markov process only if all uncertainty were removed.

Second-order analysis showed a small drop to 0.21 bit/note, meaning that long-range constraints are relatively unimportant in the calls. Put differently, the next note to occur can be predicted well from the previous one but knowing longer ordered-strings of previous notes hardly improves predictability.

OPENNESS

A major finding in the Black-capped Chickadee was that the call system is "open" (Hailman et al. 1985): as the sample size of calls is increased, the number of different call types increases without demonstrable bound. A call type is defined as any different combination of notes; thus A, CC, AC, AAACC and ACCCCCC are all different call types. In this study we found 60 different call types in the 2,071 calls recorded, and as in the Black-capped Chickadee these call types varied widely in frequency of occurrence. For example, there were 783 calls of the type AD but only one of the type ADDDD.

The test for openness is made by a Zipf-Mandelbrot plot of the probability of occurrence (*P*) as a function of occurrence rank (*r*) on log axes. Mandelbrot's (1953) formula $P = i(r + k)^{s}$ for a fitted function has three constants: the intercept (*i*), curvature factor (*k*) and asymptotic slope (*s*), which is always negative. To show openness it is not necessary to provide a fitted function but merely to show that the plotted curve reaches a non-zero asymptotic slope. Figure 4 shows this property for the Mexican Chickadee, both with all data combined (top curve) and plotted separately by the six contexts. Even the curves themselves for the different contexts are remarkably similar, reaching about the same asymptotic slopes at their right-hand sides. The curves demonstrate that the call system of the Mexican Chickadee, like that of the Black-capped Chickadee, is open and hence more new call types will be found if the sample is increased.

DIFFERENCES AMONG CONTEXTS

The distribution of calls among the sequence types differed according to context of recording (Fig. 5). For purposes of statistical comparison among contexts, calls were considered in five categories: [A], [C], [A][D], [A][C] and "other" (all the remaining sequence types combined). As each recording context was independent of the others, every possible pair of contexts was compared in a 2 × 5 contingency table using the Monte Carlo technique (see Methods). All pairs of contexts differed significantly (*P*'s < 0.001) except two involving the small sample size of lone birds: the difference from "with mate" is marginal ($P = 0.06$) and from "fall flocks" non-significant ($P = 0.19$).

When undisturbed on territory with the mate, almost three-quarters of calls were of the [A][D] sequence type (Fig. 5a). When in mixed-species fall flocks (Fig. 5b) or alone (Fig. 5c), only about half of calls were [A][D], with [A] and [C] calls making up most of the other half. In the former case, there were also a few calls of the [A][C] type and other types. When there was an external disturbance (right column of diagrams in Fig. 5), the distribution of sequence types was markedly different, with [C] and [A][C] together always making up at least half of all calls. When disturbed by a Great Horned Owl model, birds gave many [A][C] calls (Fig. 5d). When mobbing a Northern Pygmy-Owl tape, [A] and [C] calls were commoner (Fig. 5e), and when disturbed by the observer sitting about 6 m from the nest, [C] calls predominated (Fig. 5f).

OWL-TAPE PLAYBACK EXPERIMENTS

Mobbing experiments provide a means of studying calls in detail because there is a specific locus in space to which the mobbing birds attend and all individuals present behave similarly. Experiments were conducted at five sites from March to May of various years. The experiments, using playback tapes of Northern Pygmy-Owl calls, generally attracted one pair of Mexican Chickadees, often with small songbirds of other species. The chickadees gave 20 to 50 calls and then departed with the playback still running. One experiment brought in several chickadees for a long period, and the results are analyzed separately below. The results of the other four experiments are shown in Figure 6, which plots the cumulative frequency of each call sequence type through the experiment.

Every experiment shown in Figure 6 yielded a similar but unique set of results. The experiment of 22 March was made about half-way on the road to Rustler Park. This playback probably evoked calls from a single bird, which did not closely approach the speaker. In all four experiments one sequence type predominated, and that type of call was given at an approximately equal rate (constant slopes in Fig. 6) throughout the experiment. The predominant type was [A][D]

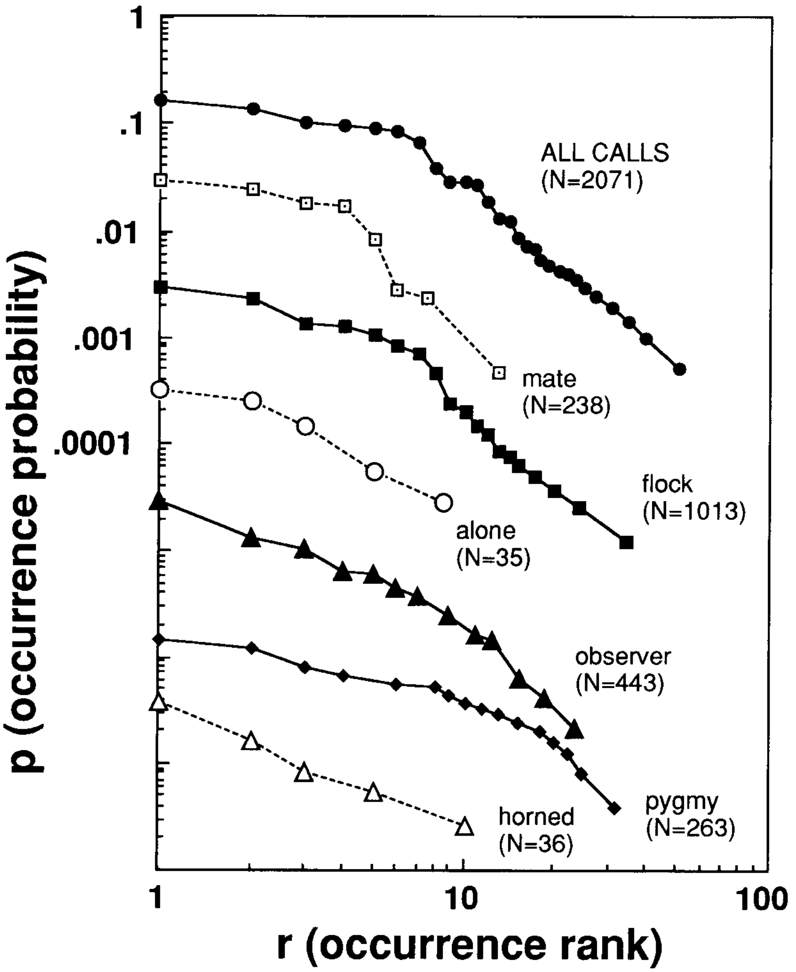

FIGURE 4. Zipf-Mandelbrot plots for all calls combined (top) and separated by contexts. Note that probability values are labeled only for the top curve; each successive curve is displaced downward by one log unit to separate the curves for clarity. The occurrence probability of the commonest call is about 0.2–0.3 for all curves. The fact that curves reach an asymptotic non-zero slope shows that the call system is "open": new call types will be found as the sample size increases.

in the March and April experiments and [C] in the experiments conducted in May. Only [A] and [C] calls were common to all experiments, [A][C] and [A][D] occurred in three experiments each, and three sequence types were unique to one experiment: [C][D] in March and [A][B][D] and [A][C][D] in April. Our qualitative observations suggested that the [C] calls were given when birds were most agitated by the playbacks and closest to the speaker. The differences among experiments may therefore indicate greater agitation during the nesting season (May) than earlier (March and April).

One experiment (Fig. 7) was unusual in several respects. First, the playback attracted at least four Mexican Chickadees (it was difficult to be certain of the precise count because of dense vegetation), instead of a single bird or a pair. Second, the birds continued mobbing for a sufficient period that we could stop the playback while they were still present, and so record post-playback calls. And third, much (but not all) of the experiment was recorded on videotape.

Birds began moving toward the site giving mainly [A] calls. While still approaching, the birds began giving [C] calls in addition to [A] calls, and

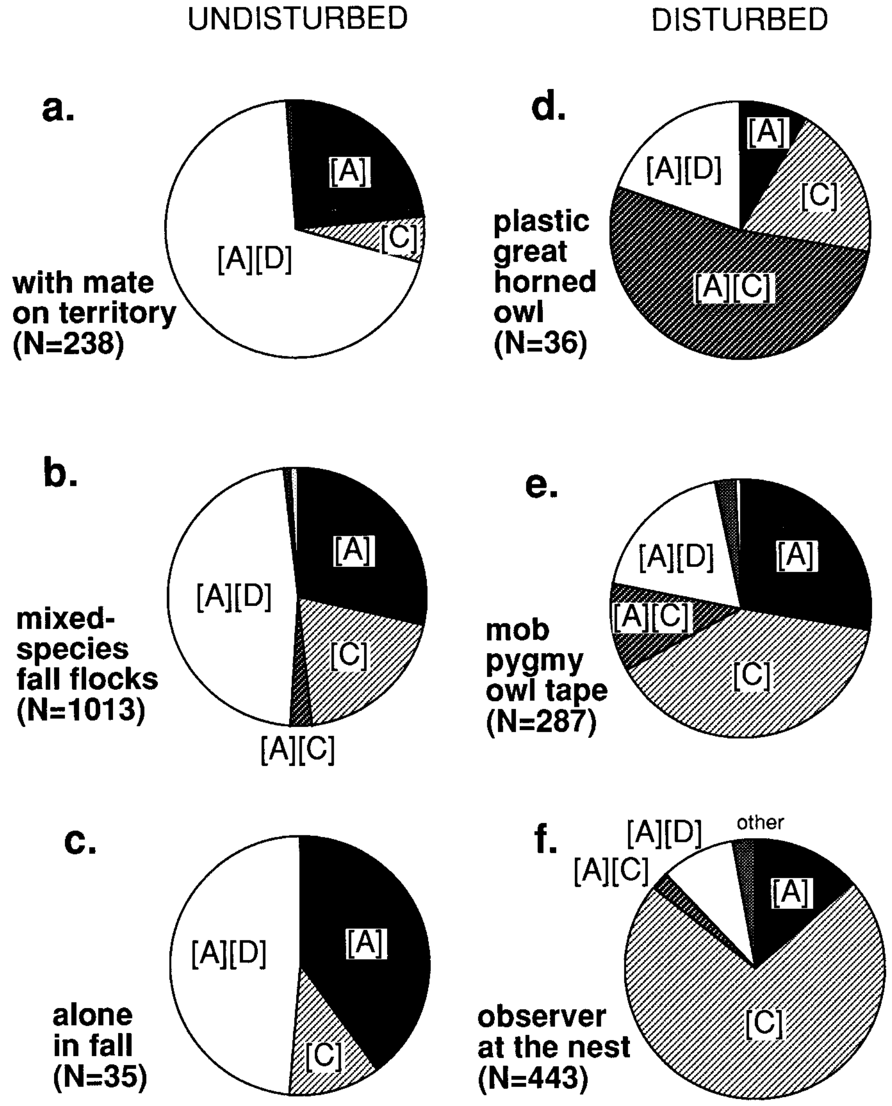

FIGURE 5. Pie diagrams of the distributions of call sequence types in six contexts of recording. (The sum of sample sizes over all diagrams is less than the total number of recordings because a few recordings do not belong in any of the six contexts shown.)

at approximately the same rate (same slopes in Fig. 7). As they moved still closer, birds began giving [A][D] calls as well, until assembled at the speaker site. Here they stopped giving [A] calls altogether (zero slope in figure) and soon after stopped giving [A][D], while abruptly increasing the rate of [C] calls (steep slope in Fig. 7). When playback was terminated, calling immediately changed again, with [A] calls immediately resuming (steep slope) and [C] calls becoming rarer (changing to a noticeably shallower slope). Taping ceased as the birds were moving off.

These results were consistent with those recorded when birds were intensely disturbed by an observer sitting under the nest hole (Fig. 5f, above), where they also gave mainly [C] calls. Videotapes of the owl-playback experiment of Figure 7 show that [C] calls were given primarily by perched birds that were pivoting on a branch, although they were sometimes given in flight. (It

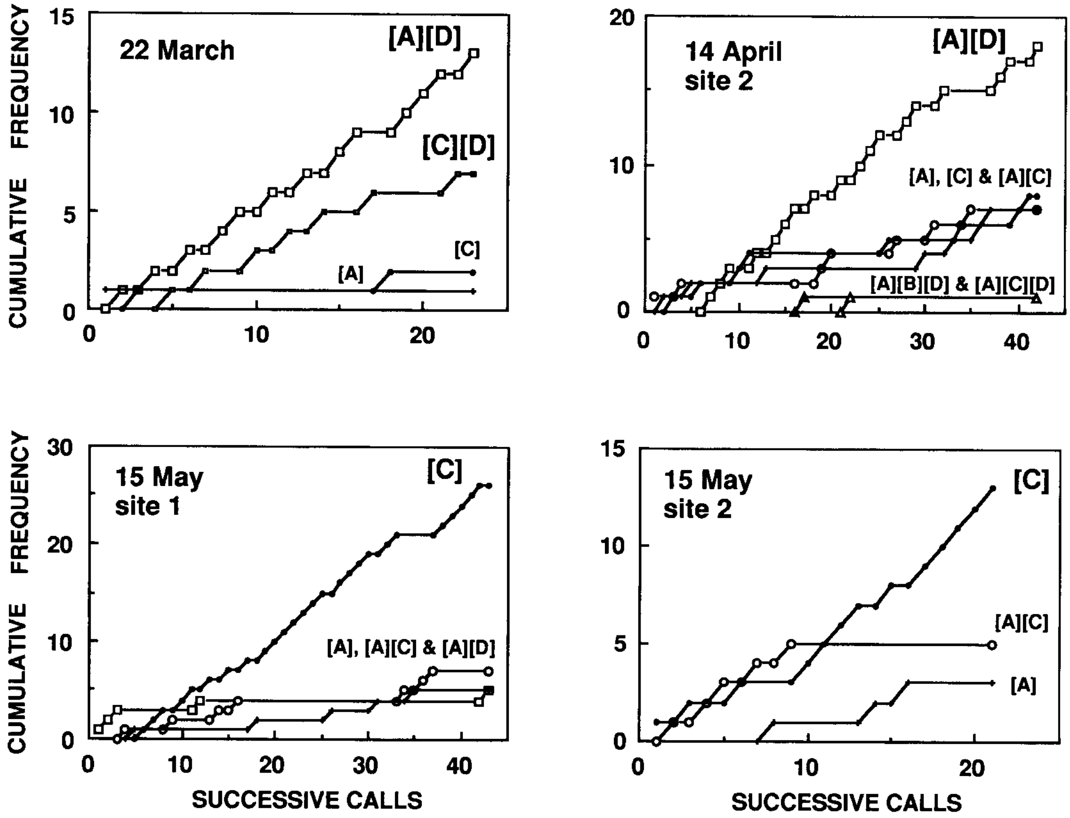

FIGURE 6. Cumulative frequency plots of call sequence types given by Mexican Chickadee pairs (a lone bird on 22 March) while mobbing a speaker playing back sounds of a Northern Pygmy-Owl. March and April experiments were dominated by [A][D] calls whereas May trials yielded mainly [C] calls.

is often difficult to tell from the videotape which call is being given by which bird.) Calls containing the A note were given during approach (and retreat) from the site, but there is a difference between [A] and [A][D] calls. In mobbing trials, [A] calls were most often strings such as AA, AAA, and AAAA, unlike single A notes given in other contexts; furthermore, A-strings given in mobbing trials seemed sometimes to be given in flight. By contrast, [A][D] calls were given only by perched birds. These birds were moving toward the site in short flights, but seemed never to utter any call containing a D note while actually in flight.

DISCUSSION

COMPARISONS WITH THE BLACK-CAPPED CHICKADEE

The overall structure of chick-a-dee calling in the Mexican Chickadee is similar to that of the Black-capped Chickadee (Hailman et al. 1985). There are four note types, they are combined into unit calls with very short internote intervals compared with intervals between calls, and they occur in the invariable sequence A-B-C-D within calls, where any note type may be omitted entirely, given once, or repeated a variable number of times. The note types are structurally similar in the two chickadees, with B and C notes being nearly identical. The calls are given by both sexes, throughout the year, and in a wide variety of contexts. In both species the [A][D] sequence type is the commonest overall. Both call systems are open to new call types as the sample size increases, and are the only communication systems outside of human language to be proven open.

The chick-a-dee calls of the two species do differ, however, in many ways. The A notes of the Mexican Chickadee are markedly different from those of the Black-capped Chickadee, and even the D notes are dissimilar (as noted by Dix-

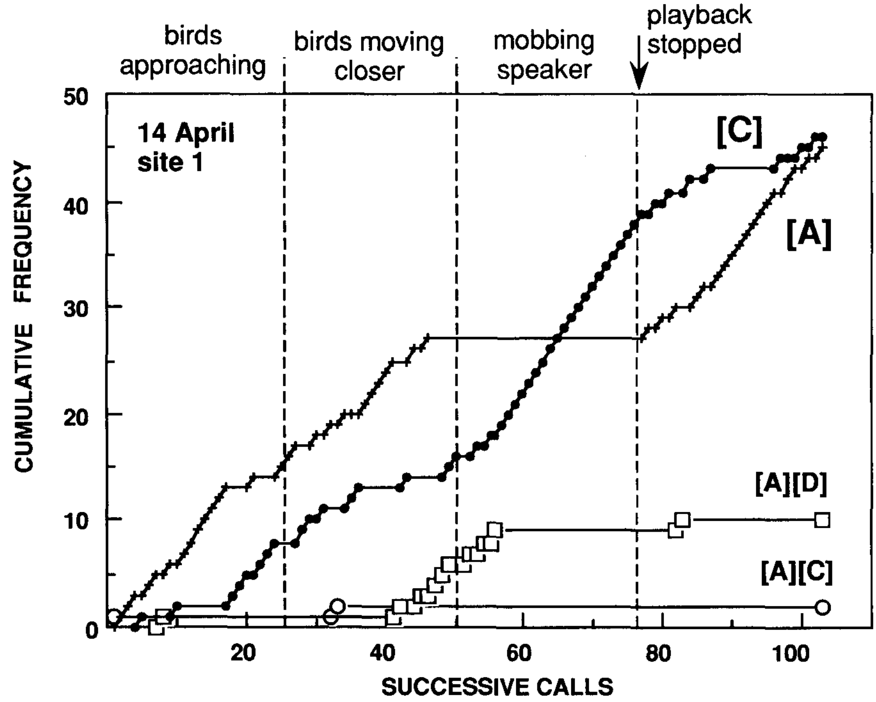

FIGURE 7. Cumulative frequency plots (as in Fig. 6) of a particularly long mobbing session with at least four Mexican Chickadees calling. Birds first gave [A] calls at a distance, then added [C] calls when drawing closer, and finally abandoned the former entirely when near the speaker. When the owl tape was turned off, [A] calls abruptly resumed.

on and Martin 1979). In both cases, though, the note types may reflect origins from a common ancestral source: the Black-capped Chickadee's A note is a single chevron, the Mexican Chickadee's a continuous chain of short chevrons run together (Fig. 1, above) so as to sound distinctly buzzing to the human ear. Similarly, the D notes of both species are the longest note type, cover a wide frequency spectrum, and may be distinctly banded into emphasized frequency components or more uniformly distributed to compose a noisy note.

Major differences are in duration, with the A notes of the Mexican Chickadee being highly variable in duration according to the other note types with which they occur (means from 120 to 170 msec in Table 1, for A notes not contracted with D's). By comparison, the A notes of the Black-capped Chickadee are uniformly shorter at about 45 msec (Hailman et al. 1985: 195, Table 1). Similarly, the Mexican Chickadee's uncontracted D note averages 270 msec (Table 1, above), whereas the Black-capped Chickadee's D notes average about 130 msec (Hailman et al. 1985: 195, Table 1).

The rarity of B notes renders the Mexican Chickadee's calls less diverse than those of its congener, and the total note length of calls is much shorter. The more variable duration of the Mexican Chickadee's notes may in some sense replace the more variable number of note repetitions given by the Black-capped Chickadee. 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 (especially if duration of notes encodes useful information).

Good contextual analyses of Black-capped Chickadee calls have not been published, but some comparison of mobbing situations between the two species may be made preliminarily. The Mexican Chickadee utters primarily [C] or [A][C] calls when greatly disturbed or mobbing (Figs. 5–7, above). An unpublished thesis of Apel (1985) showed that Black-capped Chickadees give primarily [D] calls or other sequence types containing D notes. Similarly, Lambrechts and J. P. Hailman (in prep.) found that the Black-capped Chickadees mobbing a stuffed owl near the nest gave elevated proportions of [D] and [A][B][D] calls, with hardly any calls of any kind containing C notes. There are important differences in the detailed contexts among these three studies, but the difference in results is so striking as to suggest a fundamentally different semantic structure in the two chickadee species. By Marler's (1955) classic criterion that mobbing calls should consist of short, broad frequency notes repeated, both chickadee species qualify. The Mexican Chickadee's D notes may be too long for effectively rapid repetition, whereas its C note more nearly meets the required characteristics. However, the C note of the Black-capped Chickadee is very similar to that of the Mexican Chickadee, so it remains unclear why the former species do not seem to employ C notes in its mobbing calls. In any case, the former impression that D and D-like notes were the "mobbing calls" of *Parus* (e.g., Thielcke 1968) is too simple a view of the complex vocalizations of tits.

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What chick-a-dee calls "mean" (what kind of information they encode) is a formidable problem because of the complexity of the calling system and the fact that chick-a-dee calls occur in virtually every definable context. At one extreme is the possibility that chick-a-dee syntax is simply some by-product of phonation, such that all calls are semantically equivalent, carrying little more information than the species identity and position in space of the caller. At the other extreme is the possibility that each of the hundreds of call types has its own distinct meaning, like words in a dictionary. Hailman et al. (1985, 1987) favored an intermediate view for the Black-capped Chickadee, suggesting that each note type means something different and repetitions of note types within calls serve as modifiers denoting "intensity." The present results on the Mexican Chickadee support this hypothesis by the findings of distinctly different suites of sequence types in different contexts (Fig. 5, above) and details of calls given during mobbing situations (e.g., Fig. 7, above). Comparable contextual differences have yet to be reported for the Black-capped Chickadee.

Even though different suites of sequence types characterize different contexts, the fact that the same note types, sequence types and call types can occur in different contexts suggests that note types encode information common to a variety of situations. Hailman et al. (1985, 1987) suggested that this encoded information related primarily to the position and movements of the caller in space, especially relative to external objects such as conspecifics, the nest, a human observer, or a potential predator. The present results on the Mexican Chickadee support that view and give it further substance. In contexts where birds are moving through the environment with little obvious disturbance except that caused by conspecifics, Mexican Chickadees utter primarily [A] and [A][D] calls (Fig. 5a–c, above). These same two sequence types characterize birds moving toward the site of an owl playback (Figs. 6 and 7, above), and sometimes when leaving the site (Fig. 7). The D note is always given while perched whereas the A note seems to be given sometimes in flight as well.

A preliminary interpretation may therefore be formulated as follows. A notes indicate a restlessness (a bird ready to fly or already in flight) whereas a D note indicates that the caller is perched and hence indexes its location in space. The [A] sequence type in undisturbed birds consists mainly of single A notes, but in birds approaching a mobbing site AA and AAA call types are especially common. Thus, the repetition of A might indicate speed of movement or high "intensity" of restlessness. The [C] calls of the Mexican Chickadee are given most commonly in disturbed situations (Fig. 5d–f, above), where [A][C] calls are also common. Furthermore, when intensely mobbing an owl playback, the birds gave nearly pure [C] calls (Fig. 7), as they did to the human observer at the nest (Fig. 5f). The C note is most often given by a perched bird that is pivoting while it calls, but may sometimes be given in flight. In the Black-capped Chickadee a C note given in flight has been correlated preliminarily with a sudden swerve or change in direction (Hailman et al. 1985), but our videotapes cannot document the same phenomenon for certain in the Mexican Chickadee. That [C] calls, and even a few [A][C] calls, occur in relatively undisturbed situations (Figs. 5a–c) may indicate mild disturbance by conspecifics. Therefore, C notes seem to indicate a disturbing stimulus and the tendency to change direction, so that when combined with A notes in [A][C] calls further indicate a tendency to move some distance, as when flying past a playback speaker or owl model.

In summary, the relatively simple structure of Mexican Chickadee calls provides a clearer picture of the information encoded by note types than is currently available from data on Black-capped Chickadees. Basically, A notes indicate a tendency to move some distance in space, C notes denote a disturbing stimulus and a tendency to alter direction, and D notes connote a perched bird. (The B note of the Mexican Chickadee cannot be analyzed because of its rarity). Repetitions of notes within calls indicate the "intensity" of the behavior that correlates with the note types. Whether or not combinations of these notes into sequence types such as [A][C], [A][D] or [C][D] encode something more than the concatenation of the separate meanings of the notes is a derivative question of considerable difficulty that cannot be addressed with present data.

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