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ORGANIZATION OF AGONISTIC VOCALIZATIONS IN BLACK-CHINNED HUMMINGBIRDS[1]

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Abstract. We describe vocalizations of Black-chinned Hummingbirds (*Archilochus alexandri*) recorded during agonistic encounters at feeders. Calls are composed of one to five different note-types that comprise a recombinatorial system exhibiting syntax. A Markov analysis revealed non-random ordering of note-types. The distribution of call-types (unique combinations of notes) illustrates openness; the number of call-types increases as more calls are sampled. Constraints on call length occur that are related to the length of individual note-types; shorter note-types are more common in calls with more notes. No sex differences occurred in the call-types with the exception of the Z note which occurred more often in male calls. The agonistic vocalizations of these hummingbirds demonstrate a level of vocal complexity comparable to songs of many passerines. We compare the vocalizations of the Black-chinned Hummingbird with studies of Anna's Hummingbird (*Calypte anna*) and point out major differences in repertoire organization. Marked similarities occur between organization of calls in certain chickadees (*Parus*) and that of the Black-chinned Hummingbird. This finding is surprising in view of their phyletic differences, but may reflect certain underlying constraints on the organization of avian vocalizations.

Key words: agonistic vocalizations; calls; syntax; Black-chinned Hummingbird; Archilochus alexandri.

INTRODUCTION

Only recently have vocalizations of hummingbirds been analyzed in detail with sonograms. All of these studies have involved "song" or vocalizations with presumed territorial advertising or courtship functions (Stiles 1982; Atwood et al. 1991; Goldberg and Ewald 1991; Gaunt et al. 1994). The best studied species, Anna's Hummingbird (*Calypte anna*), shows a high level of vocal complexity and song learning (Baptista and Schuchmann 1990).

In contrast, no detailed analyses exist for the agonistic vocalizations of hummingbirds. To quote Greenewalt (1990) who wrote a fascinating account of plumage iridescence and general hummingbird biology, "Finally, I must come, however, reluctantly, to a serious deficiency in this otherwise striking family, and that is their vocal performance. In the sense in which our songbirds have a voice, hummingbirds have none at all. They do indeed chatter, particularly when they are annoyed and chasing each other, but the sound is scarcely musical." To our ears, hummingbird agonistic vocalizations are indeed squeaky or chattery. However, we show here that calls given during agonistic encounters by Black-chinned Hummingbirds (*Archilochus alexandri*) rival the songs of some passerines in both acoustic complexity of notes and organization of note-types within the call. This is the first case of which we are aware showing complex syntax in a non-passerine vocalization.

The Black-chinned Hummingbird is the western counterpart of the Ruby-throated Hummingbird (*A. colubris*), and is common in arid regions of the southwestern United States and Mexico. Both sexes defend a small feeding site, the strength of defense increasing as the breeding cycle progresses (Bené 1947). At nectar feeders they are often territorial (Bené 1947, Ewald 1985, Ewald and Bransfield 1987). If there are many individuals, as at our study sites, they do not appear to be territorial, but aggressive interactions occur frequently.

We performed a sonographic analysis of the vocalizations given during agonistic encounters at feeders. Our objectives were to: (1) describe the acoustic structure of the note-types, (2) describe the sequences of the note-types comprising the individual calls, (3) determine the organi-

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zational properties of the calls using sequential analyses, (4) test whether differences in call structure are correlated with sex or behavioral context, and (5) compare the agonistic vocalizations of this hummingbird species with those of other species, particularly Anna's Hummingbird and some members of the passerine genus *Parus* (chickadees).

METHODS

We recorded hummingbirds at feeding stations at Ramsey Canyon Preserve and Patagonia (Cochise County), Arizona on 24 May 1992, 18–19 April 1993, and 15–23 May 1993.

Black-chinned Hummingbirds are sexually dimorphic. Individuals in this study were not color-banded and therefore the number of individuals recorded is unknown. However, banding studies conducted at Ramsey Canyon Preserve indicate that about 120 Black-chinned Hummingbirds are present from April through August. We undoubtedly recorded vocalizations from many different birds as we visited different feeders and often more than 10 birds were present at any one time. Our sampling period covered a sufficient length of time that we recorded many individuals. Our studies were early in the breeding season (Bent 1940), so that it is unlikely that young hummingbirds are included in our sample. If any were included, they would be indistinguishable from females.

We recorded and observed the birds throughout the day from approximately 06:00 MST to 20:00 MST. Recordings were made using a Sony Digital Audio Tape Recorder (TCD-D3), and a Sony Walkman Professional cassette tape recorder (WM-D6C) with a Nakamichi cardioid microphone and an Audio Technica directional microphone. Agonistic encounters occurred all day with slight peaks at dawn and dusk. Microphones were either hand-held approximately 4 m from the feeder or attached approximately 20 cm from the feeder. Two feeding stations about 20 m apart were used at the Ramsey Canyon Preserve. Feeders were filled with 33% sucrose solution without dye. Black-chinned Hummingbirds were seen flying between all feeders and no site specificity was apparent. At the Patagonia site, where we obtained fewer recordings, there were multiple feeders and a high visitation rate. The feeders at both sites were utilized by several other hummingbird species.

In addition to noting sex and number of birds involved in interactions, we categorized interactions based on the outcome of the encounter: (1) Confrontation: a bird flies to a feeder that is already occupied and is chased by the feeding bird. The bird that was originally present may either resume feeding or abandon the feeder. (2) Displacement: a bird approaches a feeding bird which then abandons the feeder, the intruder taking a position at the feeder. Vocalizations occurred during both types of interactions. Due to high speeds, we could not distinguish whether the vocalizer is the 'displacer' or the 'displaced,' the 'confronter' or the 'confronted.' But in about one third of the data collected for this study, both birds in an encounter were vocalizing at the same time giving no clear difference between the vocalizer with the 'winner' or 'loser.' These overlapping vocalizations were not included in our analysis.

We analyzed recordings with a Kay Elemetrics 7800 Digital Sona-Graph and a Kay Elemetrics 5500 Digital Sona-Graph with a 16 kHz frequency range and 300 Hz filter. Note-types were discrete and were distinguished by combinations of frequency and temporal characteristics. Calls were defined by typical beginning and ending notes and contained no gaps greater than 0.2 sec.

We examined the order of note-types using transitional analysis and a computer program that determined the frequencies and probabilities for first and second order Markov chains. In rare cases where note-types were fused, they were counted as individual notes.

RESULTS

AGONISTIC ENCOUNTERS

Although all our observations were made at feeders, agonistic encounters also occur under more natural conditions during the defense of flower patches. At feeders the encounter rate and agonistic vocalization rate were much greater than under natural feeding conditions (pers. observ.).

Several kinds of agonistic interactions occurred, and not all included vocalizations. Because many encounters involved high speed chases over a large area, complete interactions of this type were rarely observed. In other encounters, birds faced each other while hovering a few centimeters apart, often with tails spread exhibiting the prominent white spots (females only) which were otherwise usually concealed. Fights with bodily contact were uncommon. On rare occasions, a bill duel occurred in which the birds flew upward face-to-face while "sword fighting" with their bills (Bené 1947; pers. observ.). In addition to vocalizations, wing buzzes often occurred and may function in communication.

A total of 320 interactions was analyzed. At least 100 others were omitted from the analysis because of overlapping vocalizations. Most interactions (96%) were among conspecifics, although other species also used the feeders. The remaining interactions (4%) were with four other species of hummingbirds. Of the Black-chinned interactions, females interacted with females (37%), males with males (17%) and females with males (27%) of the interactions. During 49 encounters (15%) sex determination could not be made because of the high speed of the interactions.

NOTE-TYPES

The note-types are structurally diverse. All cover a wide frequency range; some are of short duration, others much longer. A call usually consists of several different note-types, some of which are repeated a variable number of times. We first describe the acoustic structure of the notes and then the results of sequential analyses.

Five distinct note-types were observed during agonistic feeding encounters. The notes (labeled C, Z, S, T and E) were named onomatopoeically (Fig. 1a and b). The data consisted of 502 C notes (20.3% of all notes), 88 Z's (3.6%), 321 S's (12.9%), 487 T's (19.7%) and 1,076 E's (43.5%). Measurements of notes (frequency and duration) are shown in Table 1.

C notes are composed of between four to eight frequency bands ranging from approximately 1 to 10 kHz. These bands have an energy distribution centered at 5–7 kHz. Each band decreases in frequency at a uniform rate within a note, allowing the slope of the frequency change for the note to be measured. The mean slope of the highest energy band was −135.6 Hz/ms ± 22.9 ($n = 29$). C notes are the only note type given by solitary Black-chinned Hummingbirds. They were produced as single notes in this context, but were repeated in series of doublets or triplets in the presence of other hummingbirds. Longer strings were observed, although they were less common.

E notes are similar to C notes in that they are short duration, composed of harmonic bands and cover a wide frequency range. The slope of the highest energy band decreased at about 247 Hz/ms ± 27 ($n = 30$), thus exhibiting a steeper slope than the C note.

The T note is a broad band noise burst with a frequency range from approximately 1.5–12 kHz. Unlike C notes, T notes only occur with other note-types. A wide band of modulated frequencies (trills) from 2–10 kHz characterizes the S note. S notes may be given alone in agonistic encounters, although only nine out of 320 (2.8%) agonistic sequences were single S notes. Occasionally, S notes may be fused to T notes. Of 254 ST combinations, 20 were S-T fusions (8%).

Z notes have the greatest degree of structural variation. They are composed of two narrow bands of rapidly modulated frequencies, separated by about 4–5 kHz and sloping together at the end of the note. The energy is concentrated in the lower frequency band and often only this band is recorded, because there is generally a high degree of degradation in the high frequency band. The note may end in a rapid trill. Z notes fuse to S notes. Of 55 ZS combinations, 20 Z-S fusions were observed (36%). The durations of the Z and S notes are highly variable. These two notes are the longest of the five note-types.

To the human ear, the C note is a higher pitched "chip" sound than the E note. The E note is tonally different from the C note due to differences in the number, frequency range, and slope of the harmonic bands. The T note sounds like a "click." Both the Z and S notes sound like buzzes, but differ in their pitch. The call as a whole has been described as "chatter" by Greenewalt (1990) and "chippering" by Bent (1940).

CALLS

The five note-types are combined into calls of variable length. Note-types may repeat in a call and all five types do not always occur in each call. The number of notes in a call ranges from 1 to 18 ($\bar{x} = 7.72 \pm 2.77$, $n = 320$). Figure 2 shows the frequency of occurrence of each call based on its length. A skew towards fewer notes is apparent, and the mode is six notes. Call length was also examined after grouping the data by sex and by outcome of the encounter (Displacement or Confrontation). All combinations of outcome were grouped, for example: female displaces female, female displaces male, male confronts male, etc. There were no significant differences in call

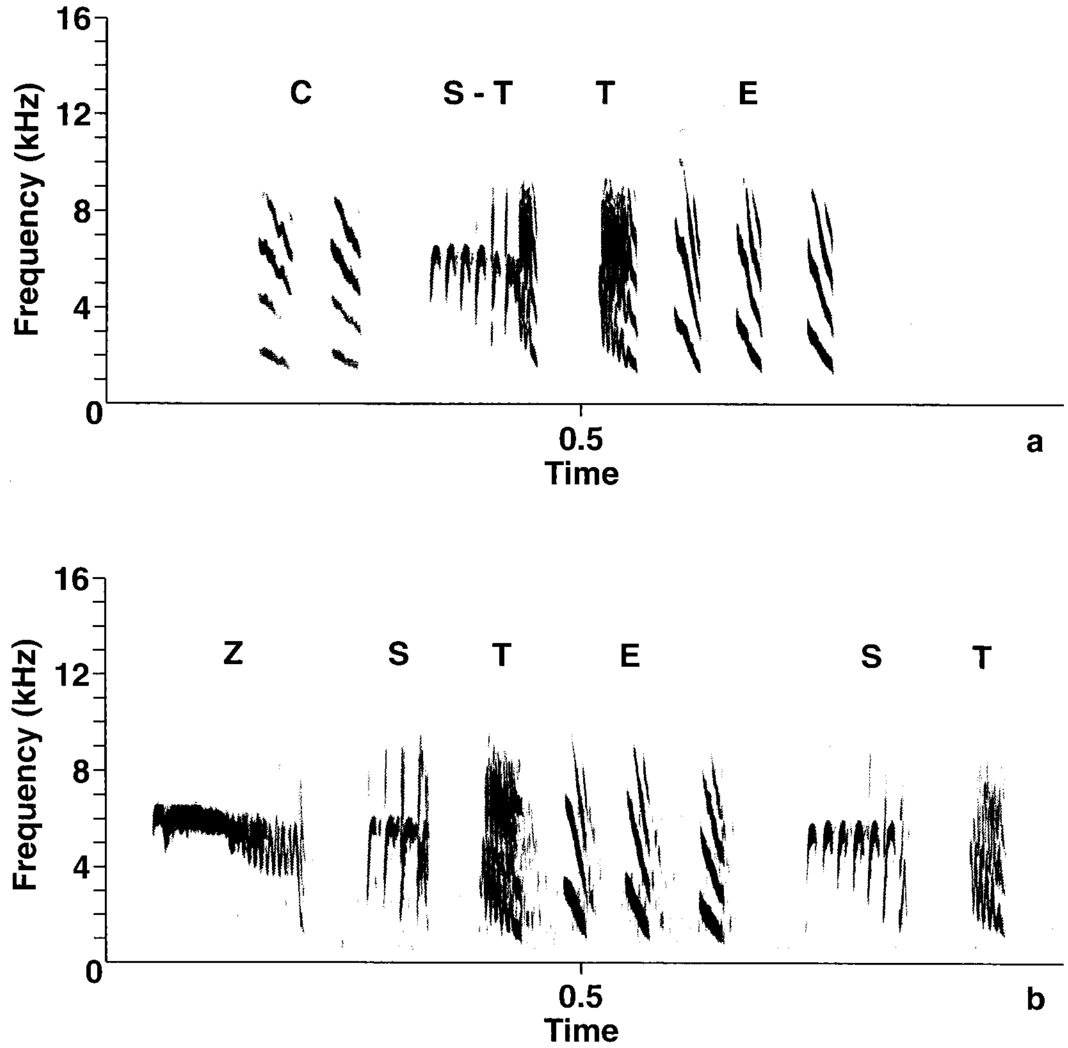

FIGURE 1a and b. Two agonistic calls of Black-chinned Hummingbirds showing note-types (C, Z, S, T and E). S-T indicates note fusion.

length among these categories (two-way ANOVA).

Males and females used the same frequencies of note-types in their calls, with one exception (Fig. 3). The Z note occurred more often in the calls of males (binomial test, $P < 0.01$). The frequency of occurrence of note-types in calls is also not related to context (Displacement or Confrontation, binomial test, $P > 0.05$). Because the frequencies of note-types showed little sexual and no contextual differences, we determined syntax rules for the data set as a whole.

Call length is highly variable. Patterns emerge in long calls (seven or more notes) that are different in frequencies of note-types and two-note combinations, or diads, when compared to short calls. The Z and S notes (long duration notes) are found more often in short sequences (binomial test, $P < 0.01$), while the E note (short duration) occurs more often in long sequences (binomial test, $P < 0.01$). These differences suggest a constraint on the length of calls. In calls with seven or more notes, long duration notes are uncommon while the short duration E note is common. In addition, certain diads occur more often in long sequences while others are more common

TABLE 1. Measurements of note-types in calls of Black-chinned Hummingbirds ($\bar{x}$ ± SD).

Note-type	Acoustic structure	n	Duration (msec)	Lowest frequency (kHz)	Highest frequency (kHz)
C	Short, banded	24	29 ± 11.0	1.6 ± 0.6	8.9 ± 1.1
Z	Long, trill	11	71 ± 32.0	5.8 ± 0.6	7.0 ± 0.5
S	Long, trill	28	98 ± 28.0	2.8 ± 1.0	11.1 ± 1.7
T	Noise burst	28	48 ± 9.0	1.9 ± 0.4	10.7 ± 1.3
E	Short, banded	27	24 ± 5.0	1.7 ± 0.3	9.9 ± 1.3

in short sequences. The following transitions occur more often in long than short calls: CZ, SE, ES, ET, EE (binomial test, $P < 0.01$). Other diads occur more often in short calls: ZS, ZT, SC, ST, TC, TT (binomial test $P < 0.01$). Frequencies of all other transitions were not significantly different between long and short calls.

NOTE TRANSITIONS

Notes occurred in a non-random order within calls. Patterns are recognized using a first-order Markov model which describes transitions between note-types and defines the system's syntax. A transition matrix shows the probability that each note-type will follow a given note-type in a diad or two-note string (Table 2). The frequencies of transitions were not random ($\chi^2 = 3532$, df = 35, $P < 0.0001$). Using the transition matrix, a kinematic diagram was constructed that represents the flow of notes in a sequence (Fig. 4). Transitions occurring less than 8% of the time have been omitted. All transitions are significant (Bonferroni test, $P < 0.01$) with the exception of the following: CZ, SZ, TZ, ZT, TE, ZZ and EZ are only significant at $P < 0.05$.

The following syntax emerges from the transition matrix. C is most often followed by C, S by T, T by E, and E by E. C or S typically begin the sequence. E usually ends the sequence. Z is the rarest note-type. It is most often followed by S and may begin a sequence. Only C notes and E notes were repeated in strings over three. Long sequences (greater than seven notes) typically contain strings of between four to nine C or E notes.

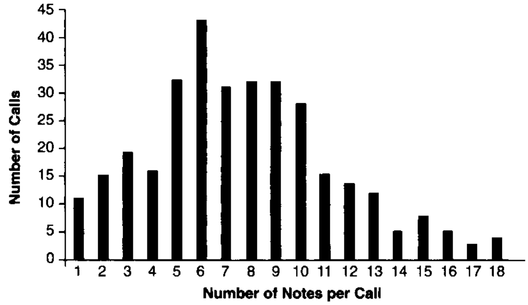

FIGURE 2. Call length defined by number of notes per call (n = 320 calls).

Uncertainty measurements (Shannon and Weaver 1949) also reveal patterns in the structure of sequences (Fig. 5). The maximum uncertainty (U_0) for the system is $\log_2 n$ where n is the number of equally probable note-types. For our system of five different note-types, $U_0 = 2.58$. The first-order estimate describing the actual frequency of note-types is U_1:

$$U_1 = \sum_i p_i(\log_2 p_i)$$

where p_i is the probability of occurrence of the

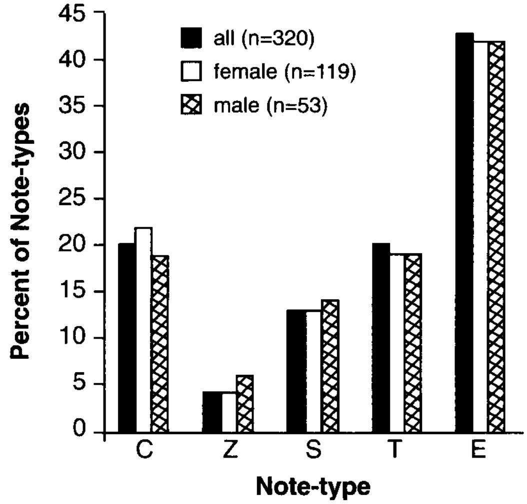

FIGURE 3. Note-types used by males and females in agonistic calls. The Z note is significant in male calls (see text). The "all" category includes males, females and unknown individuals.

TABLE 2. Frequency and probability of occurrence of note-types in agonistic calls ($n = 320$) of Black-chinned Hummingbird (above line). Transitional probabilities include repetitions for two-note combinations (below line). Silence to silence transition is an undefined state.

	Note-type					
	Silence	C	Z	S	T	E
Overall frequency	320	502	88	321	487	1,076
Overall probability	0.115	0.180	0.031	0.115	0.174	0.385
	Transitional Probabilities					
	Following note:					
Preceding note:	Silence	C	Z	S	T	E
Silence		0.406	0.078	0.459	0.056	0
C	0.093	0.654	0.022	0.186	0.043	0.002
Z	0	0.012	0.071	0.647	0.247	0.024
S	0.074	0.019	0.003	0.015	0.784	0.105
T	0.103	0.066	0.01	0.066	0.285	0.47
E	0.186	0.004	0.005	0.02	0.032	0.755

*i*th note-type. If note-types occur with the same frequency, then U_1 would equal U_0. In our system, $U_1 = 2.32$ demonstrating asymmetry in the frequency of the different notes.

The second-order estimate of uncertainty, U_2, accounts for information in diads:

$$U_2 = \sum_{ij} p_{ij}(-\log_2 p_j|_i)$$

where p_{ij} is the joint probability of the *i*th preceding note and the *j*th following note and $p_j|_i$ is the conditional (transitional) probability of *j* given *i* as tabulated in Table 2. In our system, $U_2 = 1.41$. The large drop in value from U_1 to U_2 indicates that a given note will predict the following note with a high degree of accuracy. This result is reasonable given the previous description of the transition matrix.

U_3 is defined by the same equation as U_2 except that *i* becomes the preceding ordered *pair* of notes. $U_3 = 1.23$ and the slight decrease from U_2 to U_3 indicates that transitional frequencies are not entirely described by a first-order transitional analysis. Second-order effects, or the prediction of

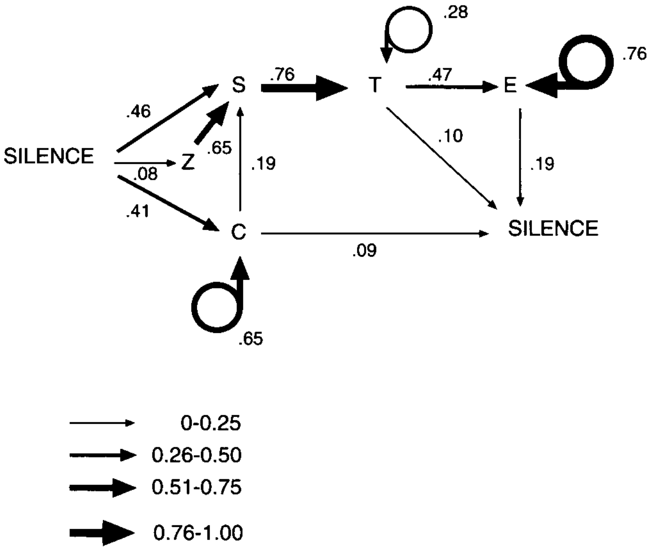

FIGURE 4. Kinematic diagram showing first order transitional probabilities among note-types. Transitions occurring less than 8% of the time have been omitted.

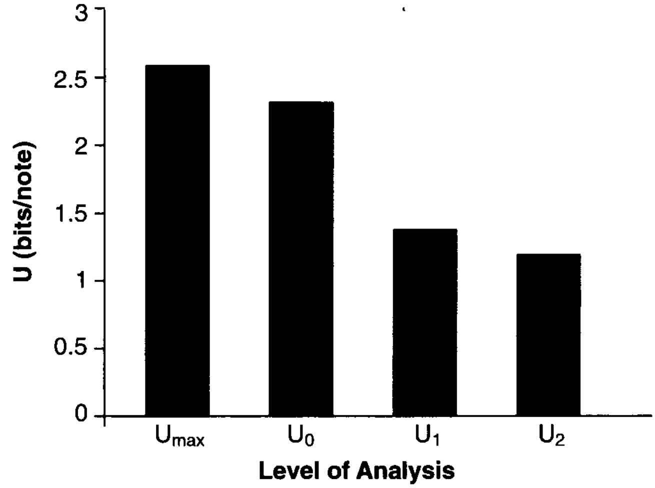

FIGURE 5. Syntax of calls shown by uncertainty measurements. A sudden reduction between U_0 and U_1 indicates a first-order Markov chain.

how a note will follow a given diad may be small but important (Table 3). The triads STE and TEE occur most frequently as well as the repetitions CCC and EEE. Some triads did not occur in our sample, and some diads were also very uncommon, indicating that all combinations are not equally probable and restrictions may occur for the formation of certain combinations.

TABLE 3. Frequency of second order transitions between notes in agonistic calls of Black-chinned Hummingbirds.

Preceding diad	Following note				
	C	Z	S	T	E
CC	180	9	82	21	1
CZ	0	3	4	4	0
CS	1	0	2	86	4
CT	4	0	6	7	4
CE	0	0	0	0	1
ZC	0	0	0	1	0
ZZ	1	0	0	2	0
ZS	0	0	1	45	2
ZT	1	1	0	7	8
ZE	0	0	0	0	2
SC	5	0	0	0	0
SZ	0	0	0	0	1
SS	1	0	0	4	0
ST	11	0	1	88	129
SE	0	0	0	0	29
TC	28	0	0	0	0
TZ	0	0	3	2	0
TS	2	0	0	9	18
TT	15	3	10	23	71
TE	1	0	0	1	215
EC	4	0	0	0	0
EZ	0	0	1	3	1
ES	0	0	0	10	7
ET	0	0	11	3	14
EE	3	5	21	33	560

CALL-TYPES AND OPENNESS

A call-type is defined as a specific sequence of notes. Brackets denote repetitions before the transition to the next note-type, so STEEEEE and STTEE are considered an [S][T][E] call-type. We recorded a wide variety of call-types with the sequence [S][T][E] occurring most frequently (61 times, or 19% of the data set). Table 4 shows other common call-types. Ninety-four call-types

TABLE 4. Common call types ($n = 320$ calls). Percent of total in parentheses. Call types that occur in less than 1% of the total are omitted. Brackets denote that a note-type may be repeated.

Call type	Frequency
[S][T][E]	61 (19)
[C][S][T][E]	46 (14)
[Z][S][T][E]	15 (5)
[C][S][T]	11 (3)
[S][T]	10 (3)
[S]	9 (3)
[C]	8 (3)
[Z][S][T]	8 (3)
[S][T][C]	7 (2)
[C][S][T][E][T][S][E]	6 (2)
[S][T][E][T][E]	6 (2)
[C][S][T][C]	5 (2)
[Z][T][E]	5 (2)

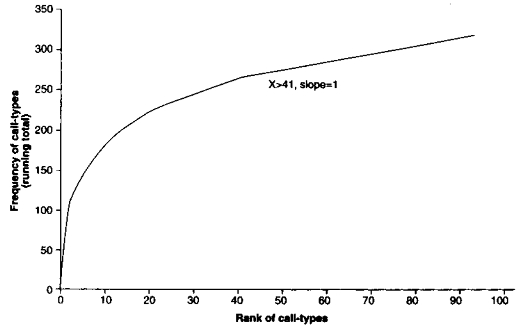

FIGURE 6. The frequency of call-types as related to rank of call-types ($n = 94$). As new calls are sampled, the number of new call-types increases showing openness. After the call-type ranked 41, a new call-type is found with every new sample.

occurred in a sample of 320 calls. Fifty-three call-types occurred only once.

Openness refers to a limitless formation of call-types. As the sample size of calls increases, new call-types are added to the system. This generative aspect can be illustrated by plotting the frequencies of call-types (running totals) against rank, or number of new call-type (Fig. 6). Call-types were sorted by frequency of occurrence. [S][T][E], the most common call type, was recorded 61 times in our data set and is graphed as the first call-type with a value of 61. [C][S][T][E], the second most common call-type, occurred 46 times and is graphed as the second call-type with a value of 107 (61 + 46). After call-type 41, each additional call-type occurs only once, giving the graph a slope of 1. A non-zero slope has an important implication in describing the nature of the call system. The system is generative or open; as more calls are sampled, new and increasingly rare call-types are encountered.

TEMPORAL AND GEOGRAPHIC STABILITY

We recorded the vocalizations over a two-year period at one site. Sonograms of nine calls made from recordings at Portal (Cochise Co.), AZ obtained in 1961 (Cornell University Library of Natural Sounds, Cat. No. RCS61-22) had the same note-types and sequences as represented in our data set.

DISCUSSION

Calls given by Black-chinned Hummingbirds during agonistic encounters are surprisingly complex. The acoustic structure of the five note-types that may be incorporated in these calls is diverse and includes white noise bursts (T note), trills (S and Z notes), and banded chips (C and E notes). The system is recombinatorial as calls are generated through the recombination of note-types. Notes are organized in calls in non-random patterns with ordering rules (syntax). The syntactical organization is based on high probabilities of certain note-types following a given note rather than on the place within a sequence based on position number. This means that notes do not have fixed positions within a call, although S and C notes often begin a sequence while E and C notes typically end sequences. The system can be described as open in that new call-types are added as more calls are sampled.

Typically, agonistic calls of passerines are not acoustically complex. In fact, one of the differentiating characteristics between the two vocal categories is that songs are usually more complex than calls (Thorpe 1961). While there is very little known about the songs used by Black-chinned Hummingbirds, the evidence that does exist suggests that the agonistic vocalizations are more complex than its songs.

Songs of hummingbirds have been divided into two categories (Wells et al. 1978). Static vocalizations are uttered when the bird is perched, while dynamic sounds occur in flight and often exhibits highly ritualized patterns. Unlike Anna's Hummingbird which uses both vocal categories, only one report exists concerning what is apparently a static song of the Black-chinned Hummingbird, described by Simmons (quoted in Bent 1940). No other reports exist despite considerable work on Black-chinned agonistic behavior (Ewald 1985, Ewald and Bransfield 1987, Stiles, pers. comm.; and pers. observ.), and this song may be very rare. Black-chinned Hummingbirds do have dynamic displays involving pendulum flights accompanied by vocalizations that are quite stereotyped in note composition. In these aerial displays, two types of notes differed acoustically (one a buzz, the other a short pure tone), but the sequence was a simple one of alternation unlike the complex combinatorial calls we describe here (Pytte and Ficken 1994).

Our findings suggest that a repertoire shift may have occurred accounting for the vocal differences between Anna's and the Black-chinned Hummingbird. The Black-chinned Hummingbird has a highly complex vocalization associated with agonistic interactions rather than a complex static territorial advertising song as in Anna's. Anna's, on the other hand, has simple agonistic calls consisting of many notes strung together to form a "chatter" consisting of an "undifferentiated series of buzzy notes" associated with chases (Stiles 1982). Perhaps this difference in agonistic vocal repertoires in the two species accounts for the findings of Ewald and Bransfield (1987) that Black-chinned Hummingbirds spent more time and energy in territorial defense, and had more invasions of their territories than Anna's. In Anna's Hummingbirds song is frequent and is apparently a territorial advertisement as shown by playback experiments conducted by Goldberg and Ewald (1991). This song may deter invaders, while Black-chinned Hummingbirds apparently lacking such vocalizations or employing them very rarely, may engage in more escalated conflicts involving fights and chases. Vocalizations are used during agonistic encounters but their role in affecting the outcome of the interactions, if any, is not known. Evidently, repertoires of different species of hummingbirds are organized in different ways. An unexplored area is the role of ritualized wing buzzing in agonistic interactions.

Numerous parallels occur between the general organization of Black-chinned Hummingbird agonistic calls and the *Chick-a-dee* calls of certain chickadees (*Parus* spp). Black-capped chickadees, *P. atricapillus* (Hailman et al. 1985), Mexican Chickadees, *P. sclateri* (Ficken et al. 1994), and the Black-lored Tit, *P. xanthogenys* (Hailman, in press) all have a recombinatorial system with a limited number of note-types (four or five, depending on the species), generating many different call-types. Syntax is more rigid in the first two species than in the Black-lored Tit. Openness occurs in the *Chick-a-dee* calls of all three parid species. Another parallel with the Black-chinned Hummingbird is that calls of the parids are organized in a fundamentally similar way based on a first order Markovian process.

Although great variety is generated by combinatorial elements, the number of possible sequences may be limited by various factors. Total call length may impose some limitations on call diversity. In Black-chinned Hummingbirds, note-types vary greatly in duration and longer calls (more notes in call) typically contain more short duration notes than calls that are comprised of longer note-types. Syntax may be another constraint on call diversity. In the Mexican Chickadee (Ficken et al. 1994) and the Black-capped Chickadee (Hailman et al. 1985) syntax is rigid and exceptions are very rare (less than 1% of Black-capped Chickadee *Chick-a-dee* calls have altered syntax). On the other hand, in some call systems a more flexible syntax may occur. Certain note sequences occur more commonly than others, but there is no rigid ordering. Such seems to be the case in the Black-chinned Hummingbird, and also in the Gargle vocalization of the Black-capped Chickadee (Ficken and Popp 1992). In both cases some note sequences are more common than others, and certain notes are more common at the beginning than the ending of the call.

Why should certain avian species, including the Black-chinned Hummingbird, produce so many call-types? In the case of the *Chick-a-dee* call of the Mexican Chickadee, it is possible that each of three more common note-types refers to locomotory tendencies (Ficken et al. 1994). Repetitions may relate to the strengths of those tendencies. Therefore, different call-types potentially encode different messages. However, the Gargle calls of Black-capped Chickadees are used in agonistic interactions and exhibit recombination of notes and syntax, but different call-types evidently have similar messages (Ficken et al. 1987).

Why are Black-chinned Hummingbird agonistic calls so complex both in acoustic structure and ordering rules? Several possibilities exist. (1) Perhaps each hummingbird has a complex repertoire, and sequence differences are products of individual variability. Testing this hypothesis would be difficult because the rapidity of interactions makes obtaining data on marked birds very difficult. (2) While no strong correlations among context and sequence were apparent in our study, this question deserves further attention using a broader variety of contexts. The fact that the Z-note was more commonly given by males indicates the possibility that certain note-types and/or sequences may be associated with subtle differences in contexts. (3) Call organization at the syntactical level could also be influenced by immediate social interactions. Trainer (1988) hypothesized that singing organization in Yellow-rumped Caciques (*Cacicus cela*) is influenced by such interactions. In Black-chinned Hummingbirds certain note-types, diads or even sequence lengths may be correlated with the intensity of the agonistic interactions and have a communicatory function, i.e., influence the behavior of the recipient. (4) Another possibility is that diversity of calls, rather than particular note-combinations, affects communication.

Additional studies of hummingbirds may show they rival passerines as subjects for vocal analysis, and many exciting questions remain about repertoires and the use of both mechanical and vocal sounds. Extending vocal analysis to some non-passerines may be important in determining if there are common underlying principles of organization of certain vocalizations, as is indicated by this preliminary comparison of agonistic calls of a hummingbird species and several species of the unrelated genus *Parus*.

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