Wilson Bull., 113(4), 2001, pp. 425–430

THE ORGANIZATION OF AGONISTIC VOCALIZATIONS IN RUBY-THROATED HUMMINGBIRDS WITH A COMPARISON TO BLACK-CHINNED HUMMINGBIRDS

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ABSTRACT.—We describe vocalizations of Ruby-throated Hummingbirds (*Archilochus colubris*) recorded during agonistic confrontations at feeders. Calls were composed of 1–5 different note types. A sixth distinct note type, the W note, was not given within a call sequence. Similar to those of Black-chinned Hummingbirds (*Archilochus alexandri*), Ruby-throated Hummingbird calls were complex, and exhibited a nonrandom organizational pattern as analyzed using a Markov model. The two closely related yet allopatric species shared similarities in the acoustic structure of note types, syntax, and call length. Slight differences occurred in the opening note types of calls in the two species. We investigated how vocalizing is associated with the outcome of encounters at a feeder and found that the vocalizer usually was the winner. *Received 26 Feb. 2001, accepted 15 Feb. 2002.*

Despite having the largest geographic range of any North American hummingbird (Robinson et al. 1996), and being a common feeder visitor in many areas, little is known about the vocalizations of the Ruby-throated Hummingbird (*Archilochus colubris*), and there are no sonagraphic studies of their vocalizations. Pitelka (1942) described their agonistic vocalizations: ‘‘Clashes and chases were accompanied by squeaks and high-pitched chatters which were more intense than the chatter given during ordinary flight.’’ While there is a scarcity of information on Ruby-throated Hummingbird sounds, agonistic vocalizations of its western counterpart, the Black-chinned Hummingbird (*Archilochus alexandri*), have been analyzed in detail (Rusch et al. 1996). Their calls are complex, consisting of an array of five note types arranged in a nonrandom pattern.

Similar to Black-chinned Hummingbirds, Ruby-throated Hummingbirds exhibit many different behavioral patterns associated with aggression at feeders supplied with sugar water. When more than one bird is at a feeder, agonistic interactions typically occur. Chases are frequent, vary in intensity and duration, and may be silent or accompanied by vocalizations and/or wing buzzes (M.S.F. pers. obs.). Face-to-face hovering with vocalizations and tail spreading is another agonistic behavior (K.T. pers. obs.). More rarely, physical contact is made with the wings or bill.

After performing sonagraphic analyses of vocalizations given by Ruby-throated Hummingbirds during agonistic encounters at feeders, our objectives were as follows: (1) describe the acoustic structure of note types, (2) determine the organization of note types within individual calls using sequential analyses, (3) describe the context associated with the calls, and (4) compare the agonistic vocalizations of the Ruby-throated Hummingbird with the Black-chinned Hummingbird.

STUDY AREA AND METHODS

We recorded Ruby-throated Hummingbirds at feeders at two sites in Wisconsin during July and August of 1997 and 1998. The southeastern Wisconsin site is the Univ. of Wisconsin-Milwaukee Field Station (Ozaukee County; 43° 25′ 53″ N, 88° 02′ 51″ W). All of the contextual data were obtained at this site because the number of hummingbird visits was low enough to record both vocalizations and behaviors of two individuals, as typically no more than two individuals were near a feeder simultaneously. The second site (Bayfield County; 46° 19′ 35″ N, 91° 17′ 46″ W) is approximately 400 km north of Ozaukee County. We recorded and observed individuals throughout the day with most recordings made during early morning or just prior to sunset. We undoubtedly sampled many individuals, as our data were collected over several weeks at each site. It was impossible to monitor indi-

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vidual birds except to identify a caller and its behavior compared to the behavior of the other bird during a single interaction. As a conservative estimate during one recording session, at least eight different individuals were noted simultaneously at Ozaukee, while 12 individuals were noted simultaneously at the Bayfield site. Because hatching year males are quite similar to females in plumage during late summer, especially when moving rapidly, we did not distinguish the sexes. Agonistic calls were given by both sexes, and a previous study of the Black-chinned Hummingbird showed no sex differences in frequencies of usage of the note types in calls (Rusch et al. 1996). A total of 286 vocalizations was analyzed (Bayfield: $n = 216$; Ozaukee: $n = 70$).

We recorded the outcome of agonistic encounters, with an individual considered a winner if it successfully ousted another bird from the feeder area. We noted if the encounters with agonistic calls were chases of $\geq$10 m or hovers, and if the vocalizing bird was present prior to the appearance of the second bird or if the vocalizer was the intruder. Because usually no more than two birds were present at the feeder at one time and the observer was using a directional microphone while seated about 3 m from the feeder, it was possible to follow interactions.

Recordings were made using Sony Professional Walkman cassette recorders, and an Audio Technica directional microphone for the Ozaukee site and a Nakamichi directional microphone for the Bayfield site. First, we analyzed recordings using a Kay Elemetrics Digital Sona-Graph 7800 with a 16-kHz frequency range and a 300-Hz filter in order to identify and catalog note types. Following the methods of Rusch et al. (1996), note types were categorized by visual examination as well as measurements of frequency and duration. Identification of note types was made independently by three different observers, one of whom had never seen this type of call previously. Sequence of the note type in a call was not a consideration in its identification. Once note types were determined, agonistic calls were analyzed using Avisoft Sonagraph Pro Windows ver. 2.5 software. We defined an agonistic call as a note or a series of notes that occurred >0.2 s after another call. Calls were distinct, as most internote intervals were <0.2 s.

We examined the sequence of note types within a call using a computer program that indicates the frequency and probability of first and second order Markov sequences. A first order Markov sequence refers to the probability of one note following another (diad level), and a second order Markov sequence deals with one note following two others (a triad). In the rare cases where note types were fused, the note type was split and counted as two individual notes. Statistical values are presented as mean ± SD. All *t*-tests are two-tailed. *P* values <5 are considered significant.

RESULTS

Note types.—Sonagrams of six distinct note types as well as their frequency and temporal characteristics are presented in Fig. 1 and Table 1. The note types were named after their similar counterparts in the agonistic call system of Black-chinned Hummingbirds (Rusch et al. 1996). Our data set consisted of 230 Z notes (11% of all notes given), 277 S notes (14%), 375 T notes (19%), 1005 E notes (50%), 129 C notes (6%), and 37 W notes (1%).

The Z note (Fig. 1A) consists of two narrow bands separated by approximately 6 kHz and sloping together at the end of the note, giving a ''zzzzip'' sound. Energy is concentrated in the lower frequency band (6.5–7.5 kHz) and in many cases only the lower band is recorded due to degradation in the high frequency band. This note may occur alone or with other note types in a call and, rarely, fuses with the S note. The Z note is the longest in duration of all the note types that comprise agonistic calls.

The S note (Fig. 1A) is a wide band of modulated frequencies and is given alone or within a call. In 20 of 277 (7%) occasions, the S note was fused with a T note.

T notes (Fig. 1A) are broad band ''click'' sounds. As is the case with E notes, T notes always occur with other note types in a call.

The E note (Fig. 1A) is similar to the C note; both are composed of bands and cover a comparable frequency range. The slope of the main energy band is −156 kHz/ms ± 81 SD ($n = 7$), giving a different tonal quality to the E sound. The E note always occurs in a call sequence with other note types, unlike the C note.

C notes (Fig. 1B) are comprised of 4–6 frequency bands. Peak energy distribution lies between 5 and 7 kHz, and the mean slope of the highest energy band is −135 Hz/ms ± 22 SD ($n = 7$). C notes usually are given at the beginning of an agonistic call sequence. This note type also may be given as a single note, or as strings of doublets or triplets, and they are given in flight or while perched.

The W note (Fig. 1C), the rarest note type, is not given within an agonistic call sequence. The note structure resembles a white noise burst and sounds like a nasal ''zeeep.'' The W note, longest in duration of all the note types, is given either alone or with another W note.

Call organization.—A typical call consists of one to several note types, and often includes some repeating note types. The number

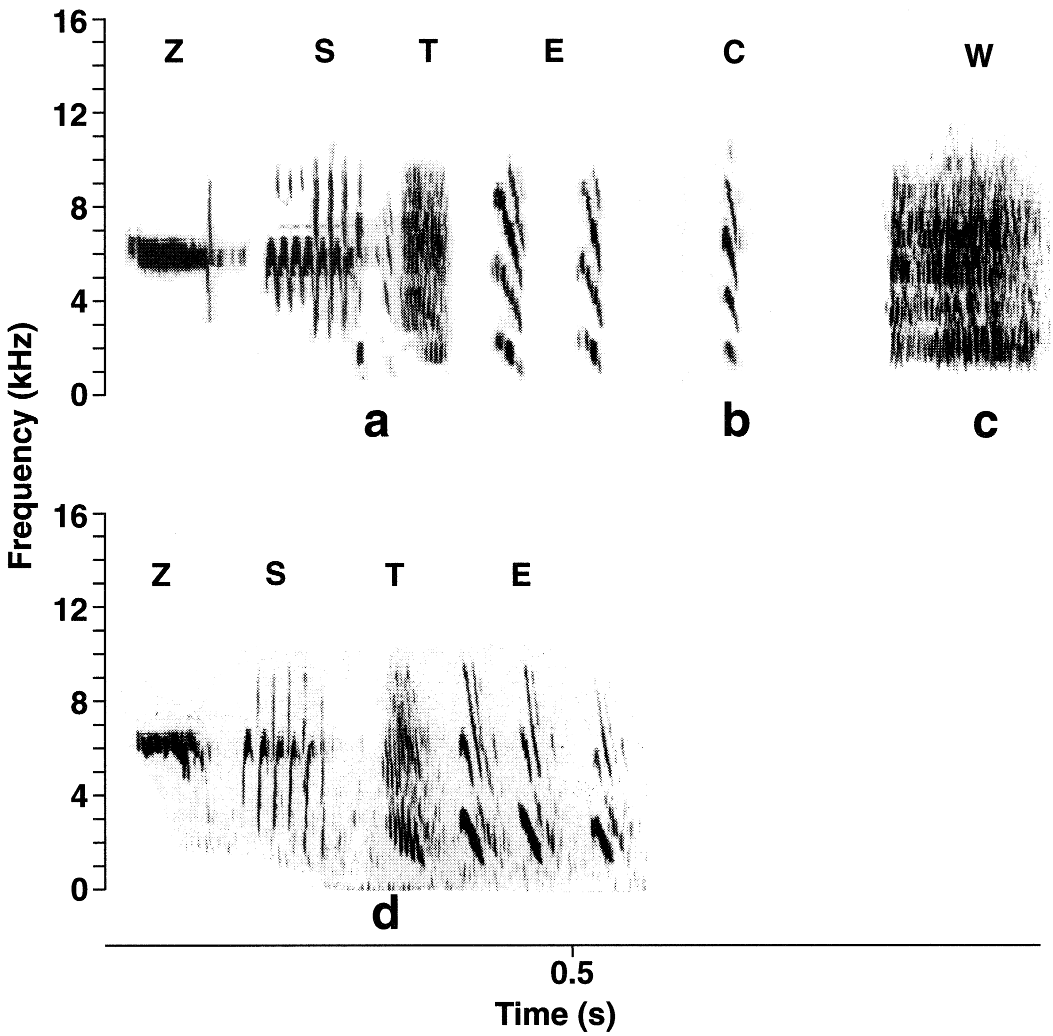

FIG. 1. Structure of note types of Ruby-throated (A–C) and Black-chinned (D) hummingbirds. (A) An agonistic call showing four note types: Z, S, T, and E. (B) C note. (C) W note. (D) An agonistic call of the Black-chinned Hummingbird, with note types that probably are homologous to those of the Ruby-throated Hummingbird. Ruby-throated Hummingbirds were recorded in Wisconsin, 1997–1998; the Black-chinned Hummingbird was recorded in Arizona, 1994. Sonagrams were produced on a Kay 7800 Sona-graph with a 300-Hz bandwidth filter.

TABLE 1. Measurements of note types in calls of Ruby-throated Hummingbirds (mean ± SD). Data are from Wisconsin, 1997–1998.

Note type	Acoustic structure	*n*	Duration (ms)	Lowest frequency (kHz)	Highest frequency (kHz)
C	Short, banded	25	20 ± 23.0	2.2 ± 0.6	9.1 ± 1.0
Z	Long, trill	25	84 ± 23.0	6.8 ± 0.6	7.5 ± 0.7
S	Long, trill	25	65 ± 24.0	3.5 ± 1.1	11.9 ± 1.8
T	Noise burst	25	42 ± 13.0	2.5 ± 0.4	10.4 ± 1.4
E	Short, banded	25	17 ± 4.0	2.2 ± 0.3	10.3 ± 1.3
W	Long, burst	12	107 ± 27.0	1.6 ± 0.2	9.8 ± 0.9

TABLE 2. Probability of occurrence of two-note (diad) combinations (n = 286) of note types in the calls of Ruby-throated Hummingbirds. Silence to silence transition is an undefined state. Data are from Wisconsin, 1997–1998.

Preceding note type:	Following note type: Silence	C	Z	S	T	E
Silence		0.16	0.71	0.10	0.03	0.00
C	0.02	0.59	0.13	0.19	0.05	0.03
Z	0.18	0.02	0.00	0.63	0.14	0.02
S	0.03	0.01	0.00	0.00	0.81	0.15
T	0.09	0.00	0.01	0.09	0.05	0.76
E	0.20	0.00	0.01	0.05	0.08	0.66

of note types per call ranged from 1–19 (mean = 6.87 ± 3.89 SD, n = 286).

To describe note transitions, we used a first order Markov model that shows the probability of occurrence for each diad (one note type following another). Diads for notes in all calls did not occur at random (χ^2 = 1124, df = 25, $P < 0.0001$; Table 2). Using transition matrices (Table 2), we created a kinematic diagram that represents the sequence of notes in calls (Fig. 2). The typical syntax of the diads was as follows: Z most often began a call and usually was followed by S, S was most often followed by T, T by E, and E by E. E usually ended the call and was the most frequently occurring note type. C typically occurred at the beginning of a call, and E and C notes commonly were given in repetitive strings of notes within a call.

To further examine syntax, we used a second order Markov model that predicts the probability of triads (one note type following a diad). The five most common triads were CCC, EEE, TEE, STE, and ZST. With 125 potential triads, 74 (60%) triads did not occur at all.

Contextual data.—We tested the hypotheses that vocalizing is associated with the outcome of encounters, prior residency at the feeder, and with the type of agonistic contest. In 39 of 41 encounters (95%), the caller was the winner of the encounter near the feeder. In some cases we were able to determine which individual had arrived first (the resident) at the feeder. The bird that vocalized was the resident in 19 of 27 (70%) of these cases. When calling occurred, the bird that vocalized

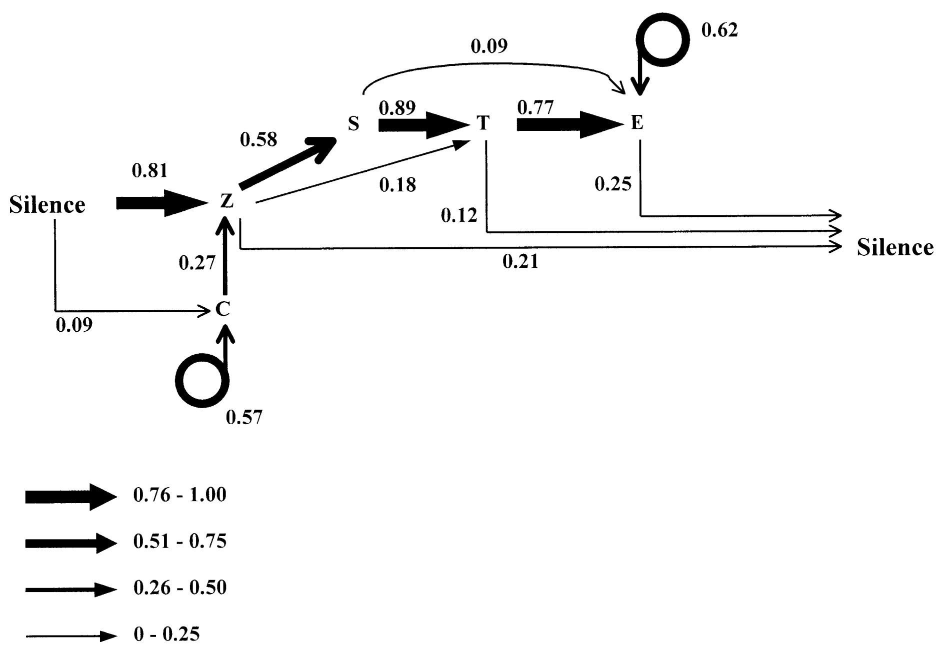

FIG. 2. Kinematic diagram showing first order transitional probabilities among note types in the calls of Ruby-throated Hummingbirds in Wisconsin, 1997–1998. This figure utilizes data from Table 2 for Bayfield County only (n = 216 calls) and is a visual presentation of sequences of note types indicating the relative frequencies of transitions. Transitions occurring <9% of the time have been omitted.

chased the intruder rather than having a contest involving hovering in 19 of 20 (95%) contests. The W note type, when it occurred, was always given by the winner ($n = 11$).

Species comparisons.—Acoustic structure of note types, call length, and syntax in calls of Ruby-throated Hummingbirds were compared with findings from our previous study of Black-chinned Hummingbirds (Rusch et al. 1996). All five note types that occur within a call sequence were found in both species and showed similar frequency bandwidth but some differences in duration. A typical Black-chinned Hummingbird call with four of the five note types revealed structural similarities (Fig. 1D). The E and the S notes were of shorter duration in Ruby-throated Hummingbird calls ($t = 3.53$, df = 50, $P < 0.001$, and $t = 3.51$, df = 51, $P < 0.001$, respectively). The W note, which also is given by Black-chinned Hummingbirds (M.S.F. pers. obs.), was not described in our previous study, as it is not a component of call sequences.

Ruby-throated Hummingbird calls were shorter than Black-chinned Hummingbird calls with a mean of 6.87 ± 3.89 SD notes/call ($n = 286$) versus 7.72 ± 2.77 notes/call ($n = 320$; $t = 3.06$, df = 606, $P = 0.002$). Ruby-throated Hummingbird calls ranged from 1–19 notes, while Black-chinned Hummingbird calls ranged from 1–18 notes per call.

In comparison to Black-chinned Hummingbirds ($n = 320$ calls), Ruby-throated Hummingbirds ($n = 286$ calls) used fewer C notes, more Z and E notes, but were similar in the percentage of S and T notes. Variations in note use for the two species typically occurred at the beginning of a call sequence. Ruby-throated Hummingbirds were less likely to begin a call with a C note than Black-chinned Hummingbirds (16% versus 41%, respectively), but were more likely to begin with a Z note (71% versus 8%, respectively). All the common note transitions were similar in both species; C was most often followed by C, S by T, T by E, E by E, and E usually ended the call. The four most common triads also were similar in both species: EEE, CCC, TEE, and STE, while other triadic combinations did not occur in either species.

DISCUSSION

Ruby-throated Hummingbirds produce agonistic vocalizations that surpass those of some oscines in complexity. The five note types comprising agonistic calls are varied in acoustic properties of duration and frequency range. Some notes have high frequency components that range above 10 kHz. Note types are very different as some are trills, others have complex banding, and one, the Z note, is almost a pure tone. Notes are organized into calls in nonrandom sequences with specific note types having high probabilities of being followed by other note types. Thus, these hummingbird calls exhibit a recombinant system with syntax. As far as is known, these agonistic calls are the most complex vocalizations in the species' repertoire.

Agonistic calls were more frequent in some contexts than others. Unfortunately, we were not able to test the association of particular call types with types of encounters, but some general patterns emerged. Winners called more frequently than losers in confrontations. The first bird that arrived at the feeder was more likely to be the winner, often calling and chasing a newcomer. Hovering was more likely when two birds arrived simultaneously. The W note, unlike other note types was not part of a sequence, and was given only by winners in our sample. This note, also given by the Black-chinned Hummingbird, has a harsh quality. The acoustic quality of this note agrees with the conclusion of Morton (1977) who studied a variety of species and found that harsh sound signals indicate that the sender is highly aggressive. Winners of encounters in many species of hummingbirds give very similar calls (M.S.F. pers. obs.). A single C note or a short series of this note may be given by a lone bird and are not associated with agonistic encounters unless combined with other note types. Perhaps C is an announcement of presence, deterring approaches. Such short, single notes are given by many species of hummingbirds in similar contexts (M.S.F. pers. obs.).

Pitelka (1942) observed that there was a higher degree in intensity of the agonistic calls associated with clashes compared to the intensity of flight calls given by lone birds, and we now are able to discern the difference through sonagraphic analysis. Agonistic calls associated with clashes and chases contain up to five note types, producing the intense ''chatter'' quality, while flight calls not associated with antagonism are simple, ''squeaky'' strings of C notes.

Short range signals may be complex in that they incorporate structural diversity as well as syntactical composition. Short range communication systems with these attributes are found in Black-capped Chickadee (*Poecile atricapilla*) gargle calls (Ficken and Popp 1992), and possibly Blue-fronted Amazon (*Amazona aestiva*) guttural calls (Fernandez-Juricic and Martella 2000). Further studies may show that they are widespread in the calls of other bird species.

The agonistic calls of Ruby-throated Hummingbirds and Black-chinned Hummingbirds show many similarities in acoustic structure of note types, call length, and syntax. The similarity of the congeners is not surprising, as a mitochondrial DNA analysis (Baltosser and Russell 2000) indicated that the two species are remarkably similar, differing in only about 2% of the base pairs of the seven genes studied. However, detailed analyses of courtship sounds, wing sounds, and postures remain to be studied and may prove to be more divergent.

ACKNOWLEDGMENTS

We are grateful to the staff of The Univ. of Wisconsin-Milwaukee Field Station for facilitating our recording of Ruby-throated Hummingbirds, and we thank the staff of Ramsey Canyon Preserve (Arizona Nature Conservancy) for use of facilities for recordings of Black-chinned Hummingbirds. We thank R. Lange, R. Sargent, and an anonymous reviewer for their helpful comments on the manuscript.

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