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BLUE-THROATED HUMMINGBIRD SONG: A PINNACLE OF NONOSCINE VOCALIZATIONS

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ABSTRACT.—Little is known about the structure and function of hummingbird vocalizations. We studied the vocalizations of Blue-throated Hummingbirds (*Lampornis clemenciae*) at two sites in southeastern Arizona. Songs were produced by males and females. Male songs consisted of arrays of notes organized in clusters of “song units.” Within sites, all males shared the same song units. Individual differences occurred in some temporal aspects of song, and slight but consistent differences in note structure occurred between the two sites. The organization of units within songs was marked by rigid syntax, and long songs were produced by agglutination of units. Male songs may function in territorial advertisement and mate attraction. Female songs were very different acoustically from those of males and typically were given when females were within a few centimeters of a male. In these situations, the female’s song often overlapped temporally with the male’s song. Of the hummingbird species studied so far, the Blue-throated Hummingbird has the most complex songs and is the only known species with complex female songs. Blue-throated Hummingbirds show convergence with oscines in vocal complexity, song organization, song function, and possible learning of some song elements. Received 25 June 1998, accepted 10 May 1999.

MOST SPECIES OF HUMMINGBIRDS are characterized by marked plumage dimorphism, polygyny, and lack of paternal care (Schuchmann 1999). Consequently, sexual selection would be expected to exert a strong influence on courtship and agonistic behavior. Although sexual selection plays an important role in the evolution of oscine song (Catchpole and Slater 1995), in hummingbirds attention has focused almost exclusively on visual signals, because many species perform complex display flights (Wagner 1954). Hummingbird vocalizations are sometimes portrayed as mere “squeaks,” assessments that probably contribute to lack of interest in detailed analysis of hummingbird sounds. Some recent studies, however, indicate a high degree of vocal complexity, and in some cases vocal learning and dialects (Gaunt et al. 1994).

The Blue-throated Hummingbird (*Lampornis clemenciae*) inhabits wooded canyons in the Chisos Mountains of Texas, the mountains of southwestern New Mexico and southeastern

Arizona, and most of Mexico west of the Yucatan Peninsula. It is the largest hummingbird that breeds in the United States, and males have iridescent blue throats that are absent in females.

In contrast to many North American hummingbirds, aerial courtship displays have not been observed in the Blue-throated Hummingbird (Wagner 1954). Therefore, we anticipated that vocalizations would be particularly important in this species’ behavior, perhaps having a dual role of territorial advertisement and mediating interactions with females (i.e. similar to the functions of oscine song). Wagner (1954) distinguished two kinds of vocalizations, songs and calls, and indicated that both are involved in reproductive activities in Blue-throated Hummingbirds. However, no detailed descriptions of vocalizations (and no sonograms) have been published for the species. Wetmore (1932) reported that these hummingbirds often utter “sharp, squeaking calls,” and that males have “. . . a simple song of three or four notes, repeated at short intervals” Blue-throated Hummingbirds have several calls and exaggerated postures and displays associated with agonistic behavior (unpubl. data), but here we deal with vocalizations that

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may be termed "songs" because of their structural complexity and the contexts in which they are used.

Our objectives include a description of acoustic structure and organization of song, analysis of behaviors associated with singing to assess usage and possible functions of song, and examination of acoustic structure of two populations to determine whether microgeographic differences occur. We also make qualitative comparisons of songs of Blue-throated Hummingbirds with those of other hummingbird species and with oscines.

METHODS

We conducted the study at two sites in Cochise County, southeastern Arizona, that are about 150 km apart: the Southwestern Research Station (SWRS) in the Chiricahua Mountains, and Ramsey Canyon (RC) in the Huachuca Mountains. Both sites have numerous hummingbird feeders distributed in both clumped and dispersed patterns. Blue-throated Hummingbirds also occur away from feeders, but almost all of our recordings were made within 10 m of feeders. All males from which songs were recorded were actively defending territories. The presence of feeders may have increased the amount of aggression and perhaps singing rates, but feeders probably did not affect the aspects of song that we studied.

We recorded songs of two males at RC in April, one in 1995 and one in 1997. The birds were unmarked but probably were different individuals because of the distance between sites. We recorded sequences of songs from these males over several days after the onset of territorial establishment. Four males were recorded at RC in late August, one in 1995 and three in 1997.

We recorded the songs of four males at SWRS in May 1995 and 1996. Three of them had distinctive color marks on the dorsum, and an unmarked male was identifiable because it sang from a specific perch. In late June to August 1996 at SWRS, DRP and SJT recorded six color-marked males, and MSF obtained recordings of a recently fledged bird in 1998.

Whenever possible, we recorded bouts of singing. A bout began with the first song and terminated when a bird flew or ceased singing. Pauses between bouts were always much longer than inter-song intervals within bouts. We also noted the rare occasions when a female was present, and whether the singing preceded or followed an agonistic encounter.

MSF and KMR used a Sony Professional Walkman WM-D6C and Audio-technica AT877 microphone and analyzed recordings with a Kay 7800 Sonagraph (8 kHz with 150-Hz filter, others at 16 kHz with 300-Hz filter for estimates of higher frequencies); mea-

surements were made on sonograms with a ruler. SJT and DRP used a Sony TCM-5000 EV cassette recorder, a Saul Mineroff BA-3 Nature Amplifier, and Sennheiser ME66 and K6 microphone modules; recordings were digitized on a Macintosh using Soundedit 2.0.3. This system was used with Canary software to determine differences among individuals in temporal aspects of A and B song units.

RESULTS

Based on both acoustic structure and usage, Blue-throated Hummingbirds have two song types. Type 1, given only by males, is much more common than type 2, which apparently is uttered only by females.

Behavior associated with singing.—Blue-throated Hummingbirds are most active at low light levels, and longer bouts of singing are more prevalent early in the morning, with a second peak in the evening during spring. However, especially during the height of the breeding season, singing occurs at other times of day. Dawn singing may be interspersed with "patrolling," i.e. flying back and forth along a creek.

Songs are given when perched and occur in a variety of contexts such as immediately after foraging, preceding or following agonistic encounters, and following preening (an activity often associated with protracted rest periods). Unlike many oscines, the bill is never opened during singing. Song often is delivered at very low amplitude. Postures associated with singing are variable. Sometimes the head is tilted slightly upward as in a normal resting posture, and the only indications of singing are very slight movements of the throat. Alternatively, the bird may lean forward with its bill only slightly elevated from horizontal; throat movements are more pronounced than when songs are delivered from the resting posture, and the songs seem louder. Perched birds often spend a great deal of time scanning, but the head is not turned during singing.

Song phenology.—Males begin singing by mid-April, and the onset of singing is associated with territory establishment that involves much chasing of other males. Singing seems to increase during May (and possibly early June, which was not sampled) and decreases in July and August. We observed the initial arrival and singing behavior of two males at RC. In one case, a new male that had just established

perches near a feeder defended his feeder against other Blue-throated males and against male Magnificent Hummingbirds (*Eugenes fulgens*). Initially, he sang very muted songs when he returned to the perch and uttered many short trills with a staccato quality similar to the B unit of type 1 song (Fig. 1A), but the units were much shorter and louder than B units. He began singing short type 1 songs after several hours, and by the next day he was singing typical type 1 songs in bouts.

The second case occurred when a male moved into an area with new feeders. Although males visited the new feeders, we saw no evidence of defense by a single male for several days. On the third day, one male began perching within 5 m of the feeder. He gave an occasional song and started defending the feeder. The following day, he gave longer bouts with longer songs, and on one occasion a female approached to within a few centimeters during his singing.

Many different sounds and visual displays occur during encounters between males. Here, we mention only those that are acoustically similar to song elements. In 14 cases during aerial encounters between males, one male gave loud B units (the same as those reported in territory establishment; see Fig. 1A). In four other cases when a perched resident male was approached by a conspecific male, he gave protracted B units without other accompanying song units. These are the only times when B units were not combined with other song units.

Acoustic structure of type 1 song.—Songs are composed of five units. Each unit was assigned a letter (A through E; Fig. 1A) based on its note composition. Note composition within units was consistent in both acoustic structure and order except for rare cases where the terminal unit lacked the last one or two notes. The note structure is remarkably stereotyped, and visual inspection of sonograms revealed no de-

tectable differences among individuals. Many notes are somewhat ill defined (i.e. fuzzy on sonograms), even under the best recording conditions.

The acoustic structure of the song units is very diverse. All units except for B, a rapid trill, are a mixture of notes, some covering a wide range of frequencies. The frequency range was from about 1.8 to 14 kHz (highest frequencies were 10 kHz for B; 12 kHz for E; and 14 kHz for A, C, and D). Most of the sound energy is concentrated below 10 kHz. A, B, C, and D units are very similar in length, as are the intervals between units (Table 1). Unit E is shorter than the others, and the interval between D and E is also shorter (Table 1). Because all songs consist of combinations of the same basic units, we were able to measure individual units to assess the length of songs that were composed of different arrays of units. Song length varied considerably: the shortest song (a single A) lasted 0.36 s, and the longest song (ABCDEBCDEBCDEABCDE) lasted 8.29 s.

Individual differences in duration of A and B units.—Significant differences occurred among individuals in some temporal attributes of songs (Table 2). Total song length, duration of B, and duration of the slur note of A did not vary among individuals, but significant differences occurred in duration of the A unit and duration of the interval between A and B. Songs analyzed in Table 2 occurred later in the season when most songs consist solely of A and B units, perhaps accounting for measurement differences shown in Tables 1 and 2.

Microgeographic patterns.—Some features of songs were highly similar at RC and SWRS, but other aspects differed between the two sites. We did a fine-grained examination of the notes from the two sites using songs recorded at RC from one bird in April and four in August. Although some August songs included some undifferentiated notes, for this comparison only

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FIG. 1. (a) Type 1 song units from a male Blue-throated Hummingbird recorded at the Southwestern Research Station (SWRS). Numbers indicate where measurements were taken for Table 2. (b) D unit from Ramsey Canyon (RC); compare with D unit from SWRS in (a). (c) A unit from RC; compare with A unit from SWRS in (a). (d) Type 2 song given by a female Blue-throated Hummingbird near a male. (e) Song of a male from RC in August showing undifferentiated notes organized in song units. Song units are separated by dots and denoted by uppercase letters above the x-axis. Sonograms produced on Kay 7800 Sonagraph on 150 Hz filter setting. Although some notes in type 1 songs have components above 8 kHz, sonograms were made on 8kHz scale for illustrative purposes.

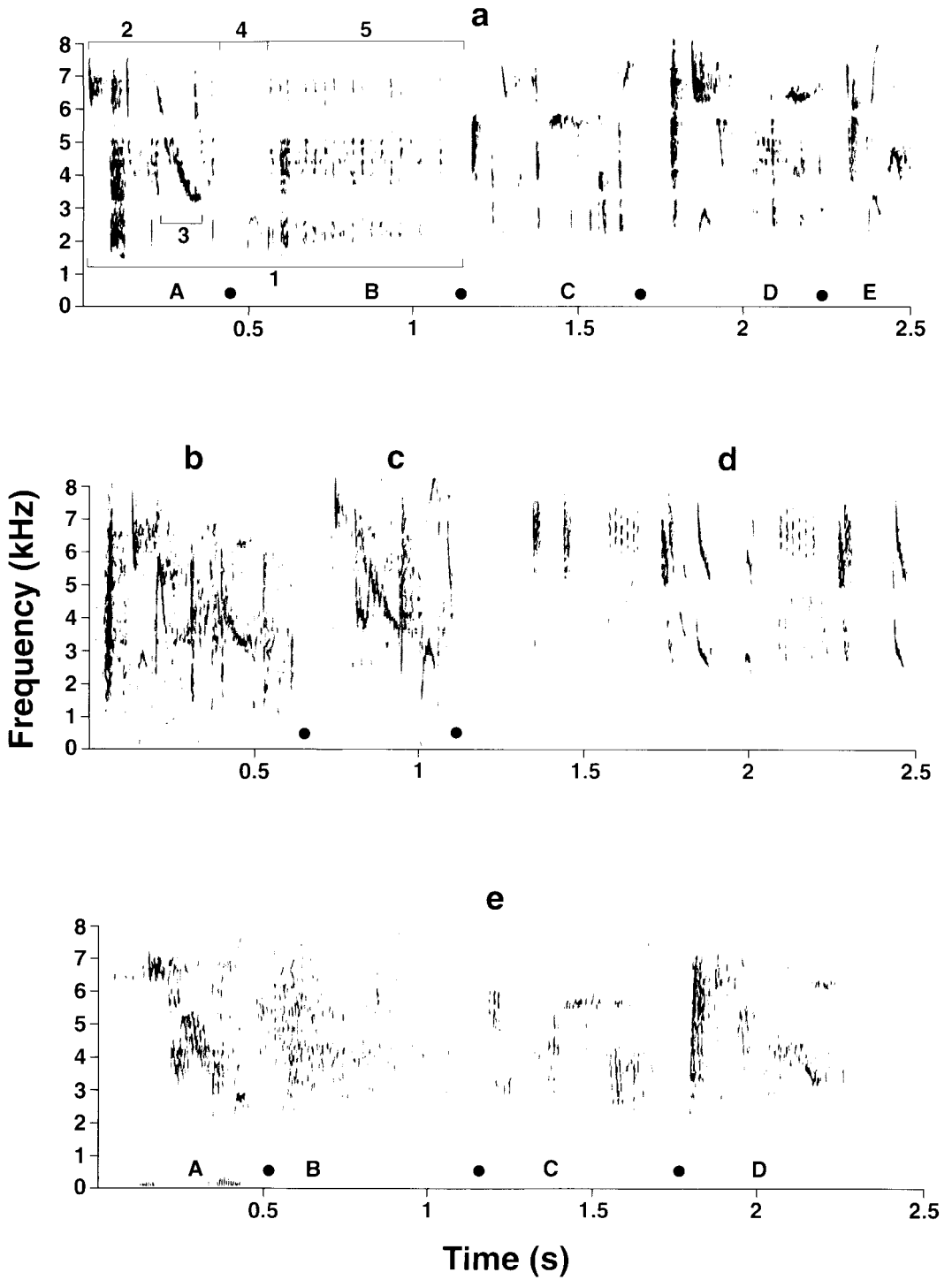


TABLE 1. Duration (in s) of the various units (A, B, C, D, E) and inter-unit intervals (A-B, B-C, C-D, D-E) in type 1 songs recorded from two male Blue-throated Hummingbirds (R and L) in May at the Southwestern Research Station. Intervals are measured from end of one unit to the beginning of the next. Values are $\bar{x} \pm SD$, with number of sonograms measured in parentheses.

Song units and intervals	Individual R	Individual L
A	0.37 \pm 0.02 (9)	0.34 \pm 0.01 (5)
A-B	0.16 \pm 0.01 (7)	0.17 \pm 0.02 (4)
B	0.43 \pm 0.09 (14)	0.53 \pm 0.04 (4)
B-C	0.20 \pm 0.03 (9)	0.16 \pm 0.02 (4)
C	0.44 \pm 0.01 (9)	0.44 \pm 0.01 (5)
C-D	0.15 \pm 0.01 (8)	0.14 \pm 0.02 (4)
D	0.45 \pm 0.01 (7)	0.41 \pm 0.02 (5)
D-E	0.09 \pm 0.01 (9)	0.08 \pm 0.01 (4)
E	0.19 \pm 0.03 (8)	0.15 \pm 0.01 (5)

August songs from birds that produced song units typical of those earlier in the season were analyzed. All nine individuals from SWRS were consistent in all of the fine details of the notes within each song unit, and all RC birds were identical to each other. Furthermore, consistency persisted in both populations over the two-year period sampled at each site.

The fine structure of all units except for B was examined at the two sites. B was omitted from this analysis because it is a simple trill, and the length varies considerably even within individuals. We detected no difference between sites in C units, even though C units are acoustically complex. D units from RC had some notes that were omitted at SWRS (Fig. 1B). A slight difference may occur in a very short note in the E units at the two sites. The major difference between sites was in the A unit, typically the introductory part of the song. The sec-

ond note of the A unit of all SWRS birds was a broad-band transient (i.e. straight line on sonogram) that had a harsh quality; a downward slur occurred in the middle of the unit. The harsh note was lacking at RC, and the downward slur showed a marked zigzag pattern (Fig. 1C) that was indicative of rapid frequency modulation (an acoustic pattern otherwise lacking in Blue-throated Hummingbird songs).

Analysis of song organization.—All individuals in both populations used all five song units, and the same units with minor variations occurred in both populations. The shortest songs consisted of a single unit. When a single A was given, it may have been part of a longer series of other songs, but a single B was only associated with agonistic encounters. A single C was given only once. The other song units (D and E) were not given as single units. The number of units given per song ranged from 1 to 18.

Song units occurred in nonrandom order, as assessed using a first-order Markov model. Of 25 possible song-unit combinations, only five occurred frequently (comprising 97% of all dyadic transitions): AB, BC, CD, DE, and EB. Ten combinations never occurred. Syntax did not vary significantly for the frequency of transitions of the five commonly occurring two-unit song combinations for four individuals ($n = 242$ songs) at SWRS ($\chi^2 = 6.38$, $df = 12$, $P = 0.91$). A kinematic diagram shows the probabilities of transitions of units for four individuals (Fig. 2). Most songs began with A and ended with any of the following units: B, C, D, or E. Second-order transitions involving three-unit strings showed syntax rigidity, with only five commonly occurring strings (ABC, BCD, CDE, DEB, and EBC) out of 125 possible combinations.

TABLE 2. Duration of song components (in s) of six male Blue-throated Hummingbirds recorded at the Southwestern Research Station in July 1996. Values are $\bar{x} \pm SD$, with number of sonograms measured in parentheses. Figure 1A indicates how measurements were made (1 = total song length of AB, 2 = A unit, 3 = slur note complex of A unit, 4 = interval between A and B units, 5 = B unit).

Male	Total song	A unit	Slur note of A	A-B interval	B unit
RVO (5)	1.21 \pm 0.24	0.29 \pm 0.13	0.14 \pm 0.02	0.24 \pm 0.09	0.58 \pm 0.13
Y (16)	1.39 \pm 0.09	0.53 \pm 0.08	0.16 \pm 0.04	0.26 \pm 0.07	0.61 \pm 0.08
UNb (5)	1.27 \pm 0.20	0.37 \pm 0.06	0.14 \pm 0.03	0.21 \pm 0.07	0.68 \pm 0.15
UNs (6)	1.52 \pm 0.16	0.45 \pm 0.03	0.14 \pm 0.03	0.38 \pm 0.10	0.58 \pm 0.16
RY (13)	1.41 \pm 0.23	0.44 \pm 0.07	0.13 \pm 0.03	0.28 \pm 0.11	0.70 \pm 0.11
OYR (4)	1.33 \pm 0.08	0.41 \pm 0.04	0.15 \pm 0.02	0.15 \pm 0.02	0.62 \pm 0.05
Overall	1.35 \pm 0.17	0.42 \pm 0.07 ^a	0.14 \pm 0.03	0.27 \pm 0.08 ^a	0.63 \pm 0.11

^a Values significantly different among individuals (ANOVA, $P < 0.05$).

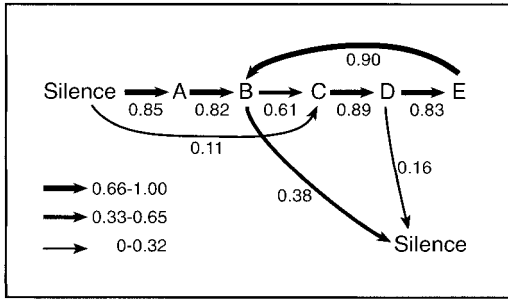


FIG. 2. Kinematic diagram showing transitional probabilities among song units. Each transitional probability is a median value for four individuals. Probabilities less than 0.1 have been omitted. The ranges for each transitional probability are: AB, 0.65 to 0.92; BC, 0.53 to 0.71; CD, 0.85 to 0.97; DE, 0.77 to 0.85; and EB, 0.84 to 1.00.

We also examined syntax at higher levels of organization. Long songs were constructed by agglutination of units. Of 216 songs with at least four units, 161 began with ABCD, 35 began with CDEB, and 20 began with some combination other than these. When units in longer songs were repeated, the initial A unit often was omitted (e.g. ABCDEBCDE).

Songs, consisting of a variable number of song units, were often given in bouts. Some songs were singles, but at other times long bouts occurred with only a few seconds separating each song. The longest bout was 18 songs, but most bouts were composed of only a few songs.

Developmental patterns.—In late summer, males sometimes produced aberrant songs that contained undifferentiated notes and poorly defined song units (Fig. 1E). Four songs were recorded from a male at SWRS that was still being fed by his mother. Most of his notes were well defined, but others were lacking. Considerable variation occurred in the number of song units given by this bird, but the syntax was the standard one.

At RC, some birds produced typical songs in all respects except for some notes in the A and D units. The three males that were sampled at RC demonstrated the same type of uncrystallized notes at the same point in the D unit, but other songs from the same individuals were normal. The A and D song units with aberrant notes in August were the same units that differed between the RC and SWRS birds earlier in the season.

Type 2 song.—This song type was rare and very different from type 1. Of the 380 total songs recorded, only 15 were type 2. The ordering of units in this song was much more variable than that of type 1 songs. Type 2 songs typically consisted of one or more trills and transients that covered a wide range of frequencies (ca. 2 to 9 kHz; Fig. 1D). In addition to acoustic differences, type 2 songs were given in different contexts than type 1 songs. Of the 12 songs analyzed, 9 were given by females, the only songs ever recorded from females (three were from birds of unknown sex). In one case, a song uttered by a lone female was barely audible by an observer 1 m away. Most other songs were given when females were a few centimeters from a male, having approached while males were singing type 1 songs (four different males were approached by an unknown number of females). In most cases when a female sang while a male was singing a bout, she overlapped her song with his. In each of these instances, the female stayed near the male less than 20 s. In the one case when visibility was good, no interactions other than singing occurred, after which the female departed. In another case, the female was not visible to us during singing, but she also left as the male continued to sing.

Females were observed to approach singing males only and not males that were silent (males spend much more time resting than singing). Males sometimes sang from conspicuous perches, but they also sang from the middle of dense junipers. In such situations, females probably located males by song. It is noteworthy that no aggression occurred during these encounters between the sexes, although males sometimes chased females at feeders. Other males sometimes approached a singer, and in contrast to the reaction of the singer when a female approached, singing males immediately supplanted the intruding males.

DISCUSSION

Songs of Blue-throated Hummingbirds are complex, certainly rivaling those of many oscines. Notes are varied in acoustic structure with many transients and trills, although pure tones are lacking. The songs cover a wide frequency range and contain higher frequencies than the songs of most oscines. Most of the dif-

ferent song units are about the same length as each other, as are the intervals between units. Such remarkably stereotyped timing in units of complex vocalizations may be unusual. Some songs last less than 1 s, but others last as long as 8 s, so total length also is comparable to songs of many oscines.

Song units consist of an array of notes that are given in a consistent sequence and are shared by all members of the population. The order of song units within songs is more varied, but the five types of units adhere to syntactical rules, with most units having a very high probability of only one other unit following them. The most frequent beginning unit is A, but endings are much more variable. Todt and Hultsch (1992) referred to songs such as these as having a "one-to-many" decisional hierarchy in which different choices are possible at later levels of song organization. Second-order transitions (probability of a dyad being followed by another song unit) are also stereotyped. Songs are composed of repeated blocks of units, e.g. ABCDEBCDEB. Thus, although very long songs may be produced, they are constructed by agglutination, often following the same syntactical rules as dyads and triads.

A considerable amount of evidence for song learning has accumulated for numerous species of hummingbirds (see Gaunt et al. 1994, Kroodsma et al. 1996), and vocal dialects, presumably the result of learning, occur in some species (Gaunt et al. 1994). Although our data on the development of song are sketchy and based entirely on field observations, some songs in late summer are similar to subsongs of oscines in that they are muted and contain undifferentiated elements (Marler and Peters 1982). Even these undifferentiated songs, however, show an organization based on units and are not just a random assortment of notes. Perhaps an innate basis exists for a certain kind of song organization, with learning from neighbors involved in defining some note types. The two populations from different mountain ranges did not have well-developed dialects, but consistent minor differences occurred in certain notes. Further evidence for song learning was that differences among birds at the two sites occurred mainly in the notes that remained uncrystallized when all of the other song units were normal.

Type 1 song was produced only by males and

was associated with territorial defense. An increase in singing occurred during territory establishment in spring before females were present. Singing continued into late summer, when sexual activity presumably had ceased. Sometimes, males sang immediately after territorial interactions. Occasionally, they sang from hidden perches within dense junipers, and immediate aggression was initiated by the singing male when approached by conspecific males. Males typically sang when no other males were nearby.

Song also appears to have an intersexual function. Males were singing, but not always readily visible, when females approached them. Males were approached by females at other times, such as near feeders, but in these cases males chased females. No copulations were observed, so the role of singing in sexual behavior remains unknown. Because type 1 songs were usually of low amplitude and emitted in a noisy environment, it is difficult to assess how females find hidden males. Their approaches to males may be facilitated by the fact that males often use a limited number of song perches and have small territories.

Type 2 song is very different from male song and apparently is given exclusively by females. These sexual differences may facilitate identification of the signaler, an important attribute in close-range interactions, because males are aggressive when approached by conspecific and heterospecific males. Often, the female's song totally overlaps the male's song temporally, which is an unusual type of singing interaction. We are not aware of other reports of female song in hummingbirds, and female singing has a restricted distribution in oscines (see Langmore 1998).

Possibilities for interspecific comparisons are limited because little is known about hummingbird vocalizations (indeed, sonographic analyses have been performed for only a few of the more than 300 species). Although the reproductive behavior of many hummingbirds is relatively simple in that males are territorial, have limited associations with females, and do not care for young, other behavior is more diverse and varies according to species. Several patterns of male vocalizations have been identified: (1) absence of song; (2) solitary singing, such as in Blue-throated Hummingbirds; and (3) singing in aggregations and leks (Atwood et

al. 1991, Gaunt et al. 1994, Kroodsma et al. 1996).

Male displays may be dynamic (aerial) or static (perched), and both types can include vocalizations and visual components. According to Gaunt et al. (1994), dynamic display vocalizations are as acoustically complex as static display vocalizations. On the other hand, Wagner (1954) indicated that the Mexican species that gave long, complex static songs did not have elaborate dynamic displays. However, Anna's Hummingbird (*Calypte anna*) has both dynamic displays (accompanied by simple calls) and a song of "three different phrase-groups, each of which contains two to four like or unlike phrases" (Stiles 1982).

Blue-throated Hummingbirds often inhabit dense vegetation and lack dynamic displays. This ecological setting may explain the complexity of male song and the phenomenon of female song. Many hummingbirds that live in upper or middle forest canopy have complex songs, but these species have not been studied in detail. Most species that have been studied congregate in leks or occur in more open habitats than those used by *Lampornis* (Kroodsma et al. 1996). No species of hummingbird for which a detailed sonographic analysis has been performed seems to have a song that approaches the acoustic and organizational complexity of the Blue-throated Hummingbird's song. However, two congeners that also inhabit Mexican forests, Green-throated Mountain-gem (*L. viridipallens*) and Amethyst-throated Hummingbird (*L. amethystinus*), also sing, the songs of the former being characterized as "melodic" (Wagner 1954).

Comparisons of song organization in hummingbirds and oscines are of special evolutionary interest at several levels, including basic design features. Blue-throated Hummingbirds have levels of organization of song units similar to those found in oscines. For example, many oscine songs are organized in unit combinations and hierarchical levels (e.g. Todt and Hultsch 1992, 1996), although extensive differences in organizational patterns among species render generalizations impossible. Complex learned vocalizations have evolved in three different groups (parrots, hummingbirds, and oscines), despite syrinx differences among groups (Baptista and Trail 1992). Resemblances between the vocalizations of Blue-

throated Hummingbirds and oscines include acoustic complexity, syntax, hierarchical levels of organization, and possible vocal learning. Because hummingbirds do not share a recent common ancestor with oscines, these similarities must be true convergence, indicating that selection favors a limited set of characteristics for effective acoustic communication.

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