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REPRODUCTIVE BEHAVIOR AND COMMUNICATION IN BLUE-THROATED HUMMINGBIRDS

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ABSTRACT.—Previous studies of Blue-throated Hummingbirds (*Lampornis clemenciae*) showed that males have elaborate songs and females also sing. Here we report complex territorial systems, sexual behavior, and communicatory repertoires of both sexes. Males typically defended territories along streams throughout the reproductive season. Time budgets revealed that males allocated more time to vocalizing in territorial advertisement than in more energetically costly activities such as chases. Both observations and playback experiments indicated that two vocalizations have different roles in territorial advertisement. Strings of chips served in long distance territorial advertisement, while the lower amplitude song, more prevalent early in the season, attracted females and also repelled males from the immediate area. Agonistic interactions included long chases, some with vocalizations. During close range encounters an array of postures and sounds occurred. Females defended territories against other females during a brief period preceding egg laying. Sexual interactions were unusually intricate, consisting of a series of activities in which the female played an active role. She delivered loud calls advertising sexual readiness and performed aerial displays. Males competed with other males for access to females. We observed four presumed copulations, all preceded by a song fragment from the male. The vocal repertoire included at least 16 different sounds, all with different functions, an unusually large number for a nonoscine. Male songs were the most complex sounds. Behaviors that differed from many other hummingbirds that have been studied included strong reliance on vocal signals, lack of male aerial displays, and female advertisement of sexual readiness. These attributes may be linked to reduced sexual dichromatism and related to the species' preference for wooded riparian habitats. Received 15 May 2001, accepted 2 April 2002.

Hummingbirds provide a fascinating and difficult challenge for behavioral ecologists. The family Trochilidae includes >300 species occupying a variety of habitats (Schuchmann 1999). Although subjects of numerous ecological and physiological studies, the reproductive behavior of relatively few species has been assessed in detail, which is not surprising considering their general tropical distribution and the difficulty of studying such rapidly moving small birds. The general picture of hummingbirds that has emerged is the conservative nature of some behavior patterns and the diversity of others (Johnsgard 1997, Schuchmann 1999). Mating systems are polygynous, and males have no role in parental care, yet other behaviors vary according to the species. For example, elaborate aerial courtship displays are performed by males of many

species, but are absent in others (Wagner 1954, Johnsgard 1997). Males of some species congregate in leks during the breeding season (Johnsgard 1997).

Detailed studies of visual and vocal signaling in reproductive interactions are lacking for most hummingbird species with the exception of comprehensive studies of courtship and aggression in Streamertails, *Trochilus polytmus* (Schuchmann 1980) and Anna's Hummingbird, *Calypte anna* (Stiles 1982). The monograph on ecological and evolutionary aspects of the lek mating system of Long-tailed Hermits (*Phaethornis superciliosus*) includes a description of the communicatory repertoire involved in reproduction (Stiles and Wolf 1979). Our present study is an initial contribution in assessing the nature and variety of hummingbird behavior.

The main focus of this study is visual and vocal signaling systems and their role in mediating territorial interactions and sexual behavior in Blue-throated Hummingbirds (*Lampornis clemenciae*). We document and discuss some previously undescribed behavior of this species that contributes new perspectives for integrating the role of intersexual communication in reproduction. Most studies of hum-

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mingbird reproductive behavior have focused almost exclusively on males, as they are much easier to observe because of brighter plumage and more conspicuous behavior. The marked sexual dichromatism of many species indicates that female choice may select for plumage and behavioral attributes. Vocal signals have received less attention. Here we suggest females have an active role in initiating sexual behavior, as may be the case in other hummingbird species as well.

The Blue-throated Hummingbird has an extensive range in Mexico but breeds in only a few localities of the southwestern United States where males typically defend territories along streams in montane regions from their arrival following migration (typically April) until departure in late summer (Williamson 2000). Eight male territories were spaced at uneven distances along 1,500 m of stream in Arizona (Williamson 2000). Territory size and structure are variable and related to the distribution of nectar supplies (Lyon 1976; DRP unpubl. data), but since birds also are breeding during their time in the southwestern United States, the functional importance of male territories probably extends beyond simple energy acquisition to include a staging ground for displays and vocalizations (Powers 1987).

The sexes are spatially segregated during most of the reproductive period, with only a brief overlap during sexual activity (Wagner 1952; MSF unpubl. data). Blue-throated Hummingbirds are unusual in having a more protracted period of association of the sexes than other hummingbirds studied in Mexico by Wagner (1954). Females defend two kinds of territories, with no temporal overlap: the immediate nesting area for a few days before egg laying (Wagner 1952), and temporary feeding territories later in the season (Lyon 1976).

Our previous studies described the structure and usage of complex male songs (Ficken et al. 2000). These songs comprised clusters of notes (termed "units") that we designated A, B, C, D, and E. Our initial observations indicated they may serve as short range territorial advertisement as well as female attraction. Other vocalizations, particularly strings of chips (the loud "seeps" of Marshall 1957), also are associated with reproductive behavior (Williamson 2000). Here we address questions concerning the different functions of songs

and chips utilizing playback experiments. Using a time budget analysis, we documented the number of these two types of male vocalizations as compared with chases and other aerial territorial behavior. We also tested the prediction that longer songs should predominate earlier in the season when sexual activity is highest, if a principal function is the attraction of females. Females also utter complex muted songs, typically when close to a male (Ficken et al. 2000), and we played back these songs to males. We describe usage of a female call (designated *Tia* following its description by Wagner 1952) and supplement observations with playbacks. In addition, we describe a variety of visual signals by both sexes, some with complex components that are important constituents of reproductive behavior.

In addition to studies of general reproductive behavior and some visual displays, we provide the first sonographic analysis of the acoustic repertoire of a hummingbird and compare the behavior of Blue-throated Hummingbirds with some other avian species regarding acoustic repertoire categories and characteristics.

METHODS

We conducted the study from 1995–2001, with the most intensive data collection during May, and some additional observations during late April and August at two sites in southeastern Arizona (Cochise Co.): Ramsey Canyon in the Huachuca Mountains (31° 50' N, 109° 10' W), and the Southwestern Research Station in the Chiricahua Mountains (31° 26' N, 110° 19' W). Both sites had numerous feeders visited by a variety of hummingbird species. Although many observations were made <10 m from feeders, others were made at a greater distance. Some behavior was much easier to observe near feeders, because the interaction rate was increased by competition for access to feeders. Feeders undoubtedly affected many aspects of reproductive behavior, such as nest site selection and population density, but we were unable to assess all these effects. We described different types of agonistic interactions, but because of the rapidity of certain types of encounters we were not always able to describe all components for both participants.

We determined time budgets for nine males at the Southwestern Research Station and two males at Ramsey Canyon that had established territories around feeders (June to July 1995). We quantified two 30-min periods for each individual, one during the morning (09:00–12:00 MST) and one during the afternoon (12:00–17:00). The observer was positioned about 20 m from the feeder being defended by the focal male. We recorded behaviors related to territorial defense. We

divided these agonistic encounters into three major categories (chases, crouches, and hovers) for analysis of their association with vocalizations. Tail spreading and sounds often accompanied these behavior patterns. We analyzed a sequence of activities of one encounter in slow motion from a published videotape (Nature Science Network, Inc. 1988).

We recorded vocalizations and notes using Sony Professional Walkman WM-D6C cassette tape recorders and either a Nakamichi directional microphone or an Audiotechnica AT 877 microphone. Some natural behavior and many playback experiments were videotaped using a Sony camcorder. We made sonograms with a Kay 7800 Sona-graph at 8 kHz with a 150-Hz bandwidth filter. For measurements of chips and *Tias*, we used Avisoft SONAGRAPH Pro (ver. 2.5).

We conducted playback experiments with the Sony Professional Walkman and a Sony SRS-27 speaker affixed about 2 m high to a branch in areas near feeders. The feeders were >50 m apart, increasing the probability that different individuals were tested.

To test whether responses differed for certain vocalizations associated with reproductive behavior, we conducted playbacks during May 1998 and May and early June 1999. We completed 14 experiments at two sites (five males at Ramsey Canyon and nine males at Southwestern Research Station). Each presumably was a different male, based on distance between playback sites. Each experiment consisted of three randomized series of vocalizations, each lasting 85 s with a 90 s interval between playbacks. Playback durations were similar to normal singing in bouts. In natural singing, a bout began with the first song and terminated when the bird ceased singing or flew. The amplitude for all playback sounds was adjusted to 70–75 dB (measured with a Yu Fung YF-20 sound level meter). For male song (Type 1 of Ficken et al. 2000), we used a common variant consisting of a string of six units (ABCDEB) repeated 11 times. Playback of female song (Type 2 of Ficken et al. 2000) lasted 1.9 s and was presented nine times, and chips were a continuous series (Serial Chips) using natural intervals. All males in the population used the same song variants, and chips were very stereotyped. Response measures for hummingbirds were necessarily different than those for oscines because of the behavioral differences between the two groups. Hummingbirds rarely perched near a speaker during playback and vocalized only infrequently. We started playbacks when a male was ≤ 15 m of the speaker. Responses included (1) no approach; (2) obvious movement away when playback started; and (3) approach to <10 m of the speaker, usually involving rapid agitated flights and hovering near the speaker. We noted the actions of the birds before playback, during pauses between playbacks, and after playback. For the analysis we used only behavior during playback.

In a separate set of experiments (June 1999) at the Southwestern Research Station we played *Tia* calls in areas where females had been observed producing these calls. These experiments were designed to test

TABLE 1. Time budgets indicate that male Blue-throated Hummingbirds (*Lampornis clemenciae*) spent more time vocalizing in territorial advertisement and defense than in active aggression (chases and other nonvocal behaviors). Values are mean number of acts per 30-min observation period for individually identifiable males. Data are from the Southwestern Research Station (birds 1–9) and Ramsey Canyon (birds 10–11), southeastern Arizona, June and July 1995.

Bird	Aggressive acts	Chipping	Singing
1	0.36	18.03	0.93
2	0.00	0.53	2.04
3	0.23	7.92	0.87
4	0.65	0.28	0.45
5	0.28	17.83	1.78
6	0.58	0.57	1.04
7	0.05	9.28	0.23
8	0.94	13.12	0.39
9	0.11	22.13	0.13
10	0.17	15.50	1.07
11	0.43	0.40	0.07
Grand mean	0.35	9.60	0.82
(SD)	(0.29)	(8.25)	(0.65)

whether both males and females responded by approaching the speaker.

We measured sonograms for comparisons of calls. Because of the extremely varied usage, we analyzed chips separately according to sex and context. Values are presented as means \pm SD. Unless indicated otherwise, *t*-tests are two-tailed. For comparisons of responses to sound playback we used the sign test, comparing approaches during playback to the nonplayback situation. *P* values <0.05 were considered significant. The data in Tables 2 and 3 are based on ≥ 8 males and ≥ 3 females. We compared the incidence of male and female agonistic behavior patterns, but because the data were not obtained from known individuals, they only suggest trends and statistical tests were not performed.

RESULTS

Territorial behavior and time budgets related to aggression.—Time budgets undoubtedly were affected by feeders, but a major trend was clear under these conditions. Males spent more time vocalizing than engaged in overt aggression. Two males spent almost the same amount of time chipping (Serial Chips) as engaged in aggressive acts, but all the others spent much more time chipping (Table 1). Similarly, singing occupied more time for 8 of the 11 males than overt aggression. Most birds (8 of 11) spent more time chipping than singing.

There may be a relationship between territory size (and possibly quality) and degree of aggression exhibited by the territory holder. The most dominant male in our study (bird 1; Table 1) defended a large territory that appeared to be about 10,000 m² in size. When bird 1 was removed, his territory was broken into several smaller pieces defended by males exhibiting less dominant behavior. Another male (bird 2) who defended a territory adjacent to a dry creek encountered substantially fewer intruders and exhibited no aggressive behavior during observations (Table 1).

Male song.—Song length was related to the stage of the breeding cycle, with shorter songs more prevalent later in the season (one-tailed $t = 1.8$, $df = 286$, $P = 0.037$). During May songs had a mean of 4.99 ± 3.46 units ($n = 242$ songs), and during July a mean of 4.09 ± 2.75 ($n = 46$). Although some long songs persisted throughout the summer, the short song of just two units (AB) was the most common song variant, and as the season progressed the proportion of AB songs increased (18% of all songs early in the season, 33% later).

Although single songs were frequent, songs also were performed in bouts. Pauses between bouts always were much longer than intervals between songs within a bout. The longest bout was 18 songs, but most bouts were composed of only a few songs. Early in the breeding season bouts were somewhat longer (mean = 4.3 ± 3.8 songs, $n = 59$) than later in the season (mean = 2.8 ± 1.4 songs, $n = 17$; one-tailed $t = 1.6$, $df = 74$, $P = 0.045$).

Single Chips.—Males often were silent when perched on their territories, unless another male Blue-throated Hummingbird or Magnificent Hummingbird (*Eugenes fulgens*) approached. The other hummingbird usually left the vicinity following one or two chips by the resident Blue-throated Hummingbird. These Single Chips also preceded flight, or were uttered as the bird approached a feeder. Females usually were silent both in the vicinity of feeders and when perched away from feeders (<1% of chips we recorded were from females).

Single Chips were very short, high pitched notes (Fig. 1a). No significant differences occurred between the sexes with respect to the mean low frequency of the chips ($t = 0.99$, df

= 28, $P = 0.36$) or the mean high frequency ($t = 0.99$, $df = 28$, $P = 0.33$), but we detected tonal differences between the sexes. Male chips sounded harsher, perhaps due to more high frequency bands than those of females, with the inclusion of a second band from 10.9–12.2 kHz (present in all 16 samples), and sometimes a third even higher band 15.9–18 kHz (present in 6 of 16 samples). We observed less banding in females, with a second band of 11.6–13.4 kHz (present in 7 of 14 samples) and no third band ($n = 14$). The most striking difference, however, was that female Single Chips were about half the duration of male Single Chips (Table 2).

Serial Chips.—Males delivered long strings of chips, particularly in the early morning and late evening, and less frequently at other times of day. Calling was most prevalent early in the breeding season. A single male called for 20 min on one occasion, and many bouts were as long as 10 min. The mean rate was 7.21 ± 1.37 ($n = 23$), and the chips were delivered at uniform intervals. Single Chips and Serial Chips did not differ significantly in frequency ($t = 1.96$, $df = 32$, $P = 0.058$), but individual chips in a series were shorter than male Single Chips ($t = 6.2$, $df = 30$, $P < 0.0001$).

Males typically perched near the creek on high perches. Serial Chipping often was accompanied by head movements (Wagner 1954; MSF pers. obs.) through an arc of about 150°. While chipping, the male occasionally altered the pitch of the call (Willard 1911), as indicated in Fig. 2. To our ears, the pitch shift and the changing amplitude during head movements produced a “stereo” effect. In fact, we believed two birds were calling when we first noted this behavior.

Female Serial Chips were rare, and all five cases occurred when a female was in the last stages of nest construction. During this time females engaged in territorial interactions with neighboring females. Female Serial Chips were associated with a head tossing movement, but unlike the males, we detected no pitch shifts in females. In females, individual chips in a series were longer than Single Chips ($t = 3.15$, $df = 30$, $P = 0.004$), in contrast to males.

Playback experiments of Serial Chips and male and female song.—Males responded significantly with approaches to male song (sign

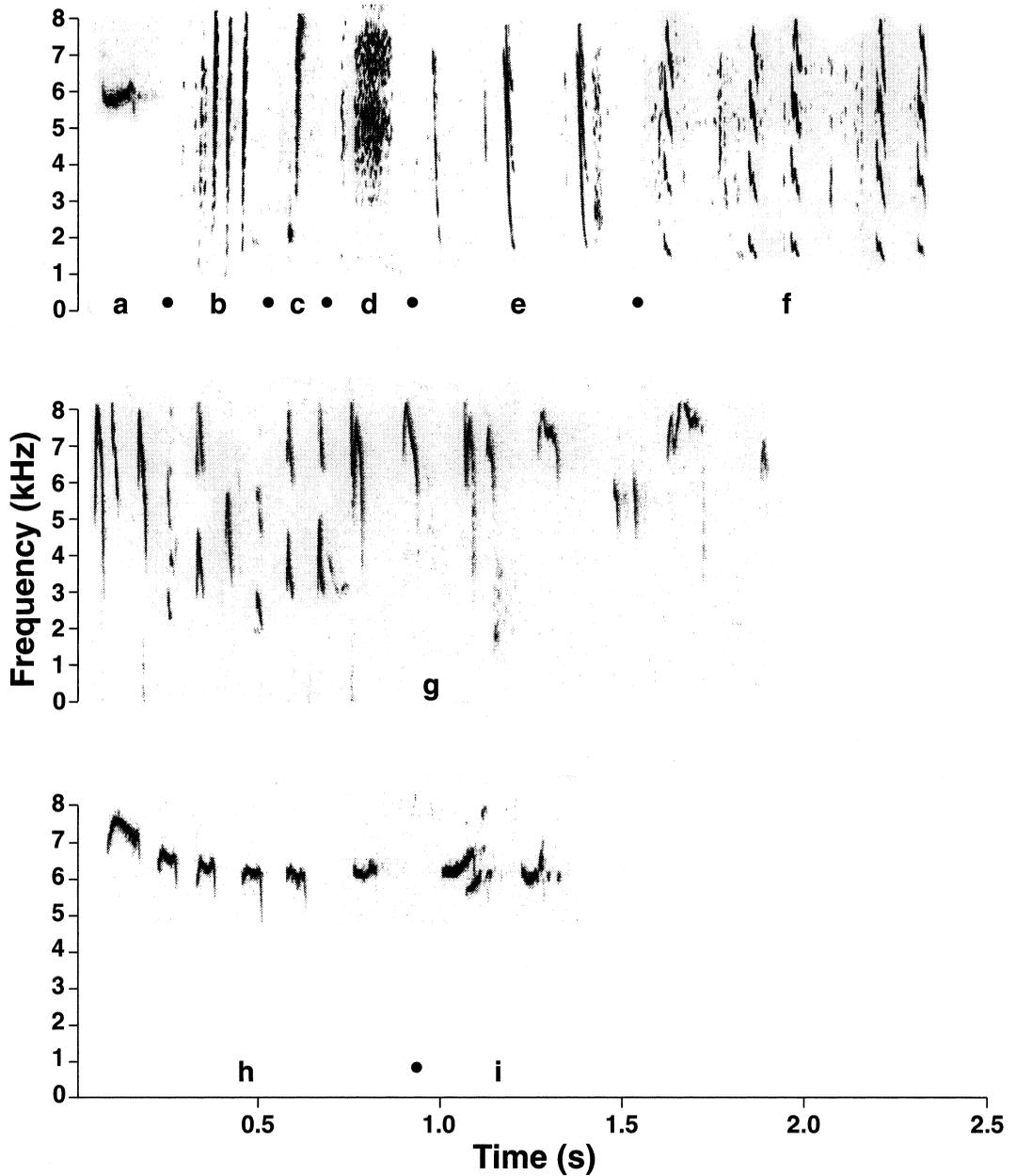


FIG. 1. Sonograms of Blue-throated Hummingbird (*Lampornis clemenciae*) vocalizations recorded at the Southwestern Research Station, southeastern Arizona, by M. S. Ficken, April through August, 1995–2001. Black circles on horizontal axis separate different kinds of calls. Sonograms were prepared using a Kay 7800 Sona-Graph with 0–8 kHz settings and a 150-Hz bandwidth. In a few cases, some elements were higher than 8 kHz. (a) Single Chip of a male. (b) Staccato Trill. (c) Bill Crack. (d) *Zeet*. (e) Short Call. (f) Long Call (most common form). (g) Complex Long Call. (h) *Tia*. (i) Mobbing Chips (more than one individual is calling).

TABLE 2. Acoustic characteristics of Blue-throated Hummingbird (*Lampornis clemenciae*) chips illustrate the variation associated with sex, age, and context. Values are means \pm SD (n). Data are from the Southwestern Research Station, southeastern Arizona, May through June, 1995–1999.

	Duration (s)	Lowest frequency (kHz)	Highest frequency ^a (kHz)
Single chips (female)	0.11 \pm 0.05 (14)	5.64 \pm 0.35 (14)	6.79 \pm 0.33 (14)
Single chips (male)	0.21 \pm 0.05 (16)	5.50 \pm 0.50 (16)	6.90 \pm 0.28 (16)
Mobbing chips	0.08 \pm 0.02 (23)	5.68 \pm 0.21 (9)	7.63 \pm 0.80 (9)
Fledgling chips	0.11 \pm 0.02 (10)	7.86 \pm 0.15 (9)	9.39 \pm 0.17 (9)
Series chips (female) ^b	0.16 \pm 0.04 (18)	5.14 \pm 0.17 (11)	6.35 \pm 0.14 (11)
Series chips (male)	0.13 \pm 0.02 (18) ^c	5.31–6.20 (18) ^d	6.44–7.10 (18) ^d

^a Energy distribution is centered in this band.

^b Mean of means for two female chip series.

^c Mean of means for five male chip series.

^d Mean of ranges for five male chip series, depicting the pitch shift for these vocalizations.

test, $L = 1$, $n = 14$, $P = 0.002$), but only two approaches by males occurred during playback of female song ($L = 2$, $n = 14$, $P = 0.012$). Responses to playbacks of Serial Chips were ambiguous, with two males leaving during playback, five males approaching, and six males not responding at all ($L = 5$, $P = 0.58$). No females responded to playbacks.

Behavior during agonistic encounters between males.—Hummingbirds exhibited an array of postures and sounds associated with agonistic interactions. Some activities occurred in conjunction with others, e.g., sounds uttered when the bird was crouched with a spread tail. Such composite displays were quite common.

We observed wing waving, in which wings

were elevated and vibrated, only eight times, but as it occurred very rapidly, many probably were not detected. Each case occurred when a resident was approached by another male, or another male flew directly over the perched resident. Usually the resident's tail was spread, and sometimes the bird emitted a Single Chip or *Zet*. The opponent then left. Tail spreading occurred alone or in combination with many other acts and exposed the prominent white tail spots. In some cases the tail also vibrated rapidly.

Chases varied greatly in duration; some were very long, apparently covering more than the length of one territory. They often were initiated by one bird flying directly toward another, but as both birds disappeared

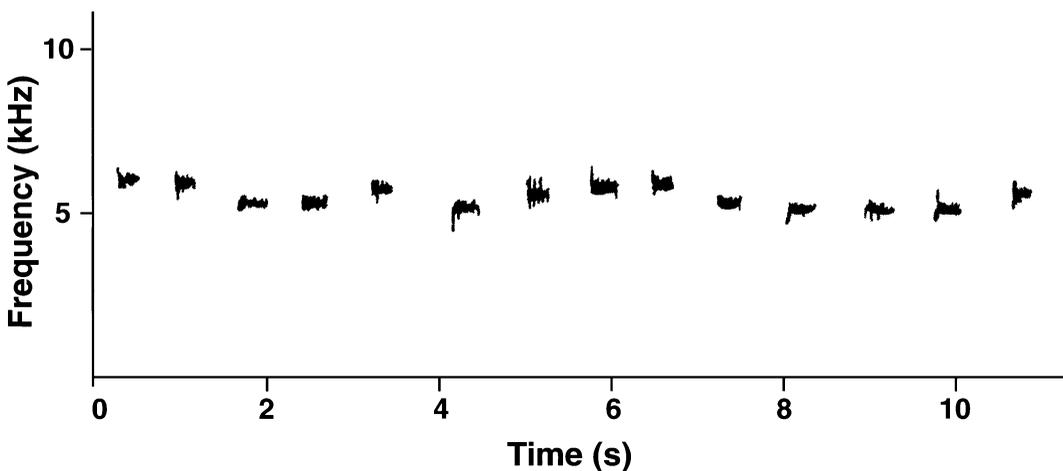


FIG. 2. Sonogram of male Blue-throated Hummingbird (*Lampornis clemenciae*) Serial Chips showing pitch shifts. Recorded by S. J. Taylor at Southwestern Research Station, southeastern Arizona, June, 1995. Prepared using Canary 1.2.

from view quickly, we could not distinguish between shorter supplantings and longer chases. Long chases involving three (and more rarely four birds) were frequent, particularly early in the breeding season, but were impossible to follow in detail. One bird chased another, with the third bird joining later. Males sometimes supplanted females, but long intersexual chases were uncommon except in a sexual context. Male Blue-throated Hummingbirds, the dominant species, sometimes chased male Magnificent Hummingbirds, but heterospecific encounters were rarer and briefer than conspecific ones. Encounters with Magnificent Hummingbird males were confined to chases and did not include hovers or crouches described below.

Another type of interaction involved crouching in which a perched bird (resident) was approached by another (intruder) that hovered within a few centimeters of the resident. The outcome was variable. A chase sometimes ensued immediately with the resident pursuing the intruder. Alternatively, the perched resident crouched with tail spread. The position of the hovering bird sometimes changed from a frontal approach to hovering directly over the resident, and in rare cases the intruder even landed on the back of the crouched bird. An even more unusual posture occurred in which the crouched bird fell over backwards and hung upside down while the opponent continued hovering over it (see drawings in Rising 1965). The bird that crouched always won ($n = 31$ encounters); the bird that approached the resident left or was chased, in contrast to Rising's (1965) conclusion that the crouched bird was the subordinate.

A published videotape of male Blue-throated Hummingbirds (Nature Science Network, Inc. 1988) allowed slow motion analysis. Initially the resident (R) was perched, the intruder (I) landed next to R, and then I flew and hovered over R. R shifted position and hung upside down with his tail spread and bill pointed upward at the hovering I, who had his bill pointed at R (at one point their bills almost touched). I changed position, and the two birds briefly were tail-to-tail (R was still upside down). I called and moved, still hovering a few centimeters above R. R righted itself on the perch but maintained tail spread

TABLE 3. Male and female Blue-throated Hummingbirds (*Lampornis clemenciae*) differed in the number of intrasexual agonistic acts and associated vocalizations. Data are from the Southwestern Research Station, southeastern Arizona, April through June, 1995–2000.

Call type	Agonistic activity					
	Chase		Crouch		Hover	
	Male-male	Female-female	Male-male	Female-female	Male-male	Female-female
Long call	13	0	0	0	0	0
Short call	4	0	9	0	3	0
Zeet	6	0	4	0	4	1
Bill crack	6	0	0	0	10	1
No calls	8	9	18	5	5	6
Total	37	9	31	5	22	8

as I hovered over it. I left and R remained. Hanging upside down was relatively rare in our sample of crouches (19.4%, $n = 31$), and we never observed one with a bill-to-bill component as in this video.

Hovering was another type of confrontation (Table 3) in which both birds flew up face to face only a few centimeters apart with widely spread tails, sometimes flying several meters into the air while maintaining the same orientation. Hovers sometimes terminated in chases.

Agonistic sounds.—Various sounds were associated with agonistic interactions. One was a trill (unit B), a common component of male songs (Ficken et al. 2000), and the only song unit delivered without any accompanying units. The B unit occurred in several different contexts. The loud Staccato Trills (Fig. 1b) occurred during some agonistic encounters. Soft Trills of much lower amplitude with shorter internote intervals than the staccato ones sometimes occurred during close range agonistic interactions between males, and all apparent copulations were preceded by these whispered sounds. We excluded these trills from the quantitative analysis of sounds during encounters (Table 3) because the soft ones were inaudible unless we were within a few meters of the bird.

Bill Cracks were nonvocal sounds (Fig. 1c) produced during hovers and chases (Table 3). In the few cases where we had good views of the combatants, the sounds were produced as the birds hovered and struck bills at about 2/

3 the length of the bill. The sounds were loud, indicating a forceful impact. Bill Cracks occurred during chases when the bird being chased turned and confronted its pursuer. Bill Cracks were not heard during crouches.

Four major types of vocalizations also occurred only during agonistic interactions. The *Zeet* was a short, harsh, snarly call of variable duration, covering a wide frequency range (Fig. 1d). Short Calls were a series of several (typically 3) transients covering a wide frequency range (Fig. 1e). Long Calls (Fig. 1f) were more protracted strings of notes with more complex structure than Short Calls. We recorded an unusually complex call only twice (both times delivered by the same male) during our extensive recording (Fig. 1g). Its rarity in our sample may be due to its occurrence in an unusual situation when two males hovered close to each other during an agonistic encounter near a sexually active female. Many of the notes in these calls are transients covering a wide frequency range. The Complex Long Call was more complex than other Blue-throated Hummingbird vocalizations except for song, as there was a mixture of note types, and some notes covered a narrower frequency range than is typical for other agonistic sounds such as Short Calls and the typical Long Calls.

Some sounds were associated with certain types of interactions more than others (Table 3). Long Calls were performed only during chases, while Short Calls and *Zeets* occurred during all three types of encounters (hovers, chases, and crouches). *Zeets* also were given when another individual flew near the caller but no obvious interaction occurred. They may inhibit approaches, in contrast to the other sounds that occurred once an interaction was already underway. Crouches often were silent, while hovers, and particularly chases, often had accompanying sounds.

Female territorial behavior.—We noted aggression between neighboring females at the time that sexual activity was occurring (late nest building and perhaps egg laying). This was the time that females uttered Serial Chips near the nests ($n = 3$ females). While feeders may have modified spatial relationships, most interactions were not near feeders. Two females were observed for several hours each on six days, and their territories did not overlap. One female had fledglings and later was

observed lining a nest adjacent to an area where another female was engaged in the same activity. Both females were involved in many agonistic interactions with each other. Both returned to their original sites following encounters. We never observed agonistic encounters between incubating females or those with nestlings, despite about 20 h of observation.

The types of agonistic encounters between females included the same general categories as those of males (Table 3), but female encounters were of lower intensity. During 22 encounters, sounds occurred only twice. Chases usually were shorter as well as less frequent than those of males.

Male-female interactions.—During a period of about two days, the male often remained near the female and in the area of the nest. We observed behavior that seemed sexual, but because most birds were unmarked and the stage of the nesting cycle for many females was unknown, we were able only to piece together a number of separate observations to produce a general pattern. Females sometimes approached singing males and produced a very distinctive but muted song that often overlapped the male's song (Ficken et al. 2000). In all cases where visibility was good, the female left after <10 s. On one occasion when there were no prior interactions, a male hovered over a crouched female. She uttered a *Zeet* and he left, but he returned about 5 min later to the same place and delivered long songs. The female then disappeared from view.

Male-male interactions near females.—The period of late nest building through nest completion coincided with sexual behavior and was marked by especially intense agonistic encounters between males, often involving long chases. This was the only time we observed physical contact between males. On three different occasions males tumbled to the ground, hitting with a strong impact ("thuds" were heard) with one grasping the other. Females always were nearby.

Female sexual invitation behavior.—An unusual aerial display that we named "River Dance" was performed only by females known to be sexually active, just following nest completion and during the period of *Tia* calling (see below). Just prior to dancing, a

female would be perched very low near a creek or would fly to the site of the dance. All dances took place over a creek, a dry creek bed, or more rarely (<10% of cases) <10 m from a creek. Dances did not take place near nests. Dances may have originated from ritualized insect-catching movements, but no insects were present as we inspected the sites carefully immediately after dances. No dances were observed during a study session in which no females were at the right stage of the nesting cycle.

River Dance was a series of short flights, usually only a few cm high and 1–3 m in diameter, often centered over the creek. The female did not vocalize during the dance, and she was quiet before starting a display. Each short flight was followed by a hover (typically <2 s long) and a change in position. During some but not all hovers, females exposed their white outer tail feathers, sometimes while flicking the tail back and forth. Dances incorporated all directions (up, down, left, right, forward, backward, and diagonals) in 3-dimensional space. Mean duration (timed from video recordings) was $12.4 \text{ s} \pm 6.0$ ($n = 19$), with about 10 movements per dance. In some cases we observed males within a few meters of the dancer, but in many cases we were not certain if males were present, as they tended to perch low in very dense vegetation and chipped only occasionally. We observed no interactions immediately following the dances.

During periods of sexual activity, females uttered special calls (*Tias*) that were not heard at other times. We measured the calls from a pooled sample of females (≥ 3 different birds, 8 sonograms); mean duration was $0.58 \text{ s} \pm 0.25$, highest frequency was $7.89 \text{ kHz} \pm 0.76$, and lowest frequency was 5.75 ± 0.09 . Unlike Serial Chips, *Tia* calls consisted of a series of rapid chip notes with the first note always longer and slightly higher pitched than the others (Fig. 1h).

The calls were given either when the bird was perched or when she flew. In contrast to many calls of this species, *Tias* were unusually loud, and functioned as long distance signals, as individuals ≥ 50 m distant approached in response to the calls. Because of observational difficulties, the stimuli eliciting the calls were not always apparent. Sometimes females

seemed to call spontaneously, but at other times they called in response to a male flying overhead. Some calls from perches elicited no apparent responses from other birds. On other occasions the female called in flight as she approached and then engaged in a chase with a male, although it was not clear which sex was the ultimate pursuer. In one case, a female uttered a very muted *Tia* as the male hovered over her, but no further interactions took place. In two instances encounters with *Tias* ended in copulations.

We also conducted seven playbacks of *Tias*. Responses occurred at all sites where we had observed females calling that day. In all cases the females approached, and in three cases she uttered *Tias*, chipping only once. In four of the seven cases a male also approached during playback. One time the male chased the female, and another time two males approached and chases ensued. In two other cases, chases occurred but the sexes of the participants could not be determined.

Copulations.—We observed three probable copulations, and E. Sandlin (pers. comm.) provided data on another. All happened during late May or early June at the Southwestern Research Station. The events occurred very rapidly and cloacal contact was not observed. All were on the ground in dense vegetation at low light levels during early morning or evening. In three cases a chase preceded copulation, in two cases *Tias* occurred, and in all four cases the male performed a soft B trill fragment.

Calls of the young.—Nestlings were silent, as was the female in approaching the nest, giving only a soft call when a human was near the nest (Wagner 1952; MSF unpubl. data). However, fledglings called prior to a feeding when the female was several meters away, and sometimes in her absence. Sometimes the female also chipped before approaching the fledglings for feedings (Wagner 1952; MSF unpubl. data). When the female was close, the young quivered their wings. The chips uttered by fledged young just before independence differed from the other chips in the species' repertoire (Table 2) in being higher pitched, with the main band between 7.9–9.4 kHz and a second band around 20 kHz.

Calls in response to a predator.—We observed only one case of a reaction to a pred-

ator, a Northern Pygmy-Owl (*Glaucidium gnoma*), which was perched about 1 m from a feeder. Five Blue-throated Hummingbirds (unknown sex) flew at the owl giving loud chips. The owl then flew and was followed closely by the chipping hummingbirds. Calls of different individuals overlapped, a pattern often associated with oscine mobbing (MSF unpubl. data). Because of these conditions, the exact number of individuals calling was unknown. Mobbing Chips (Table 2) were of shorter duration than either male or female chips ($t = 11.3$, $df = 37$, $P < 0.0001$) and were higher in frequency ($t = 3.38$, $df = 23$, $P = 0.030$) compared to female Single Chips. Mobbing Chips also differed from other types of chips in having a second band ranging from 7.8–9.3 kHz ($n = 10$; Fig. 1i), instead of the usual harmonic band for Single Chips or Serial Chips.

Another type of call, described as a "squeal," is uttered by both sexes and young in stressful situations, such as being handled (Williamson 2000).

DISCUSSION

Reproductive behavior.—As hummingbirds are polygynous with no pair bonds and no male parental care, females would be expected to exert strong selection for male traits. In many hummingbirds extreme sexual dimorphism, brilliant male colors, and often acrobatic aerial displays are associated with courtship (Wagner 1954, Johnsgard 1997, Schuchmann 1999). In Blue-throated Hummingbirds, sexual dichromatism is minimal, the male being distinguished from the female by a blue gorget, and in the dim light of its typical habitat even that difference may not be readily apparent. No aerial displays or exaggerated visual signals by males are associated with courtship (Wagner 1954; MSF unpubl. data).

Our observations of the reproductive behavior of Blue-throated Hummingbirds revealed some new aspects of hummingbird behavior. Unusual features included female territoriality near the nest, active and complex role of females in initiating sexual encounters (including aerial displays), courtship occurring in several stages, and the diversity and complexity of communicatory signals.

Males of many hummingbird species are territorial, and Blue-throated males are noted

for being very aggressive. However, time budgets showed that the use of more energetically expensive behavior involving flights (short chases, hovering, and the long chases characteristic of this species) were rarer than the presumably lower cost vocalizations. The discovery that vocalizations are an important component of hummingbird territory maintenance is not new, having been suggested previously for the highly vocal Anna's Hummingbird (Stiles 1982, Powers 1987).

These hummingbirds were unusual in having two different vocal systems involved in territorial behavior. Oscine song typically serves dual roles in territorial advertisement and mate attraction (Catchpole and Slater 1995). Blue-throated Hummingbirds have partitioned these functions in a different way, with song mediating close range interactions between males and attracting females. Serial Chips, on the other hand, were involved only in long distance territorial advertisement.

Males advertised territorial boundaries through strings of loud Serial Chips often from an exposed perch near a stream, whereas songs were low amplitude and sometimes were delivered when a male was hidden. Blue-throated Hummingbirds preferred riparian habitat, a noisy environment in which chips probably were effective for long distance communication. Head turning movements during chipping broadcast the signal in many directions and increased its effectiveness. Even when silent, they were alert and surveyed their environment, immediately pursuing conspecific interlopers. Chipping birds usually were not approached by conspecifics.

Playback results also strengthened our interpretations that Serial Chips and song had different roles in territorial behavior, as close approach to playback was associated only with song. Serial Chips seemed to transmit the message of territory occupancy, and may inhibit intrusions by other males. Song also indicated ownership, but was not the primary means of excluding other males, serving instead as a short distance threat (characterized by very low amplitude). Song often was associated with agonistic encounters, and other males sometimes approached a singer. Other indications for song playing a strong role in sexual behavior were that longer songs (hence more complex ones), and longer singing bouts

occurred when reproductive activity was at its height. In oscines, female preference for song complexity is an important component of sexual selection for many species (Catchpole and Slater 1995). In Blue-throated Hummingbirds where the male and female may not share feeding areas (Wagner 1952), sexual contact is limited, and the male does not participate in parental care, female choice may be based at least in part on characteristics such as song composition, song length, and bout composition.

Males did not respond to playback of female song. Under natural conditions female singing usually occurred only when she was close to the male (Ficken et al. 2000), so it is not surprising that males did not respond to playback of this song in her absence.

Females defended an area near the nest against other females from late nest building until completion of egg laying (Wagner 1952; MSF unpubl. data). Serial Chirps by females evidently serve as territorial advertisement during the few days of sexual activity. The most likely hypothesis for this short term defense of a site where sexual activity occurred is that females competed for access to males. As nests had already been constructed, females' competition for access to nest locations is an unlikely explanation for female aggressive behavior.

Montgomerie and Thornhill (1989) noted that loud calls of female Red Junglefowl (*Gallus gallus*) and Lapland Longspurs (*Calcarius lapponicus*) during the fertile periods attracted males, and suggested that the phenomenon is more widespread, and that the calls advertise fertility and incite male-male competition. They predicted that such calls should be most common in species that are not strictly monogamous. They noted the difficulty of studying such calls in the wild because fertile periods of birds are so short. We heard calls only when females were in the preincubation period. The calls were exceptionally loud for hummingbirds, and experiments supplemented our observations that males approached calling females and if more than one male was present intense male-male competition resulted (MSF unpubl. data). As the sexes often were spatially segregated, vegetation was dense, and females were sexually receptive only a few days for each brood, the impor-

tance of female signaling sexual readiness was apparent. Females may be unreceptive to male approaches, even reacting with snarling attacks (Williamson 2001; MSF unpubl. data).

The traditional view of hummingbird courtship is of advertising males and relatively passive females (Johnsgard 1997, Schuchmann 1999). In contrast, female Blue-throated Hummingbirds were very active in initiating sexual activities. Females may evaluate a male's fitness based on his singing, by his response to her behavior, such as *Tias* and River Dance, and by his pursuit chases. Furthermore, as male-male competition also was intense during this period, females may selectively mate with the winners of those contests, as those males were more likely to remain nearby. Males on the other hand, had the opportunity to assess female fitness based on her precopulatory activities.

While there were no reports of copulations for this species in the literature (there are very few for any hummingbird species), these events shared some similarities with a report of copulation in the Magnificent Hummingbird (Stiles pers. comm. in Powers 1996), another species lacking male aerial courtship displays. The sexual behavior followed singing by the male who then chased the female to a low perch and uttered whisper songs while facing her. Cloacal contact followed alighting on her back, with only a few seconds of contact.

Communicatory repertoire.—We have described the major communicatory signals of this species, allowing us to assess repertoire size, diversity, and usage, and make preliminary comparisons with some other species. Indications that hummingbirds are a neglected group is provided by the most recent bibliography of avian vocalizations that lists 359 publications, with only one on hummingbirds (Hansen 1997).

Decisions on classifying and determining the size of vocal repertoires often are difficult because of intermediates (grading) and other problems arising from the lack of distinct categories (Hailman and Ficken 1996). On the basis of acoustic properties and usage, we identified 16 acoustic signals in Blue-throated Hummingbirds (male song, female song, female *Tia*, male Soft Trill, Staccato Trill, *Zeet*, Long Call, Complex Long Call, Short Call,

female Single Chip, male Single Chip, male Serial Chip, female Serial Chip, Fledgling Chip, Mobbing Chip, and distress Squeal). Bill cracks occur during agonistic encounters as an outcome of physical contact, but may have communicatory salience. In addition, wing buzzes could have signal functions.

Many of the sounds produced by these hummingbirds were acoustically simple. The most complex vocalization, male song, consisted of an array of different notes with a precise syntax (Ficken et al. 2000). Female song consisted of a more limited number of different notes and was of shorter duration (Ficken et al. 2000). The Long Call occurring in agonistic encounters usually was a repetition of a single note, but more rarely an array of diverse notes (Complex Long Call).

Some diversity of messages may be achieved by slight modifications of acoustic structure. For example, the B unit, a common element in male songs (Ficken et al. 2000), served as a precopulatory call when at low amplitude and not accompanied by other song elements. On the other hand, a loud version with longer internote intervals and a staccato quality (Staccato Trill) was associated with aggression and never with sexual encounters (Ficken et al. 2000). These hummingbirds utilized chips, some with slight but consistent differences in several contexts, and some differences probably were indicative of different messages. For example, Fledgling Chips were higher pitched than other chips, as might be expected of a short range signal. Single Chips may serve as an announcement of presence, and here the sexes differed. Females not only chipped much less frequently than males, but their chips also were much shorter, although about the same pitch as those of males. Serial Chips by both sexes were delivered in different circumstances than Single Chips, and evidently served as territorial advertisement. The female sexual call (*Tia*) was a string of very rapid short chips of a different quality than other sounds in the repertoire. Mobbing Chips exhibited some frequency and temporal differences when compared with other chips.

Interspecific comparisons of vocal repertoires are even more difficult than intraspecific ones, but some insights may arise from generalities among communicatory categorization in unrelated species. In petrels, a well-studied

group of nonpasserines, functional categories of vocalizations include food begging of young, copulation calls, agonistic calls, contact calls (to avoid others during flight), and those used in courtship and agonistic behavior for a total of 6–8 different calls (Bretagnolle 1996). Blue-throated Hummingbird vocalizations fell into similar general functional categories, but this species lacked contact calls and had more elaborate sexual and agonistic signals than petrels, as well as two calls used for predators (mobbing and distress). A non-oscine passerine, the Eastern Phoebe (*Sayornis phoebe*), has nine vocalizations (Smith 1977). The Black-capped Chickadee (*Poecile atricapilla*) has a repertoire of about 13 different vocalizations (Hailman and Ficken 1996). A pinnacle of repertoire size is the 26 sound signals of the Village Weaver, *Ploceus cucullatus* (Collias 2000). With about 16 different vocalizations, Blue-throated Hummingbirds were at the high end of the number of different acoustic signals in an avian species' repertoire, although the complexity of the sounds (except for male song), was not as great as that of most oscines. It is impossible to do more than approximate the actual number of signals based on structure and usage without performing experiments to determine how Blue-throated Hummingbirds categorize calls.

The variety of visual signals was more limited than the vocal repertoire and involved tail, wing, and body movements. Tail spreading and rapid tail shuffling occurred in several contexts and exposed the large white tail spots of both sexes. Wing waving served as a threat when another hummingbird approached. Crouching was more graded, varying from a slight crouch to the bird actually falling over backwards on the perch. Not only was this a complex series of postures, but the message potential also was extended by a variety of sounds associated with these acts. Such multimodal signals can provide more information than signals using only one sensory modality (Partan and Marler 1999).

Some differences between hummingbird species with aerial displays and Blue-throated Hummingbirds may be related to ecological conditions. Those with aerial displays often inhabit more open areas than Blue-throated Hummingbirds. Blue-throated Hummingbirds

favor shaded riparian areas, and their plumage dichromatism is limited. The evolution of complex song probably was related to difficulties in detection of visual signals in these dense habitats (Ficken et al. 2000).

Complex signals by females may be related to being multibrooded with little territorial overlap with males. In the absence of female signals, such as *Tias* and River Dance, the male would have little opportunity to assess female reproductive state. In addition, the complex interactions of the sexes allowed both the male and female to assess fitness attributes of the other, and thus affect mate choice. Until recently, most studies of bird behavior, particularly those of vocalizations, have focused on songbirds. Clearly, other groups, such as hummingbirds, warrant more attention.

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