MALE SONG VARIATION OF GREEN VIOLETEAR (*COLIBRI THALASSINUS*) IN THE TALAMANCA MOUNTAIN RANGE, COSTA RICA

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ABSTRACT.—We studied variation in acoustic and temporal characteristics of the static male song of the Green Violetear (*Colibri thalassinus*) in a single population in Costa Rica. The static song of 19 males was extremely variable. The song has two elements: the first was delivered exclusively at the beginning of each song while the second was present once, twice, or three times in the song of different males. Low frequency (LF), song duration (ΔT), and high frequency (HF) varied significantly among most individuals. The male population of Green Violetear has four song types that differ in acoustic and temporal characteristics. The great inter-male song variation suggests this type of vocalization may be under sexual selection. *Received 2 February 2007. Accepted 17 January 2008.*

Song variation among individual birds is well known for oscine and psittacid species (Farabaugh and Dooling 1996, Kroodsma 1996). Learning in these birds has an important role in syntaxes and structure of the song. This variation may have evolved to facilitate social interactions and/or by intra- or inter-sexual selection (Kroodsma 2004). Male reproductive success in birds is often associated with striking displays, such as complex songs, resulting from sexual selection (Catchpole 1982, Searcy and Yasukawa 1983, Johnsgard 1994, Kroodsma 2004).

Individual song variation is relatively unexplored in hummingbirds, another song-learning bird group (Baptista and Schuchmann 1990, Gaunt et al. 1994, Jarvis et al. 2000). Gaunt et al. (1994) showed that male Green Violetear (*Colibri thalassinus*) in neighboring populations share song types and similarity decreases with geographical distance. The extent of intra-population variation in male song has not previously been reported for this hummingbird.

Male Green Violetear show little (if any) aggressive physical interactions with other males during the breeding season (e.g., darting chases) and visual displays are apparently absent. Territorial males sing nearly continuously during courtship from before dawn until sunset (Slud 1964, Feinsinger 1977). Males begin to sing in September and some continue until the end of March, investing up to 84% of daily time to this activity (Skutch 1967, Wolf 1976). The objective of our study was to describe the variation in male song features within a population of Green Violetear.

METHODS

We conducted fieldwork at the Estación Biológica Cuericí, Talamanca Mountains, Costa Rica (09° 33′ N, 83° 40′ W; elevation 2,600 m) during the dry season in January 2004. The area is dominated by oak (*Quercus* spp.) forest intermixed with several successional growth stages with abundant flowering plants: *Fuchsia paniculata*, *Bomarea costaricensis*, *Lamourouxia lanceolata*, and *Centropogon* spp. We recorded the static songs (song uttered by perched birds) from 19 males singing from exposed perches, ranging from 8 to 25 m in height, on a 1.5-km transect along the primary road (4 m wide); 12 males were recorded one morning and seven the next morning. Singing males were separated by 20–100 m and perched at most 10 m into the forest ($n = 17$), facing the main road, or in a forest gap ($n = 2$). Each bird was recorded once for

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at least 2 min or until the bird became silent. We recorded the hummingbirds sequentially as we walked along the road to avoid recording the same individual more than once. Because of their high density, we could, in most cases, listen to the hummingbird previously recorded when we began to record the next focal individual. We considered singing males as territorial individuals following Skutch (1967); however, identifying territory limits was difficult, due to few aggressive interactions by males of this species. We define a male territory as a circular area of 20 m in diameter around the perch the singing male was most frequently using.

We recorded songs using a Telinga Pro II Parabola and a Marantz PMD-222 tape recorder, and analyzed the songs using the program CANARY Version 1.2.1 (Charif et al. 1993). Tapes were deposited at the Laboratorio de Bioacústica, Escuela de Biología, Universidad de Costa Rica. Spectrograms were obtained with a filter bandwidth of 349.70 kHz, frame length of 256 points, and a sampling rate of 44,100 Hz. We identified the elements of the song, defining a song as a string of notes or elements, temporally separated from other such strings; an element was the shortest consistently recognizable trace on a sound spectrogram (Marler and Peters 1982). We randomly selected five songs separated by at least 10 sec to analyze the among-individual song variation from the total record of each hummingbird. We measured eight variables for each complete song: high frequency (HF), low frequency (LF), frequency range or bandwidth (ΔF) (HF-LF), peak frequency (PF, frequency with highest amplitude), peak time (PT, time with maximum amplitude), duration in seconds (ΔT), time elapsed between two consecutive songs (T1), and time between the first and the second element (T2). We also quantified the number of songs and elements delivered in a random selected minute for each individual.

We used a multiple analysis of variance (MANOVA) on six song variables (ΔT, LF, HF, PF, T1, and T2) to examine the difference of these variables among individuals (based on a Discriminant Function Analysis (DFA), ΔF and PT were excluded because they did not differ among individuals). One-way analyses of variance and *posteriori* tests (Duncan)

were conducted to examine which particular variables differ among individuals. We classified the song of the hummingbirds into four types based on sonogram images, and used stepwise Discriminant Function Analysis (DFA) to test whether hummingbirds could be separated into four groups by their song features. We also recorded the following information during 6 days: non-systematic observations of aggressive interactions and presence of flower patches near perches of singing males. Means $\pm$ SD are presented.

RESULTS

The 19 male Green Violetears apparently held the same territories for at least 6 days as the same perches were occupied by singing males day after day and we assumed the same males were present. Territories included 2–3 perches from which males sang; they spent most of their time on one of them. The number of males singing appeared to decrease from the forest border to the interior, except when a gap was present, in which case the number of males singing increased near the gap edge.

Territories of the 19 recorded males varied by presence of flower patches used as nectar sources for hummingbirds. Twelve territories (main song perches) were within 10 m of large patches of *Fuchsia paniculata*, which were frequently visited by Green Violetears and Volcano Hummingbirds (*Selasphorus flammula*). Attacks between individual Green Violetears were rarely seen although the presence of an individual in a flower patch occasionally triggered an attack by a singing male. The absence of obvious sexual dimorphism prevented us from knowing whether these few attacks were directed preferentially at males.

Males sang from before dawn until dusk, only abandoning their perches to briefly visit nearby flower patches for feeding or to capture insects on the wing with short sallies. The song of all males included two different elements (Fig. 1). The first element (a) was produced only once in the song of all individuals. Element (b) occurred once in the song of nine males (song type 1), twice in the song of seven individuals (type 2), three times in two other males (type 3), and one or two times in songs produced by another male (type 4). On average, males produced 64.2 ($\pm$ 8.8, range:
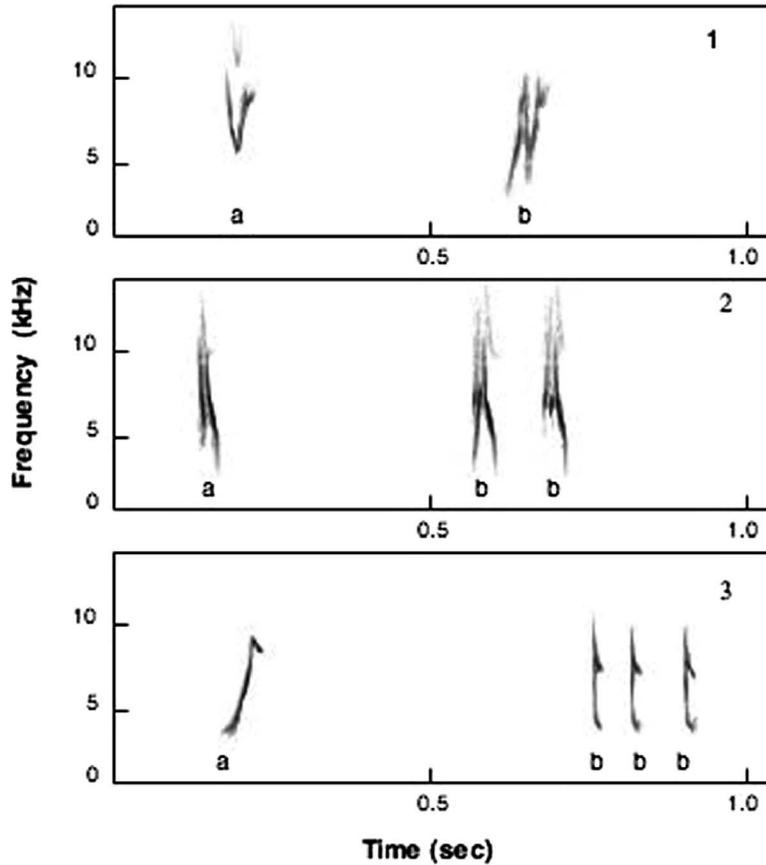
FIG. 1. Spectrograms of the variation in number of elements, and structural characteristics of elements and songs of three male *C. thalassinus*. Element (a) was present only once, at the beginning of each male's song, while presence of element (b) varied from one to three in songs of different males.

42–76.5) songs and 163.6 (± 33.7, range: 126–231) elements per minute.

Structurally, the frequency range and highest frequency were features of the static song that had the largest range (max-min values) for the 19 males: 11.06 and 9.08 kHz respectively (Table 1). The time between the first and the second element (T2), followed by frequency range (ΔF), had the largest variation (CV) among individuals. Number of songs delivered by individual per minute decreased with song duration ($r = -0.41$, $n = 19$, $P = 0.08$). However, the number of elements ($r = 0.17$, $n = 19$, $P = 0.49$) produced per minute was not related to ΔT. The large variation in ΔF was primarily caused by individual variation in both HF and LF.

We compared six characteristics of the complete song (ΔT, LF, HF, PF, T1, and T2) among individuals using a MANOVA. The comparison of all song features showed significant differences among individuals ($F_{108,414} = 21.66$, $P < 0.001$). Significant differences were also found among individuals when variables were analyzed separately (one-way ANOVA and Duncan tests). Variables that differed among most individuals were LF (16 males: $F_{18,76} = 57.64$, $P < 0.001$), ΔT (14 males: $F_{18,76} = 47.27$, $P < 0.001$), and HF (13 males: $F_{18,76} = 77.56$, $P < 0.001$). Variation among individuals was lower for PF (8 males: $F_{18,76} = 6.32$, $P < 0.001$), T1 (4 males: $F_{18,76} = 2.59$, $P = 0.002$), and T2 (4 males: $F_{18,76} = 26.62$, $P < 0.001$).

Male Green Violetears were divided in subgroups based on structural and temporal characteristics of their song. DFA separated the males of this population into four groups

TABLE 1.   Characteristics of high frequency (HF), low frequency (LF), bandwidth (ΔF), peak frequency (PF), time duration (ΔT), time between two consecutive songs (T1), and time between the first and the second element (T2) for the complete song of 19 male Green Violetears in Costa Rica.

	HF (kHz)	LF (kHz)	ΔF (kHz)	PF (kHz)	ΔT (sec)	T1 (sec)	T2 (sec)
Mean	10.98	3.16	7.82	6.11	0.58	0.37	0.33
SD	2.19	0.57	2.36	0.81	0.10	0.03	0.15
CV	19.90	17.98	30.17	13.31	17.73	8.86	44.41
Range	9.04–18.12	2.08–4.82	4.28–15.34	4.05–8.53	0.42–0.95	0.30–0.51	0.069–0.84

($F_{15,240}$ = 11.98, P < 0.0001) based on six variables (ΔT, LF, HF, PF, T1, and T2), and classified 82% of the songs correctly.

DISCUSSION

The difference in characteristics of the static song among male Green Violetears was high. This difference individualizes most singing males in the population, suggesting a possible role of inter- and intra-sexual selection (Morton 1986, Searcy and Andersson 1986); however, other factors such as age may also affect song characteristics. Frequency range in the song of *C. thalassinus* is possibly the feature from which the receiver (e.g., a female) obtains greater information, particularly when the song is composed by short, broad bandwidth elements or notes (Fig. 1, Table 1). This characteristic permits more precise location of singing males (Smith et al. 1978, Richards and Wiley 1980). Additionally, males producing songs with a wide frequency range may conceal the songs of other males, if these males' songs have a narrower bandwidth that fit in part of the range of frequencies of other males.

Despite the high variation in this population of male Green Violetears, groups of males produced similar song types. This suggests the presence of "different dialects" in a single population. However, causes of inter-group song differentiation are difficult to explain. Dialects usually evolve through geographic or microgeographic isolation (Kroodsma 1996) but, in this case, geographic isolation seems not to be the cause, since this species breeds in the area and then migrates to lower elevation during the non-breeding season (Skutch 1967). In addition, young hear songs of adult males as males sing well beyond when fledglings abandon their nests (GB, pers. obs.). A possible explanation is the "song relearn hypothesis" proposed by Kroodsma (2004) to explain temporal song variation in dialects of the Three-wattled Bellbird (*Procnias tricarunculatus*). This hypothesis proposes that adult birds "relearn" their songs throughout their life, and modify their songs through competition (by imitation) with familiar rivals. For this hypothesis to be possible, groups of males have to hear and recognize neighboring males (Aoki 1989); this is the case with Green Violetear. Consequently, at a particular time lag, different songs could be present in a single population. However, spatial distribution of song types is needed to begin testing this hypothesis.

The information available allows us to compare variation of song traits of *C. thalassinus* with other Trochilinae hummingbirds. The number of elements in the song of *C. thalassinus* is small compared to songs of Anna's Hummingbird (*Calypte anna*) (Stiles 1982), Blue-throated Hummingbird (*Lampornis clemenciae*) (Ficken et al. 2000), Amethyst-throated Hummingbird (*L. amethystinus*), and Green-throated Mountaingem (*L. viridipallens*). The number of elements is similar to Magnificent Hummingbird (*Eugenes fulgens*) (Ornelas et al. 2002) and more complex (e.g., more elements and frequency modulation) than the static song of its congener Sparkling Violetear (*Colibri coruscans*) (Gaunt et al. 1994). A characteristic present in all songs of this small sample of hummingbirds is the wide frequency range (bandwidth), although both species of the genus *Colibri* present the narrowest bandwidth. Song complexity is not higher in those species lacking visual displays, such as *C. thalassinus*, when compared to species with complex visual displays, such as *C. anna* and *L. amethystinus*. These results should be viewed with caution because number of elements and acoustic structure of hum-

mingbird songs may be strongly influenced by environmental and phylogenetic features (Irwin 1988, McCracken and Sheldon 1997). These aspects can be more closely analyzed within the monophyletic genus *Colibri*. When features of the song are compared between *C. thalassinus* and *C. coruscans*, the two highland species of the genus (Gaunt et al. 1994), the static song of *C. thalassinus* has a higher number of elements. However, *C. coruscans* produces a ''dynamic song'' that males sing during a diving flight as part of the courtship display, which is absent in *C. thalassinus*. This supports Wagner's (1954) suggestion that species lacking elaborate dynamic songs have complex static songs, and suggests the two highland species of the genus have evolved different courtship strategies. The other two species in the genus, *C. delphinae* and *C. serrirostris* are mid-elevation and apparently territorial (Stiles and Skutch 1989, Schuchmann 1999). Little is known about the vocalizations of these two species.

ACKNOWLEDGMENTS

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