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TEMPORAL PATTERNS OF SINGING ACTIVITY AT LEKS OF THE WHITE-BELLIED EMERALD

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ABSTRACT.—The White-bellied Emerald (*Amazilia candida*), a sexually monomorphic, dull-plumaged hummingbird, forms singing assemblies that are assumed to function as leks. Within each lek, individuals use and defend specific display perches throughout the day. These perches are visually isolated from one another, and song is the principal form of display. Although some song is given throughout the day, peak activity occurs during the first hour of daylight; a second, more protracted period of display occurs during the 3 hours preceding sunset. The number of songs given by individuals is positively correlated with the number of birds present on the lek, and individuals that are consistently present throughout the day sing more songs when present than do birds that attend the lek only sporadically. *Received 5 Sept. 1990, accepted 19 March 1991.*

RESUMEN.—Amazilia Pechiblanca, un colibrí de plumaje apagado y sin diferenciación sexual, se congrega en formaciones de canto que se asume tienen funciones reproductivas (asambleas reproductivas ó "leks"). Dentro de cada una de estas asambleas reproductivas, los individuos utilizan y defienden perchas específicas a lo largo del día. Estas perchas están aisladas visualmente las unas de las otras, y el canto es la forma principal de exhibición. Aunque cantos aislados ocurren durante el día, la actividad máxima occure durante la primera hora de luz en la mañana; un segundo período de actividad ocurre durante las 3 horas previas a la puesta del sol. El número de cantos que cada individuo exhibe está positivamente correlacionado con el número de aves presentes en cada una de estas asambleas reproductivas, y los individuos que están presentes en estas asambleas reproductivas en forma constante cantan mas que los individuos que están presentes solo en forma esporádica.

Bird species with lek mating systems are often characterized by pronounced sexual dimorphism (Payne 1984). However, Trail (1990) found that approximately one-quarter of all lekking birds were sexually monomorphic in size and plumage, thus raising the question of how monomorphism may persist under the intense pressures of sexual selection that generally characterize lek systems (Bradbury and Gibson 1983, Beehler and Foster 1988). Höglund and Lundberg (1987) and Höglund (1989) proposed that vocal behavior may represent "an alternative target of selection" in monomorphic lek species. In contrast, Trail (1990) suggested that monomorphism in lek birds may result from intense intrasexual competition among both males and females; in this assessment, "social

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selection on females has counterbalanced sexual selection on males to produce monomorphism as an evolved dynamic equilibrium."

Further debate about these hypotheses is hindered by the general lack of data concerning monomorphic, lekking species (Trail 1990). The White-bellied Emerald (*Amazilia candida*) is a small, sexually monomorphic, dull-plumaged hummingbird distributed in Central America from southern Mexico to Nicaragua (American Ornithologists' Union 1983). Although Stiles and Skutch (1989) briefly mentioned that "males may form loose courtship assemblies," no other information appears to be available concerning the behavior of the species. In this study, we present a preliminary description of song behavior in White-bellied Emeralds, including evidence that singing assemblies function as leks. Furthermore, we summarize available data concerning the occurrence of lek behavior in the Trochilidae.

STUDY AREA AND METHODS

We studied White-bellied Emeralds in the Rio Bravo Resource Management and Conservation Area of the Orangewalk District of northwestern Belize (17°50'N, 88°55'W) from 14 February–16 March 1990. On average, these dates coincide with the beginning of the dry season (<100 mm rainfall per month) (Wright et al. 1959). Daily temperatures ranged from approximately 18–27°C; on the night of 18 February, temperatures dropped to approximately 10°C as a result of a major cold front. The moist, subtropical habitat of the Rio Bravo area has been described as "medium-high, semi-deciduous forest" (Pennington and Sarukhan 1968) or "upland broadleaf forest" (N. Brokaw, pers. comm.). Although the area was probably cleared to varying degrees by the Mayan civilization, for the past 900–1000 years the forest has experienced relatively undisturbed regrowth with managed selective logging, and it presently is in a late successional stage. Vertical structure of the habitat is heterogeneous; most upper canopy trees range from 20–30 m in height, with a fairly dense understory of shrubs and saplings. Important families of trees represented in the upland broadleaf forest include Sapotaceae, Leguminosae, Moraceae, Apocynaceae, Meliaceae, and Palmae (N. Brokaw, pers. comm.).

We identified, marked, and mapped the locations of song perches used by White-bellied Emeralds during several days of preliminary observations at each of three leks (A, B, C). Later, on two consecutive days at each lek, we counted the number of songs delivered by six birds at Lek A, three birds at Lek B, and four birds at Lek C; counts recorded the total number of songs delivered by each bird during 48 consecutive, 15-min periods, from 06:00 to 18:00 h. We were unable to capture and uniquely mark individual birds. However, we assumed that we could distinguish individuals based on their highly stereotyped use of specific song perches and our frequent ability to have all singing birds under simultaneous observation by up to seven assistants. In addition to the 312 h of focused observations, supplemental data were collected during numerous, shorter visits to nine additional leks.

Temporal patterns of singing behavior were analyzed using a standardized index of daily song activity, as measured by the percent of an individual's daily total songs that were delivered during each 15-min period. Birds that gave many songs during a day were thus weighted equally with birds that sang few songs. Individual percentages were then used to calculate a mean percentage for each period on a given date. Because low light intensities

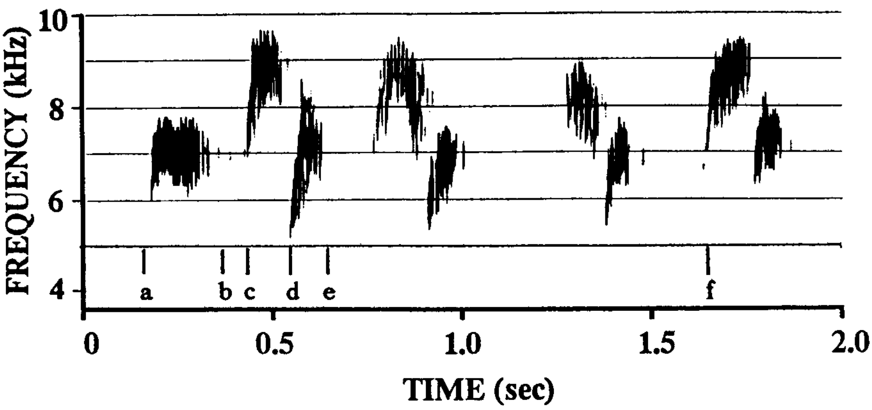

FIG. 1. Song characteristics used in analysis of temporal variation. INTRO = average frequency (kHz) of introductory note, located between a and b; FREQ-I = average frequency (kHz) of first syllable of first paired phrase following the introductory note, c–d; FREQ-II = average frequency (kHz) of second syllable of paired phrase, d–e; LAG = time (sec) between starts of the first and second syllables, d–c; DELIVERY = number of paired phrases delivered per sec, based on time interval from c–f. Additionally, the number of paired phrases delivered in each complete song (PAIRS) was counted.

made it impossible to locate singing birds immediately prior to sunrise, we excluded songs given before 06:00 h.

To evaluate daily variation in vocalizations, we tape recorded songs given from a single perch, presumably by the same individual, at five different times on 10 March. Recording equipment consisted of a Marantz PMD221 cassette recorder, a Sennheiser ME88 directional microphone, and TDK IECII/Type II High Position tapes. We used a Kay Elemetrics DSP Sona-Graph model 5500 to analyze five randomly selected songs representing each time period. Song parameters measured directly from the digital display (Fig. 1) included (1) INTRO—average frequency (kHz) of single, introductory note, (2) FREQ-I—average frequency (kHz) of the first syllable of a song's initial paired notes, (3) FREQ-II—average frequency (kHz) of the second syllable, (4) LAG—time (sec) between start of the first and second syllables, and (5) DELIVERY—number of paired notes given per second. Additionally, we counted the number of paired notes (PAIRS) in all songs recorded during the five time periods.

RESULTS

General description of lek behavior.—A total of 12 White-bellied Emerald leks were observed. Eleven leks were located adjacent to abandoned logging roads where the forest canopy was intact overhead; one lek was found along a 2-m-wide dry stream bed, again with a closed canopy. We found no leks in approximately 10 km of edge habitat located adjacent to a large (15–20 m wide) road where the forest canopy was broken; most display territories within leks were not situated in distinct open areas or edge habitat. The two closest leks were separated by approximately 0.5

km of continuous forest habitat. However, because our exploration of the Rio Bravo area was essentially limited to irregularly spaced roads or trails that provided access into the dense vegetation, we have no data regarding the actual density of White-bellied Emerald leks.

At three intensively studied leks, minimum estimates of the number of birds regularly present were six (Lek A), three (Lek B), and seven (Lek C). Lek members appeared to defend territories of up to approximately 450 m^2 that included two to three specific song perches. The location of these perches appeared to be largely stable throughout the month-long period of our study. Nearest neighbor distances between the approximate center of each territory varied from 14–32 m ($\bar{x} = 25.8 \pm 6.5$ [SD], N = 13). Territories on Leks A and C were spatially distributed such that one or two individuals held what might be considered "central" locations; no central territory was evident in Lek B, which included only three birds dispersed approximately equidistant from each other.

Typical song perches were located on slender, bare branches or lianas that extended into relatively open portions of the mid-canopy. Most were 10–15 m above ground level, although three birds with territories located in lower (3.5–6 m), seasonally inundated riverine vegetation sang from perches only 3 m high. Because of dense vegetation, distance, and in some cases topography, most displaying individuals probably could not see their nearest neighbor. Although each lek member was in audio contact with at least one, and usually more, adjacent territory holders, some birds were separated by as much as 120 m and probably could not hear each other's songs.

Lek displays appeared to consist entirely of song, which generally included a variable number of repeated, paired notes (Fig. 1) that were usually delivered while perched. Detailed characteristics of these songs differed dramatically among leks but were consistent within leks; these data will be presented elsewhere. Singing birds rapidly moved their heads from side to side, but this hummingbird species has no irridescent gorget, auricular, or crown feathering that might be flashed by such movement, nor is the dull pinkish base of the mandible evident except at close range. No pronounced flicking of wings or tail occurred while singing.

Interactions between White-bellied Emeralds on the lek consisted of high speed chases through the forest mid-canopy, accompanied by rapid, chattering calls. Such chases were especially common immediately prior to dawn, when birds arrived in the area and presumably re-established ownership of specific display territories. Because we could not distinguish sexes, we are unable to exclude the possibility that some chases may have involved male–female interactions or males attempting to disrupt courtship activities elsewhere on the lek. However, in most cases birds returned to their perch and resumed singing within seconds of initiating a chase, suggesting that most of these interactions represented defense of a display territory from intruding males. We were unable to determine whether visual or vocal cues generally caused a singing bird to leave its perch. We observed no copulations during more than 300 h of focused observations.

Life history and foraging ecology.—Little is known about the life history of the White-bellied Emerald. We found a single nest, containing two young, that was located 2 m above the ground on a small branch of a 2.6-m-tall *Guettarda Coombsii* sapling. One of the two juveniles present in this nest fledged on 4 March; three days later the empty nest was collected and is now deposited in the collection of the Western Foundation of Vertebrate Zoology. No leks were found within earshot of the nest site. E. Mallory (pers. comm.) noted a general decline in White-bellied Emerald singing activity in the Rio Bravo area between early February and mid-April 1990.

Nearly all White-bellied Emerald foraging activity occurred away from the leks. Birds occasionally hovered near their song perches and appeared to glean arthropods from nearby foliage; very few flowers were present within the general vicinity of the leks themselves. Several flowering *Trichospermum mexicanum* (Tiliaceae) trees were found in the Rio Bravo Conservation Area, and White-bellied Emeralds were consistently observed feeding at these trees. No leks were found within hearing distance of the *Trichospermum* trees, and no songs were given by the foraging birds. Although we saw Rufous-tailed Hummingbirds (*A. tzacatl*), White-necked Jacobins (*Florisuga mellivora*), and Wedge-tailed Sabrewings (*Campylopterus curvipennis*) feeding on flowers of *Lisianthus axillaris* (Gentianaceae) and *Pseudobombax septenatum* (Bombaceae), we did not observe White-bellied Emeralds regularly visiting these species.

Temporal variation in lek display.—Based on data collected during a single day from individual C1, there appears to be no significant temporal variation in song characteristics (Table 1). However, singing activity showed a definite temporal pattern that was similar among leks and among days (Fig. 2). On most days (excluding 19 February, see below), over 20% of the total songs given on a lek occurred during a 1-h period beginning immediately prior to sunrise ($\bar{x}$ = 22.6% [2.5], N = 5). Following this intense initial surge of singing activity, leks became virtually silent as all individuals left their display territories within an approximately 10-min period. Moderate levels of singing activity later resumed during mid-morning and continued through early afternoon; a secondary peak of song, more protracted but less intense than the early morning singing bout, occurred during the three hours preceding sunset.

Individuals sang more during intervals when larger numbers of birds

TABLE 1

TEMPORAL VARIATION IN SONG CHARACTERISTICS OF INDIVIDUAL C1 ON 10 MARCH 1990

	Song characteristics[a]					
Time	INTRO (kHz)	FREQ-I (kHz)	FREQ-II (kHz)	LAG (sec)	DELIVERY (number/sec)	PAIRS
06:00	6.99 (0.07)	8.81 (0.10)	7.21 (0.09)	0.108 (0.01)	0.42 (0.04)	3.35 (1.5)
06:50	6.98 (0.05)	8.78 (0.06)	7.14 (0.31)	0.108 (0.01)	0.39 (0.01)	3.43 (1.7)
09:50	6.95 (0.09)	8.70 (0.22)	7.22 (0.23)	0.113 (0.00)	0.40 (0.03)	3.30 (1.4)
13:30	7.03 (0.11)	8.75 (0.27)	7.11 (0.11)	0.111 (0.01)	0.43 (0.04)	3.47 (1.4)
16:20	6.99 (0.08)	8.74 (0.24)	6.99 (0.23)	0.118 (0.00)	0.53 (0.26)	3.94 (1.8)
P[b]	0.693	0.924	0.464	0.096	0.401	0.458

[a] Song characteristics as defined in Methods. Mean, with standard deviation provided in parentheses. Sample size (N) = 5 for all characteristics except PAIRS; for PAIRS, N = 43 (06:00), 60 (06:50), 37 (09:50), 53 (13:30), and 32 (16:20).

[b] Probability of differences among times based on nonparametric ANOVA.

were displaying on the lek (Lek A–N = 93 periods, Spearman rank correlation $r_s = 0.252$, $P = 0.015$; Lek B–N = 95, $r_s = 0.251$, $P = 0.014$; Lek C–N = 78, $r_s = 0.448$, $P = 0.0001$). Also, combining data from all three leks, there was a significant positive correlation between the number of 15-min periods an individual was present during the day and the mean number of songs it delivered during those periods of lek attendance (Fig. 3). That is, individuals that were consistently present on the lek sang more during their periods of attendance than did birds that were only sporadically present. However, we note that this relationship was not clear when each lek was analyzed separately (Lek A, $P = 0.642$; Lek B, $P = 0.048$; Lek C, $P = 0.251$), suggesting either a spurious correlation associated with the combined sample or failure to detect a pattern caused by smaller within-lek sample sizes.

Although patterns of activity were similar on five of the six days included in the analysis, behavior of Lek C was dramatically different on 19 February (Fig. 4). Approximately 55% of the total number of songs on this date were given during the first 30 min following sunrise, as compared to a mean of 18% on the other five days. Similarly, only 2080 songs were delivered on 19 February vs 6594 on the preceding day. The singing behavior of one bird (C2) had returned to a more typical pattern on 14 March (Fig. 4), and our subjective impression was that this was also true for other members of Lek C.

DISCUSSION

Bradbury (1981) listed three main characteristics of species that form leks. These included (1) absence of male parental care, (2) spatial clustering of displaying males within habitat that included no resources required by

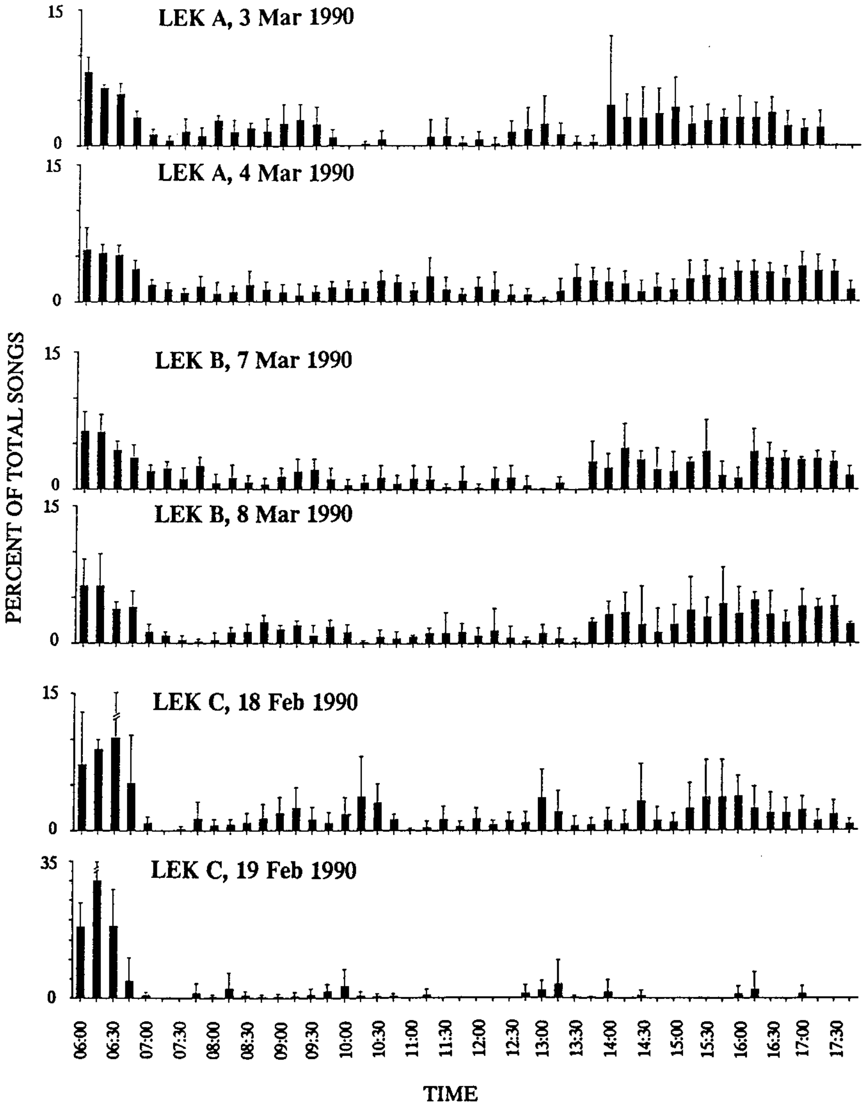

FIG. 2. Temporal distribution of singing activity in White-bellied Emerald leks. Each bar represents the mean percent of total songs occurring during a given 15-min period (+2 SE), based on standardized values for each individual in the lek (Lek A, N = 6; Lek B, N = 3; Lek C, N = 4).

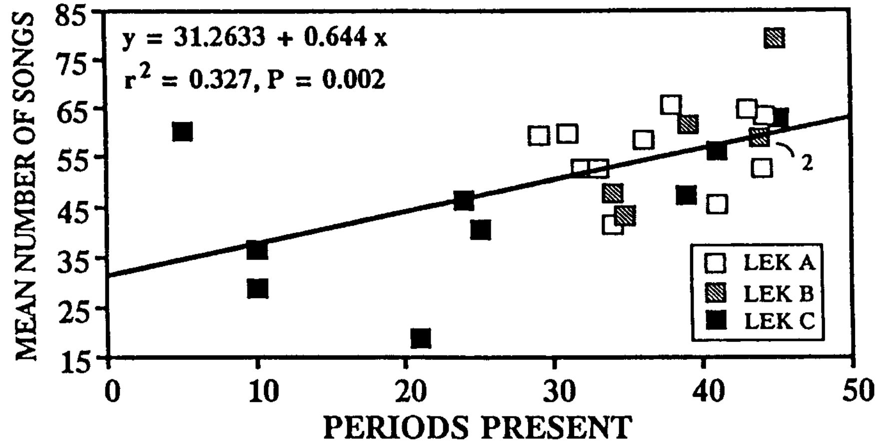

FIG. 3. Relationship between song delivery and lek attendance in White-bellied Emeralds. Mean number of songs given by each bird based on song counts during periods of attendance; "Periods Present" represents the total number of 15-min periods an individual was present during the day. Point labelled "2" represents exact coincidence of two data values at the given plot resolution.

females, other than the males themselves, and (3) ability of females to select a mate from a group of displaying males.

White-bellied Emeralds meet most, and probably all, of these criteria. In the majority of hummingbirds males do not participate in nesting or rearing of the young (Pitelka 1942), and we assume this to be the case with *A. candida.* White-bellied Emerald singing assemblies were spatially clustered, with no indication that this clumping was related to localized concentrations of food or other resources. Although the locations of singing assemblies may have been somewhat influenced by the slight forest gaps afforded by abandoned logging roads, White-bellied Emerald groups were clearly not uniformly distributed along these roads; furthermore, singing assemblies may have been found adjacent to abandoned roads simply because these trails were our almost sole means of access into the dense vegetation. Because we could not distinguish sexes of White-bellied Emeralds in the field, we can only assume that singing birds were males and that females visited assemblies for the purpose of selecting mates. However, the similarity of White-bellied Emerald behavior to that of several more thoroughly studied species of lekking *Phaethornis* hummingbirds (Snow 1968, Snow 1974, Stiles and Wolf 1979) suggests this is a reasonable assumption.

Few quantitative data have been presented regarding most aspects of

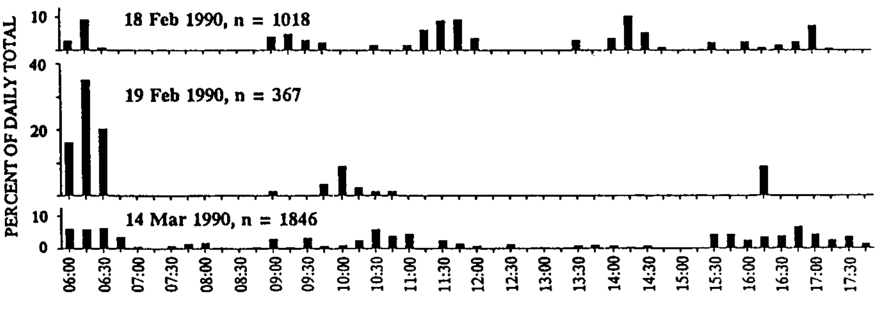

FIG. 4. Temporal patterns of singing by individual C2 on three dates. Each bar represents percent of total songs for indicated date occurring during a given 15-min period.

hummingbird lek behavior. White-bellied Emeralds and other described species of lekking hummingbirds are generally characterized by "exploded" lek systems (*sensu* Gilliard 1969), in which most displaying males are in audio contact with each other, but where direct visual interactions are limited or precluded by the combined effects of distance, terrain, or vegetation. Nearest neighbor distances between displaying White-bellied Emeralds varied from 14–32 m, with visual contact between adjacent individuals generally prevented by dense vegetation. Males displaying on presumed leks of the following species have been described as being separated by distances >15 m: Violet Sabrewing, *Campylopterus hemileucurus* (Skutch 1972); Blue-chested Hummingbird, *A. amabilis* (Skutch 1972); Rufous-tailed Hummingbird (Skutch 1981); Blue-throated Goldentail, *Hylocharis eliciae* (Skutch 1972); White-eared Hummingbird, *H. leucotis* (Skutch, in Bent 1940); Scaly-breasted Hummingbird, *Phaeochroa cuvierii* (Skutch 1964); and Violet-headed Hummingbird, *Klais guimeti* (Skutch 1958). Display territories in the genus *Phaethornis* (Long-tailed Hermit, *P. superciliosus*; Little Hermit, *P. longuemareus,* and Green Hermit, *P. guy*) may be separated by as little as 10 m (Wiley 1971, Snow 1974, Stiles and Wolf 1979), but visual contact between singing birds is, nonetheless, generally prevented by dense vegetation (Stiles and Wolf 1979).

The daily pattern of activity on White-bellied Emerald leks resembled that described for the Long-tailed Hermit (Stiles and Wolf 1979). In both species, an intense period of song and territorial defense began immediately prior to sunrise. About 1 h later, singing declined sharply as birds left the lek almost synchronously for what Stiles and Wolf (1979) termed a "breakfast break"; these authors found the timing of this break to coincide with the period of maximum nectar production in the flower species used by Long-tailed Hermits. Moderate levels of song activity resumed after the "breakfast break" and continued through early afternoon; a secondary peak in singing, more protracted but less intense than the morning display period, characterized the hours prior to sunset. Stiles and Wolf (1979) hypothesized that these daily patterns of activity resulted from selective pressures associated with (1) the unpredictable appearance of females on the lek, (2) the recurring need to defend dominance and territory ownership, and (3) the optimal timing of foraging periods relative to food availability.

Activity patterns observed at Lek C on 19 February contrasted markedly with those seen on the previous days at this site and with patterns observed on four other days at Leks A and B. The cause of this anomaly, in which very few displays were given after the early morning "breakfast break," is uncertain. However, the night of 18 February was unusually cold (approximately 10°C), and we speculate that the approximately 3.7-g hummingbirds' metabolic reserves may have been depleted to such a point that most of the following day was devoted to foraging rather than display. Wetmore (1968) observed a similarly sized (3.1 g) tropical hummingbird (Garden Emerald, *Chlorostilbon assimilis*) that was immobilized under windy, 20.8°C conditions.

As in the 21 other species of Central American hummingbirds that are known or suspected to form leks (Table 2), song appears to be the primary form of advertising display used by White-bellied Emeralds. Skutch (in Bent 1940), noted that hummingbird courtship displays were either "static" (song delivered from a fixed perch) or "dynamic" (aerial flight displays). We know of no species of lekking hummingbirds that use courtship flight displays.

Based on our observations, and descriptions of *Phaethornis* lek behavior provided by Snow (1974) and Stiles and Wolf (1979), we postulate that persistent and vigorous singing may determine which individuals succeed in gaining copulations with visiting females. Song delivery by individual White-bellied Emeralds was greatest during those periods when maximum numbers of lek members were present. Furthermore, birds that consistently displayed throughout the day sang more, when present, than did individuals that were only sporadically present on the lek. We suspect that display frequency and intensity may define dominance relationships among displaying males or be used by females as cues by which to select mates. Unfortunately, observed copulations at hummingbird leks are typically rare (Stiles and Wolf 1979), making it virtually impossible to directly compare the actual reproductive success of different males.

Höglund and Lundberg (1987) and Höglund (1989) proposed that sexual differences in vocal displays might be substituted for plumage or size

TABLE 2

SEXUAL DIMORPHISM IN CENTRAL AMERICAN HUMMINGBIRDS KNOWN OR SUSPECTED TO FORM LEKS

Species	Source[a]	Plumage[b]	Size[c]
Band-tailed Barbthroat (*Threnetes ruckeri*)	7	M	S
Green Hermit (*Phaethornis guy*)	9	D	M
Long-tailed Hermit (*P. superciliosus*)	11	M	M
Little Hermit (*P. longuemareus*)	8	M	M
White-tipped Sicklebill (*Eutoxeres aquila*)	11	M	S
Scaly-breasted Hummingbird (*Phaeochroa cuvierii*)	5	M	M
Rufous Sabrewing (*Campylopterus rufus*)	7	S	M
Violet Sabrewing (*C. hemileucurus*)	6	D	S
Brown Violet-Ear (*Colibri delphinae*)	2	M	M
Violet-headed Hummingbird (*Klais guimeti*)	4	D	S
White-eared Hummingbird (*Hylocharis leucotis*)	3	D	S
Blue-throated Goldentail (*H. eliciae*)	7	S	S
White-bellied Emerald (*Amazilia candida*)	1	M	M
Blue-chested Hummingbird (*A. amabilis*)	7	D	S
Charming Hummingbird (*A. decora*)	10	D	M
Cinnamon Hummingbird (*A. rutila*)	10	M	M
Rufous-tailed Hummingbird (*A. tzacatl*)	7	S	S
White-tailed Emerald (*Elvira chionura*)	10	D	S
Coppery-headed Emerald (*E. cupreiceps*)	10	D	S
Snowcap (*Microchera albocoronata*)	10	D	M
Amethyst-throated Hummingbird (*Lampornis amethystinus*)	6	S	n/a
Wine-throated Hummingbird (*Atthis ellioti*)	7	D	n/a

[a] Presence of lek behavior based on following references: 1 = present study; 2 = ffrench (1980); 3 = Skutch, in Bent (1940); 4 = Skutch (1958); 5 = Skutch (1964); 6 = Skutch (1967); 7 = Skutch (1972); 8 = Snow (1968); 9 = Snow (1974); 10 = Stiles and Skutch (1989); 11 = Stiles and Wolf (1979).

[b] Plumage characteristics: D = dimorphic; S = slightly dimorphic; M = monomorphic. Based on descriptions provided by Ridgway (1911).

[c] Size characteristics: D = dimorphic (female : male wing length ratio ≤ 0.90); S = slightly dimorphic (ratio = 0.91–0.94); M = monomorphic (ratio ≥ 0.95). Based on measurements provided by Ridgway (1911); n/a = data not available for both sexes.

dimorphism in lekking birds. That is, vocalizations could serve as an alternative "target" on which selection could operate, thereby allowing monomorphism to persist even in the context of the strong sexual selection found in lek mating systems. Trail (1990) argued against Höglund's (1989) hypothesis, instead suggesting that monomorphism might evolve in lek systems where there was strong selection for females to share male morphological characteristics. However, Trail's (1990) arguments focused primarily on the existence of monomorphic lek species in which both sexes possess exaggerated plumage characters; little attention was given to the problem of drab, monomorphic lek birds such as the White-bellied Emerald.

Twelve of the 22 species (55%) of known or suspected lekking hummingbirds in Central America, including the White-bellied Emerald, are sexually monomorphic or only slightly dimorphic in plumage (Table 2). All of the 20 species for which measurements were available are sexually monomorphic in size, based on Trail's (1990) criterion of 10% difference in wing length; using Höglund's (1989) more restrictive cutoff of 5%, 10 species (50%) are monomorphic, and 10 (50%) are slightly dimorphic in size (Table 2).

Unfortunately, few careful studies have been made of the social behavior of known or suspected lekking hummingbirds, and many authors have failed to distinguish between resource-centered groups, such as occur near localized food sources, and leks (Pitelka 1942). For example, Skutch (in Bent 1940) described White-eared Hummingbirds as forming song assemblies that were spatially clustered in areas of uniform habitat and compared the functioning of these groups to manakin (Pipridae) leks; however, Stiles and Wolf (1979) thought this species "probably" exhibited food-centered mating territories. Barash (1972) described what he considered lek behavior in the Broad-tailed Hummingbird (*Selasphorus platycercus*), but did not specifically exclude the possibility of adjacent, food-centered mating territories. Stiles (1973) and Stiles and Wolf (1979) suggested that the normally non-lekking Anna's Hummingbird (*Calypte anna*) may switch from typical food-centered mating territories to a lek mating system, depending on the spatial dispersion of available nectar resources. Even for species in the fairly well-studied genus *Phaethornis,* it is somewhat unclear whether lek behavior may be abandoned under certain ecological conditions and replaced by resource-oriented mating strategies (Davis 1934; Oniki 1970; Stiles and Wolf 1979; L. Wolf, in Bradbury 1981).

Stiles and Wolf (1979) discussed the evolution of hummingbird lek behavior and sexual dimorphism in the context of foraging ecology. These authors concluded that "the critical determinant" of whether a species exhibits a lek social system or food-centered mating territory was "whether breeding males can control rich feeding areas which then serve as mating stations." Furthermore, Wolf (1969) and Stiles and Wolf (1979) suggested that sexual dimorphism in hummingbirds is often related to agonistic behaviors associated with defense of feeding sources; the monomorphic Long-tailed Hermit seldom exhibited intraspecific territoriality at flowers. Similarly, Bleiweiss (1985) hypothesized that the bright male-like plumage of females in some populations of the Tourmaline Sunangel (*Heliangelus exortis*) may reflect the results of nonsexual social competition for food.

The preliminary data presented here underscore the need for further study of monomorphic, lekking birds, including species such as the White-bellied Emerald that lack exaggerated plumage characters. Available information is inadequate to address the relative merits of Höglund's (1989) behavioral transference hypothesis vs Trail's (1990) social selection hypothesis. Nonetheless, the intriguing diversity of mating and foraging systems exhibited within the Trochilidae, coupled with plumage characteristics that range from drab to extremely elaborate, suggest that behavioral studies focused on this family would provide valuable insights into sexual selection and the evolutionary basis of lek behavior.

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