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SINGING BEHAVIOR OF LEKKING GREEN HERMITS[1]

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Abstract. We examined temporal and spatial variation in singing behavior of lekking Green Hermits (*Phaethornis guy*). Song production by individual males was correlated to song production by their neighbors on the lek. There was significant variation among territories in the amount of time that males on these territories devoted to singing and the total number of songs produced. This variation appears to be related to territory location on the lek: males on sites near the center of the lek spent more time singing and produced more songs than did males on the periphery. Males also varied in the frequency (pitch) of songs produced, but this variation did not appear to be related to territory location.

Key words: *Green Hermits, leks,* Phaethornis guy, *song production.*

In many animal species, males gather in a lek, defined as an aggregation of displaying males that females attend primarily for the purpose of fertilization (Höglund and Alatalo 1995). Lek mating systems are extremely widespread taxonomically and have been observed in such diverse taxa as insects, cichlid fish, amphibians, mammals, and birds. Lek systems frequently are characterized by an extreme skew in mating success among males (Emlen and Oring 1977). Male mating success is correlated with numerous factors, including morphology, age, behavioral displays, and territory location (Höglund and Alatalo 1995).

Green Hermits (*Phaethornis guy*) are relatively large (6 g), sexually dimorphic hummingbirds which inhabit dense vegetation in highland Neotropical forests. During the breeding season, males form singing aggregations or leks, consisting of about a dozen males defending small territories from which they sing and perform visual displays. The ecology and breeding biology of Green Hermits have been described by Snow (1974, 1977) and Harger and Lyon (1980).

We examined temporal and spatial variation in singing behavior of Green Hermits in a highland cloud forest. We investigated (1) the correlation between song activity of individual males and the song activity of their neighbors on the lek, (2) variation across territories in singing activity and song frequency, and (3) whether this variation is correlated to territory position on the lek.

METHODS

We studied a lek of Green Hermits located along the Quebrada Aleman Trail, near Los Planes, Chiriqui, Panama, between 20–22 January 1997. The lek was located along both sides of a 70 m section of trail. During periods of peak activity, we estimated membership on the lek to be 12–15 birds. We assessed singing behavior at six focal territories, designated A, B, C, D, E, and F (Fig. 1). These focal territories were surrounded by several territories at which singing behavior was not measured. However, our study site bisected the lek as shown in Figure 1, so that sites designated as "central" or "peripheral" were in fact central or peripheral with respect to the lek as a whole. Males consistently sang from one or a few perch sites

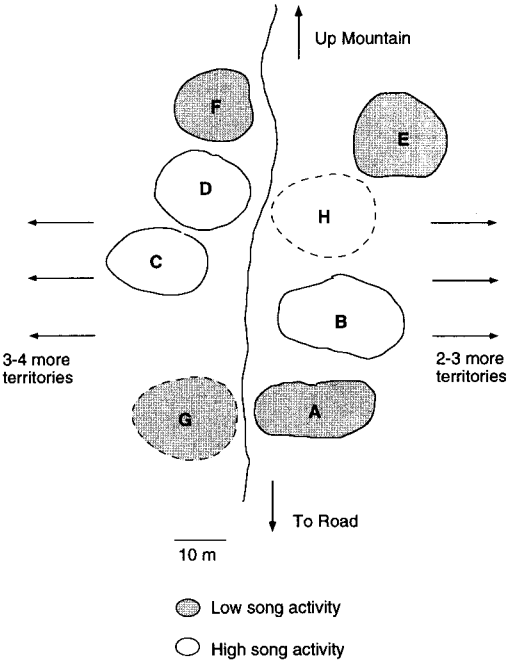

FIGURE 1. Approximate boundaries of six focal territories at which singing behavior was measured and song recorded (A–F, solid outlines), 2 additional territories at which song only was recorded (G and H, dotted outlines), and the approximate locations of the remaining territories which were not studied.

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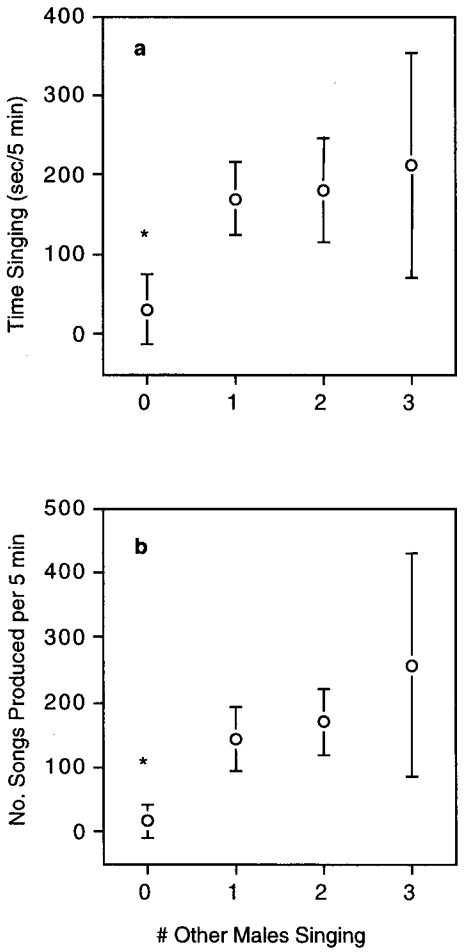

FIGURE 2. Relationship between the number of other males audible on the lek and (a) time spent singing and (b) number of songs produced on focal sites. Values are means ± SE. Asterisk indicates significant difference ($P < 0.05$), $n = 6$ territories, 12 observations each.

within these territories, enabling us to estimate singing rates at focal territories even though the birds were not individually marked.

We performed a total of 12 5-min watches at each focal territory, between 07:30 and 10:30 on three consecutive days. These watches were performed sequentially along the trail, so that all territories were sampled within 40 min of each other and effects of weather and time of day would be minimized. Weather conditions ranged from bright sun to moderate rain, but were generally consistent between days of the study. During each observation, we recorded the proportion of time that a male was singing at a given site, the number of songs produced during the 5-min interval, and the number of other males audible. Simultaneously, a second observer hiked quickly along the length of the trail and recorded which territories contained singing males at a given point in time; 45 such observations were made.

We investigated individual variation in song characteristics by recording the song produced by each focal male (at territories A–F), as well as that of two additional territory holders (at territories G and H; Fig. 1). Recordings were made with a Sennheiser ME-66 directional microphone and a Sony TCM-5000EV cassette recorder. Songs then were analyzed using Avisoft-Sonagraph Pro software (Avisoft, Berlin, Germany), using a sampling rate of 22,050 Hz and a sample size of 16 bits to digitize the sounds. Green Hermits produce a monosyllabic, broadband song with several harmonic overtones visible on the spectrogram. For each bird, we measured the mean frequency of the first harmonic in 10 songs, because in all cases the highest intensity of sound was contained in this first harmonic.

In cases where we used parametric statistics, we square-root transformed data in order to approximate normal distributions. All statistical tests are two-tailed.

RESULTS

To examine the relationship between the singing behavior of individuals and the number of other males audible at a given time, we calculated the mean time spent singing by each focal male when 0, 1, 2, or 3 other males were audible. A repeated measures ANOVA indicated that individuals' time spent singing varies with the number of other audible singers on the lek ($F_{3,15} = 5.59$, $P < 0.02$; Fig. 2a). Post-hoc analyses revealed that individuals spend significantly less time singing when no other males are audible than when at least one other male is singing (Fisher PLSD, $P < 0.05$). Similarly, the mean number of songs produced by individuals is related to the number of other males audible on the lek ($F_{3,15} = 5.92$, $P < 0.02$; Fig. 2b). Again, individuals produce more songs when one or more other males are audible than when no other birds are audible (Fisher PLSD, $P < 0.05$). Thus, a given male's tendency to sing is related to whether or not any other males are currently singing.

We found significant variation among territories in the time males spent singing at those territories ($F_{5,66} = 2.59$, $P < 0.04$; Fig. 3). Post-hoc analyses revealed that birds on territories A and F spent significantly less

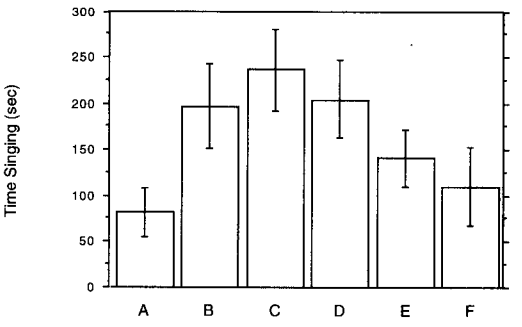

FIGURE 3. Variation in time spent singing (per 5 minutes) by males on focal territories. Values are means ± SE, $n = 6$ territories.

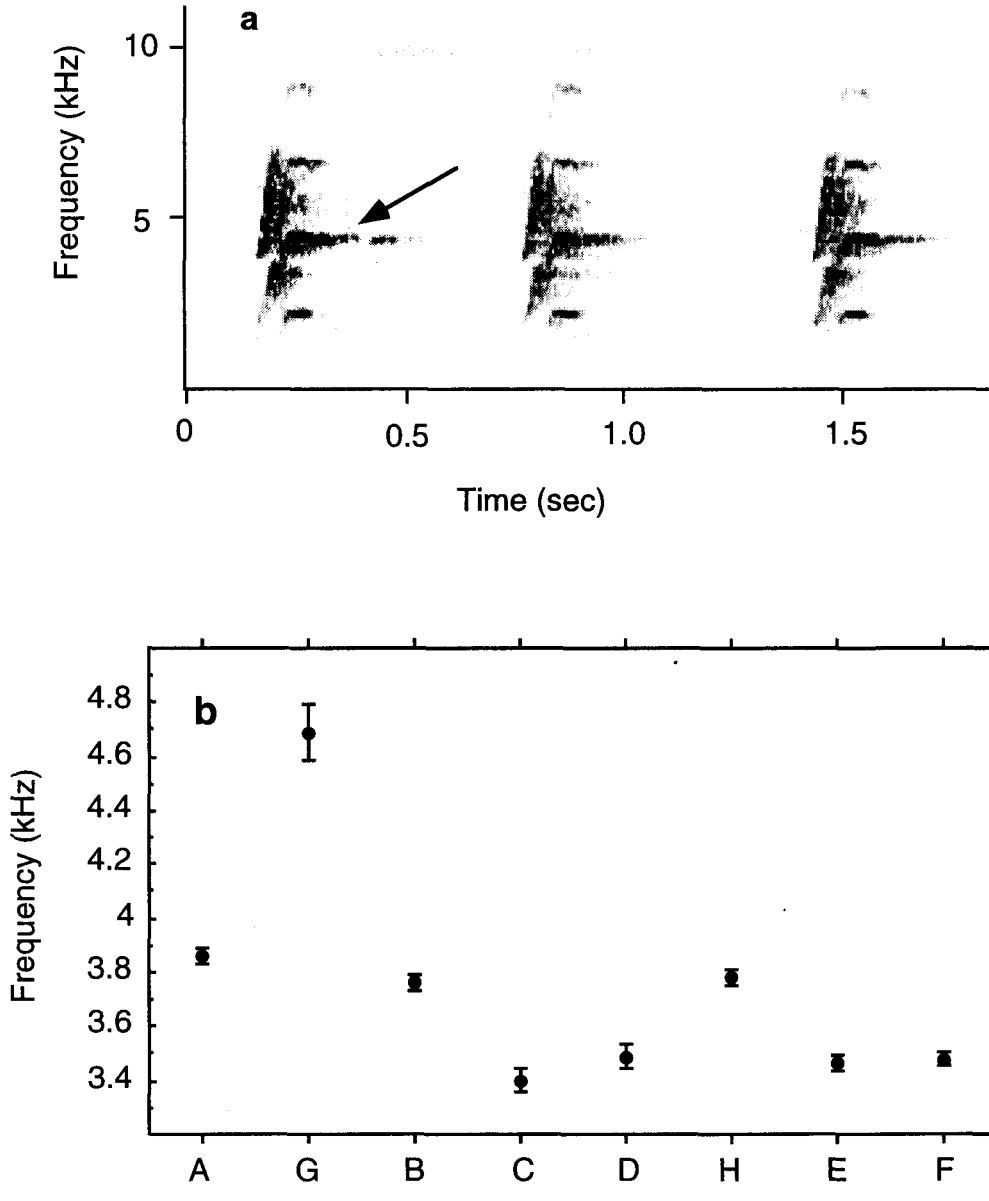

FIGURE 4. (a) Sample spectrogram of Green Hermit song. Arrow indicates the first harmonic, which in all cases was the frequency of maximum intensity. Harmonic structure: 2.19, 4.39, 6.58, 8.78 kHz. FFT length: 256 points. (b) Individual variation in the frequency of the first harmonic. Values shown are means ± SD, $n = 10$ songs per individual.

time singing than did birds on territories C and D (Fisher PLSD, $P < 0.05$). The variation among territories in the total number of songs produced per 5 min approached significance ($F_{5,66} = 2.03$, $P < 0.09$); again, males at territories A and F produced fewer songs than did males at C and D (Fisher PLSD, $P < 0.05$). Because males were not individually marked, undetected territorial turnovers may have occurred between days during the study. Therefore, in order to address variation in singing behavior among individuals, we also analyzed each of the three days separately. When the data were analyzed in this way, we found significant variation among individuals in both time spent singing ($F_{5,18} = 9.02$, $P < 0.01$) and songs produced ($F_{5,18} = 7.57$, $P < 0.01$) on the third day of the study, but not on either of the first two days (Day

1 time spent singing $F_{5,18} = 1.66$, $P > 0.05$; songs produced $F_{5,18} = 1.60$, $P > 0.05$; Day 2 time spent singing $F_{5,18} = 0.44$, $P > 0.05$; songs produced $F_{5,18} = 0.36$, $P > 0.05$).

Further analyses revealed that the variation observed in singing behavior among territories can be explained in part by position on the lek. Using the number of song censuses in which a given site had at least one neighbor singing, we categorized focal territories as experiencing either high or low neighboring song activity (mean number of censuses with neighboring song = 38.0 and 33.3, respectively). Thus we defined the center of the lek as the center of singing activity; this also corresponds to the approximate geographic center of the lek (Fig. 1). Males on sites defined as central (B, C, and D) had higher median proportions of time spent singing (Mann-Whitney U, $z = -1.96$, $P = 0.05$) and higher median numbers of songs produced ($z = -1.96$, $P = 0.05$) than did males on sites at the periphery of the lek (A, E, and F). On several occasions females were seen to visit the lek. Copulations were observed on only one of the focal sites (site D, on two different mornings); this site also had the highest incidence of chases and fights.

Individuals also varied in the nature of the songs produced. For each individual, we measured the frequency of the first harmonic overtone, which was in all cases the harmonic of most intensity, in 10 songs (see sample spectrogram, Fig. 4a). We found significant variation in frequency among individuals ($F_{7,72} = 735.6$, $P < 0.01$, Fig. 4b). However, this variation does not appear to be related to spatial position on the lek, as males occupying center territories (B, C, D, and H) did not sing at higher or lower frequencies than did males on edge territories (A, E, F, and G); ($z = 0.73$, $P > 0.30$).

DISCUSSION

Males spent more time singing and produced more songs when there was more singing activity by other birds on the lek (Fig. 2a, 2b). This correlation of individual singing with surrounding singing activity may or may not reflect a causal relationship. Males may increase their own rates of song production in response to the activity of their neighbors, either to announce ownership of their territories to other males (Westcott 1992) or to outcompete their neighbors in advertising for mates. Males on adjacent territories were frequently heard countersinging, a phenomenon also common in the closely related Long-tailed Hermit *Phaethornis superciliosus* (Stiles and Wolf 1979). This suggests that individuals may increase song production in response to elevated song activity by their neighbors. However, the synchrony of song production on the lek probably also is influenced by factors other than neighbor activity. Song production in Long-tailed Hermits is affected by time of day, and more specifically by nectar availability (Stiles and Wolf 1979); other variables such as weather and the presence of females on the lek also may affect the level of song produced (Snow 1974). Social stimulation and synchronous male presence on the lek may thus combine to create a high degree of synchrony in song.

We found significant variation among territories in song production (Fig. 3). When data were analyzed separately by day, we also found significant inter-individual variation for one of the three days of the study. Furthermore, differences in the amount of song produced on different territories appear to be related to territorial position, such that birds in the center of the lek sing more than do birds on the periphery. It also is interesting that one of the central territories was the site of all the copulations seen and also had the highest incidence of fights and chases, although these data are anecdotal. As the birds in this study were not individually marked, we cannot rule out the possibility that undetected territorial change-overs occurred between days of the study. Regardless of whether such change-overs did occur, the gradient in activity from the center to the periphery of the lek reported here is similar to that found by Stiles and Wolf (1979) for Long-tailed Hermits. Individual males also varied in the frequency (pitch) of song produced (Fig. 4b), but this did not appear to be related to territory position. High annual mortality in tropical hummingbirds may limit the formation of age-structured dominance hierarchies, and Stiles and Wolf (1979) suggested that the skew in male mating success may therefore be less extreme among hummingbirds than among longer-lived birds. Nonetheless, there appears to be considerable variation among individuals in song production and song frequency, both of which are potential determinants of male mating success.

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