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# THE DAWN LEK OF THE SWALLOW-TAILED HUMMINGBIRD

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ABSTRACT.—We studied the lek behavior of the Swallow-tailed Hummingbird (*Eupetomena macroura*) in an urbanized area in São Paulo state, southeastern Brazil. During the 22-month study we identified a total of 26 lekking territories in one lek that covered an area of approximately 12 ha. The lek was active throughout the year; the number of singing males per morning ranged from 6–15. The abandonment of territories and the establishment of new ones caused continuous rearrangement of lek boundaries. Lekking territories had a mean size of 217 $m^2$ and were separated from each other by 24–120 m. On average, males started singing 27 min before sunrise and kept singing for 17 min. At the end of this period and after a few minutes of silent perching, they abandoned their lekking territories until the next morning. During the singing period, males spent 72–100% of the time inside their territories. The lek behavior of *E. macroura* is unusual compared to other lekking hummingbirds because of the short daily period of lekking, restricted to just before sunrise. Since males and females of *E. macroura* possibly defend feeding territories throughout the rest of the day, the short lekking period may represent a tradeoff between two different time budget pressures from lekking and feeding activities.
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A lek mating system is characterized by the spatial aggregation of males in an area (the arena or lek) where they defend individual territories. These territories do not contain any other resources required by females except the males themselves. Females visit the leks to choose a mate freely, and males are released from any further parental investment (Höglund and Alatalo 1995). The attendance of males at their territories on the lek is important in achieving mating opportunities (see Théry and Vehrencamp 1995 and references included). So, the adoption of a lek as a mating system generally requires that males have access to easily reached abundant or exclusive food sources that do not take much time to be found and exploited (Snow 1962). Lekking hummingbirds are thought to fulfill this requirement by adopting a nonterritorial foraging mode, following a regular foraging route along which dispersed but rich and predictable food sources are exploited (high-reward traplliners *sensu* Feinsinger and Colwell 1978; see Stiles 1975, Stiles and Wolf 1979). As an alternative to lekking, males of most hummingbird species defend feeding territories, while females exploit less rich food patches or are temporarily hosted in male territories for mating purposes (Wolf and Stiles 1970).

The Swallow-tailed Hummingbird (*Eupetomena macroura* Gmelin 1788; placed in the genus *Campylopterus* by some authors; e.g., del Hoyo et al. 1999) is a large hummingbird (total length 15–17 cm; male, 8–9 g; female, 6–7 g; del Hoyo et al. 1999) with a deeply forked tail, which in adult males takes up almost two-thirds of the total length (Sick 1993). Dark blue and dark green predominate in body coloration. Sexes are alike except that adult males have longer outer rectrices and the rachis of the first remiges are slightly expanded and flattened. Immature males resemble females (Grantsau 1988). The species occurs from Guyana south to Bolivia and Paraguay. It is present throughout most of Brazil, from some parts of Amazonia to Rio Grande do Sul (Sick 1993). *E. macroura* inhabits open habitats such as *cerrados* (savanna-like vegetation) and second growth forests and its borders, and it is one of the commonest hummingbirds in urban areas, where it can be found in squares, gardens, parks, and orchards (Sick 1993).

In this paper, we describe for the first time the lek behavior of *E. macroura*, which is unusual compared to most other lekking hummingbirds because activities on the lek take place only during a short period of the day, just before sunrise. We hypothesized that this short daily lek period represents an evolutionary solution to accommodate two time-consuming, apparently incompatible activities: lekking and feeding territoriality.

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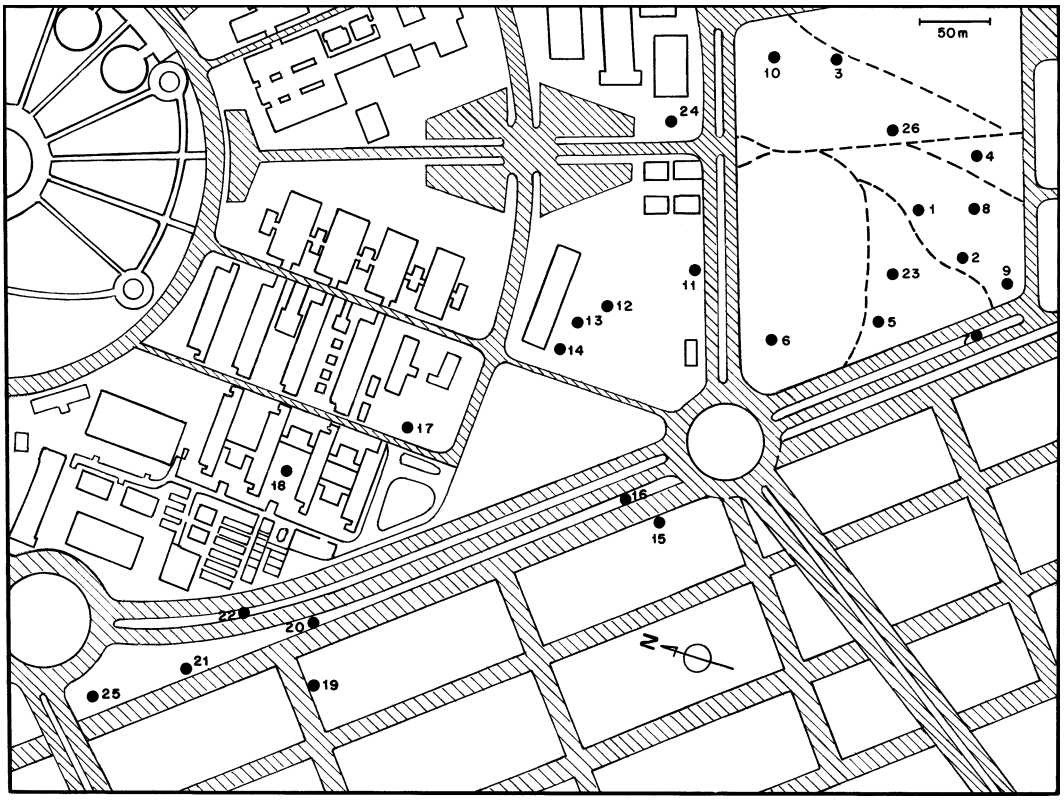


FIG. 1. The area of the Swallow-tailed Hummingbird (*Eupetomena macroura*) lek at the campus of the Univ. Estadual de Campinas and nearby residential blocks, São Paulo state, southeastern Brazil. Hatched areas correspond to streets and avenues, broken lines represent pathways, and the numbered dots indicate the location of territories recorded on the lek during 1990–1991.

## STUDY SITE

The lek was located on the campus of the Univ. Estadual de Campinas and adjacent residential areas, approximately 12 km north of central Campinas (22° 55′ S, 47° 03′ W), São Paulo state, southeastern Brazil. The climate is characterized by a dry-cold season from April through September (winter), and a wet-hot season from October through March (summer). Mean (± SD) annual rainfall for 1990–1993 was 138.1 ± 16.5 cm. Mean monthly temperatures for the same period ranged from 11–28° C during winter and from 14–30° C during summer. The temperature occasionally dropped below 10° C in winter and rarely reached 38° C in summer.

The lek site was located in an urbanized area occupied by several buildings interspersed with streets and avenues. Extensive open areas formed by lawns ornamented with scattered native and exotic plants dominated approximately half of the lek site; the other half was strictly residential (Fig. 1).

## METHODS

*Territory mapping and lek dynamics.*—From March to December 1990 we made 29 visits to the lek in an effort to locate all the territory owners present. Intervals between consecutive visits ranged from 1–3 weeks. During each visit we walked separately and arbitrarily through the lek site, visiting established territories and looking for newly settled ones. Locations of occupied territories were recorded on a 1:5000 map. The presence of a territory owner was almost always detected by its song since the detection of silent birds was difficult due to twilight conditions, the short duration of the lekking period, and the large area to be censused (see below). Neighboring territories were assigned to different owners only if they were detected simultaneously. We recorded the time of first and last vocalization on the lek, which was then compared to sunrise times obtained from an almanac. Similar censuses also were conducted when the lek was discovered in June 1987 (four visits) and 10 years later, during November and December 1996 (five visits).

*Behavior of territory owners.*—Observations of the lek behavior of five territory owners (territories 1, 2, 3, 5, and 23 in Fig. 1) were conducted by MAP between March 1991 and February 1992. These individuals were chosen based on their attendance at territories on the lek, as shown by the censuses conducted

the previous year, and their conspicuousness inside the territory, which facilitated observation. We made no attempt to mark these birds due to the difficulty of seeing any mark under the twilight conditions prevailing during the lekking period. Thus, we assumed that the same individuals were observed throughout the study. We also assumed that the occupants of these territories were males because in lek-breeding birds only males are known to defend territories on the lek (Stiles and Wolf 1979, Höglund and Alatalo 1995). Supporting this assumption is the fact that one territory owner collected (see below) was an adult male with full-sized testes.

For each observation session the observer arrived at the focal territory prior to the arrival of the bird and recorded (1) the time of the bird's first arrival and last departure from the territory, (2) the time of first and last advertisement calls, (3) the number of advertisement calls emitted during 1 min and recorded at 3-min intervals, (4) the number and height (visually estimated to the nearest 0.1 m) of perches used to emit the advertisement call (calling posts), and (5) the number and duration of departures from the territory. At the end of each observation the air temperature and degree of cloudiness (whether more or less than 50% of the sky was cloudy) were recorded. At the end of the study we measured the area of the five focal territories, considering them rectangles and taking the outermost calling posts used by the territorial birds as boundaries. In June 1992 we collected one territorial bird (territory 18 in Fig. 1) and deposited it in the collection of the Museu de História Natural of Univ. Estadual de Campinas (ZUEC no. 1820). We tape recorded the advertisement calls of several birds. Recordings were made using a magnetic tape at 19 cm/s with a Nagra E tape recorder and a Sennheiser ME88 directional microphone. Sonograms were made with a Uniscan II sonograph. Recordings are deposited in the Arquivo Sonoro Neotropical, Lab. of Ornithology and Bioacoustics, Univ. Estadual de Campinas.

To document that the lek was not active after the early morning period of activity, we censused the lek site throughout the day searching for individuals of *E. macroura* occupying the known territories. These censuses were conducted monthly from April 1991 to February 1992 during three periods of the day: just after activity on the lek had apparently ceased (between 06:00 and 08:00, 23 censuses totaling 13 h of searching), during the midafternoon (13:00–15:00, 9 visits, 5.5 h), and just prior to dusk (17:00–18:00, 7 visits, 4 h).

We used parametric statistics whenever the assumptions of normality and equality of variances were not violated. We used a two-way ANOVA to test the effects of cloudiness and season on the amount of time that calling initiation preceded sunrise and duration of the calling period at the lek. Results are reported as means ± 1 SD. We consider $P$ values $<0.05$ significant.

## RESULTS

*Lek dynamics and structure.*—We plotted a total of 22 territories on the lek from March to December 1990, plus four additional territories during 1991. Ten of the territories recorded during 1990 (38.5%) had been in use during 1987, when a total of 15 territories were recorded. During 1996 we recorded 13 territories on the lek, four and five of which were occupied in 1987 and 1990, respectively. During the 1990 study period 6–15 males called on a given morning. As a consequence the lek was never deserted. Some territories were quite constant over time (e.g., territories 1–3 in Fig. 1), whereas others were abandoned or newly established on the lek. For instance, six new territories were established during the dry season of 1990. Half of these territories persisted until the end of the study in February 1992.

The lek was structurally dynamic as territories were abandoned and established. By March 1990, the lek apparently was a single unit composed of 12 males (Fig. 2A). As new territories were established by July, the lek area expanded eastward, occupying its largest total area (approximately 12 ha; Fig. 2B). During October 1990, as some males were present irregularly at their territories, two distinct subleks separated by approximately 300 m (I and II in Fig. 2C and D) were formed. The separation between subleks was still apparent five months later with the abandonment of additional territories (Fig. 2D).

Territories were not closely adjacent and neighbors frequently were separated by more than 50 m (mean distance to the nearest neighbor = 54.9 m ± 26.4 SD, range 24–120, $n$ = 15). Thus, males definitely were not in visual contact with their counterparts on the lek and, with the exception of nearest neighbors, most presumably also were beyond hearing the others.

Males typically chose an isolated group of trees and shrubs to establish their territories, which had a size of 216.6 ± 50.5 $m^2$ (range 132.9–266.0 $m^2$, $n$ = 5). Most territories (77%) were ≥10 m distant from any artificial illumination. Inside the territories males used 1–8 calling posts/lekking period (mean = 2.7 ± 1.5, $n$ = 27), which typically consisted of twigs at a mean height of 1.9 ± 0.9 m (range 0.3–4.2 m, $n$ = 21). The density of vegetation in the immediate vicinity of calling perches varied, but males never were totally exposed while calling, and some of them were hard to

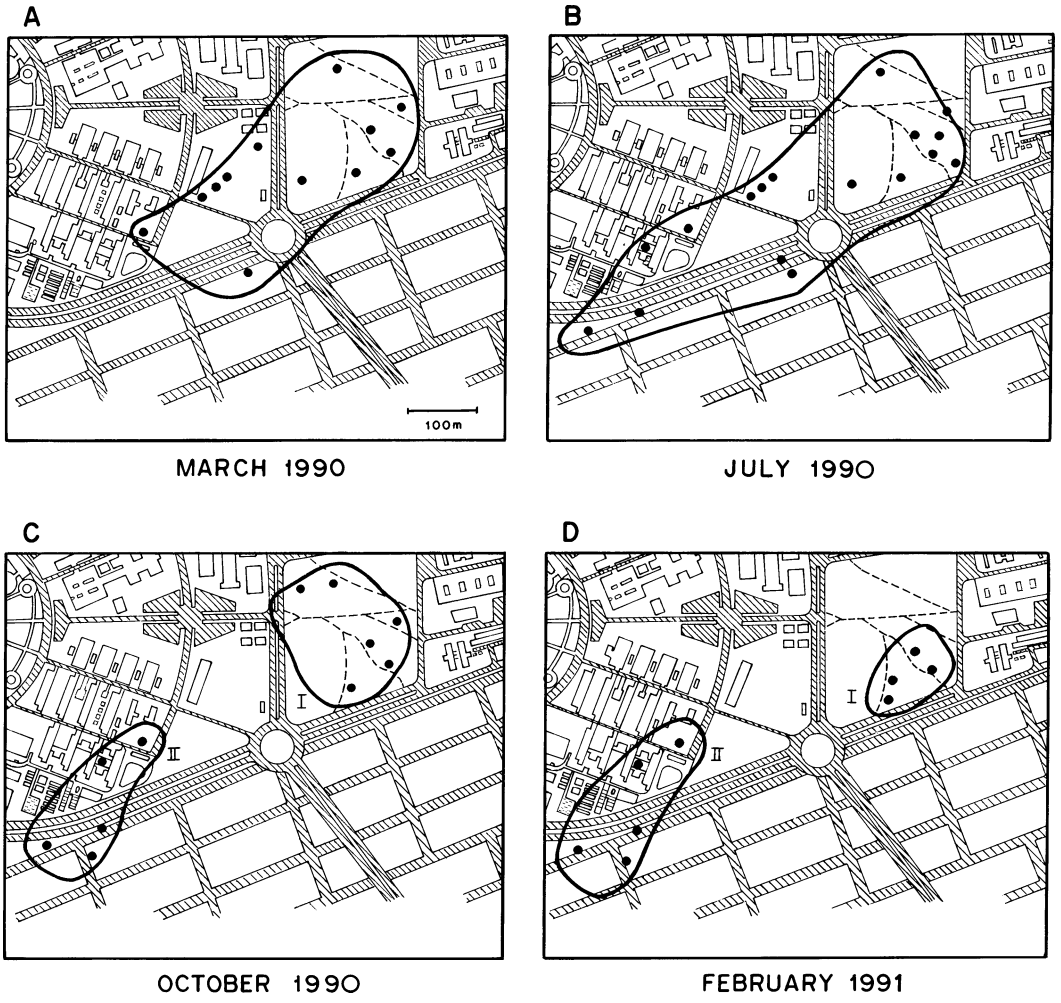


FIG. 2. Temporal variation in the area occupied by the lek of the Swallow-tailed Hummingbird (*Eupetomena macroura*) at the campus of Univ. Estadual de Campinas and nearby residential blocks, São Paulo state, southeastern Brazil. The rearrangement of the lek boundaries over time created two distinct subleks (I and II in C and D). Hatched areas correspond to streets and avenues, broken lines represent pathways, and black dots indicate the location of lekking territories.

locate amidst the vegetation. No male was observed feeding inside its territory on the lek at any time.

*Behavior of lekking males.*—Males did not spend the night inside their territories. The activity on the lek began with the arrival of males 1–2 min before they started to call, when, in the darkness that precedes dawn, they flew through the territories, sometimes emitting alarm notes (Vielliard 1983). The time of calling initiation in relation to sunrise was significantly related to cloudiness, but not by season or the interaction between these two variables (Table 1). Calling began 30.8 ± 2.8 min (range 27–37 min, $n = 15$) before sunrise on mornings with ≤50% of the sky cloudy, and 23.2 ± 4.1 min (range 16–29 min, $n = 10$) on cloudier mornings, suggesting that calling initiation was, at least partially, controlled by light intensity. As a consequence, the time of calling initiation varied throughout the year, occurring earlier in summer and later in winter (Fig. 3). Males of the same sublek started calling almost at the same time, and neighbors often did so simultaneously. Both subleks, however, differed in the time of call-

TABLE 1. Two-way ANOVA for the effects of season (summer and winter) and cloudiness (more or less than 50% cloudy) on the amount of time that calling initiation preceded sunrise, and the duration of the calling period in the lek of the Swallow-tailed Hummingbird (*Eupetomena macroura*) at the campus of the Univ. Estadual de Campinas São Paulo State, Southeaster Brazil, during 1991.

| | Time of calling initiation | | | | Duration of calling period | | | |
|---|---|---|---|---|---|---|---|---|
| Effects | df | MS | *F* | *P* | df | MS | *F* | *P* |
| Season | 1 | 0.03 | 0.00 | 0.95 | 1 | 40.74 | 2.61 | 0.12 |
| Cloudiness | 1 | 514.62 | 42.92 | 0.00 | 1 | 5.70 | 0.37 | 0.55 |
| Season × cloudiness | 1 | 30.79 | 2.57 | 0.12 | 1 | 81.98 | 5.25 | 0.03 |
| Error | 25 | 11.98 | | | 25 | 15.62 | | |

ing initiation (paired *t*-test: $t = 3.84$, df = 10, $P = 0.003$). Calling started 4.5 ± 3.4 min (range 0–12 min, $n = 13$) earlier in sublek II.

Males spent 88.5 ± 8.7% (range 72.2–100%, $n = 19$) of the lekking period perched inside their territories. Once calling started, males left their territories only to chase trespassing conspecifics or to visit neighbors. These temporary absences, however, did not occur until 6.0 ± 3.3 min (range 2.6–12.5 min, $n = 11$) after they had started to call and were very brief, lasting a mean of only 32.4 ± 31.4 s (range 5–128 s, $n = 47$). Males left their territories in this manner 3.0 ± 3.0 times (range 0–12, $n = 12$) during the period of lek activity.

The initial period of activity at the lek was one of intense calling. Advertisement calls were uttered at a frequency of 36.6 ± 10.1 calls/min (range 10–58 calls/min, $n = 72$). There was a general tendency to decrease the rate of advertisement calling toward the end of the lekking period, although the trend was not significant (Kruskal-Wallis test with chi-square approximation: $\chi^2 = 2.94$, df = 5, $P = 0.71$; Zar 1984). In 13 of 38 mornings (34.2%) the first male to start calling at sublek I also was the last to stop. Males differed in time

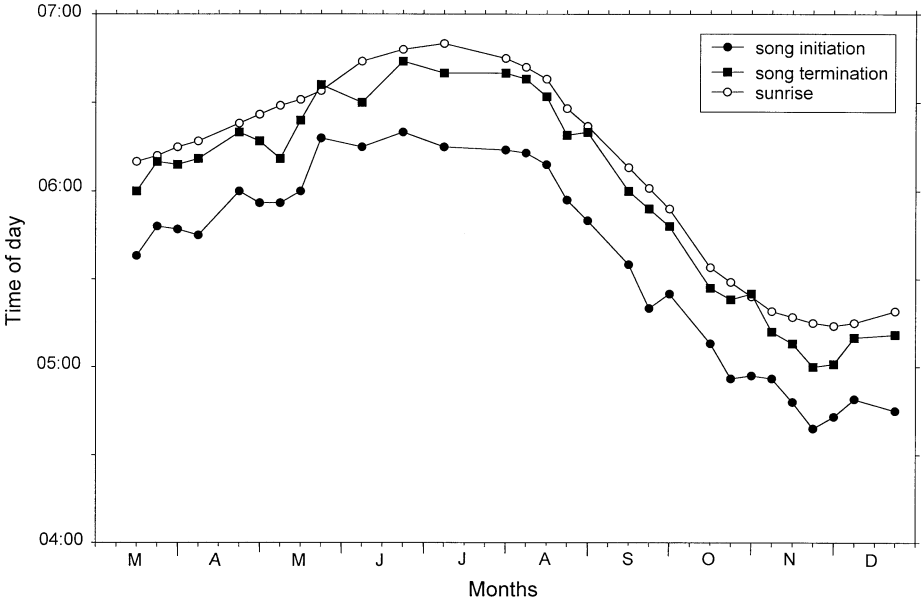


FIG. 3. Seasonal variation in sunrise and time of calling on the lek of the Swallow-tailed Hummingbird (*Eupetomena macroura*) at the campus of Univ. Estadual de Campinas, São Paulo state, southeastern Brazil, from March to December 1990. Intervals on the x-axis denote weeks. The number of sampling weeks per month varied from two to four.

spent calling. At sublek I, for example, the four males for which we have sufficient data (territories 1, 2, 5 and 23) sang from a mean of 17.0 ± 5.5 min to 9.0 ± 3.2 min (one-way ANOVA: $F_{3,40} = 4.13$, $P = 0.01$). A multiple comparison test revealed that the difference was due to the brief calling time of male 23 (Tukey test for unequal sample sizes: $q = 3.79$, $P < 0.05$; Zar 1984), which was first detected on the lek in April 1991 and was perhaps a young male. After a male had stopped calling it either immediately abandoned its territory or spent ≤11 min (5.2 ± 3.3 min, $n = 12$) perched silently prior to definite abandonment. The period of activity on the lek, measured by the time elapsed between the first and last call in a given sublek, lasted 19.8 ± 4.0 min (range 11–28 min, $n = 41$) in sublek I, and 18.1 ± 5.2 min (range 7–26 min, $n = 13$) in sublek II, a nonsignificant difference ($t = 1.17$, df = 52, $P = 0.25$). Therefore the cessation of lek activities, with few exceptions, occurred shortly before sunrise (Fig. 3), and after that the lek was completely silent. Contrary to calling initiation, the duration of the calling period was significantly related to only the interaction between season and cloudiness, not the main factors (Table 1). Our general impression was that the combination of cloudiness, wind, and low temperature acted to shorten the period of activity on the lek. Supporting this suggestion, we found a positive although not significant correlation between air temperature and duration of lekking period (Pearson correlation: $r = 0.52$, $P = 0.08$, $n = 12$).

The visits we made to the lek after lekking activities apparently had ceased revealed that territories on the lek rarely were occupied again by silent birds during the late afternoon, just prior to dusk (17:00–18:00). During these visits we compiled 63 records of *E. macroura* flying or perched in the area of the lek, but only four of these records were of birds perched, always silently, inside known lekking territories. All four records occurred during the late afternoon. In contrast, we observed many individuals throughout the day defending feeding territories centered on flower rich ornamental plants (e.g., *Erythrina speciosa* Fabaceae, *Callistemon viminalis* Myrtaceae, and *Clerodendron* sp. Verbenaceae) in the gardens surrounding the lek site.

*Vocalizations and display.*—The advertisement call is composed of a single note rapidly modulated between 3.5 and 9.0 kHz, lasting approximately 0.3 s (Fig. 4A–C). This call was the most frequent vocalization emitted on the lek by males, but it occasionally was heard outside the lek in what seemed to be aggressive encounters between two or three individuals. Individual variation in the structure of the advertisement call was detected (Fig. 4A–C), making it possible to distinguish some males from the others by voice alone. A brief and high-pitched whistle (Fig. 4D) occasionally was uttered during encounters on the lek but, unlike the advertisement call, we never heard it in another context.

The most characteristic display observed on the lek, which we called tail-flashing display, involved a territory owner and an intruding individual. The former remained perched as the visitor made a series of rapid lateral flights, forming 15- to 20-cm arcs just in front and slightly above the territory owner. At the ends of each arc, the flying bird opened widely its deeply forked tail. After 5–10 s, the flying bird either was chased by the territory owner or retired in a ''trembling,'' irregular and ascending flight. No sound was emitted during the entire display. This display was not restricted to the period of activity on the lek. During our visits to the lek site just after lekking activities had finished (i.e., between 06:00 and 08:00) we watched four more instances of this display being performed in what again seemed to be aggressive encounters. We observed no copulation attempts at any time during or after the lekking period.

## DISCUSSION

The aggregate distribution of male territories, which have no food resources and were used solely for male advertisement, coupled with the release of *E. macroura* males from parental care (Oniki and Willis 2000), fits well into the definition of lek (Höglund and Alatalo 1995). More precisely, the lek of *E. macroura*, as with other hummingbird leks (Atwood et al. 1991), may be best characterized as an exploded lek (*sensu* Gilliard 1969) in which individual territories are well separated from each other, permitting only acoustical contact between neighboring territory owners.

The establishment and abandonment of ter-

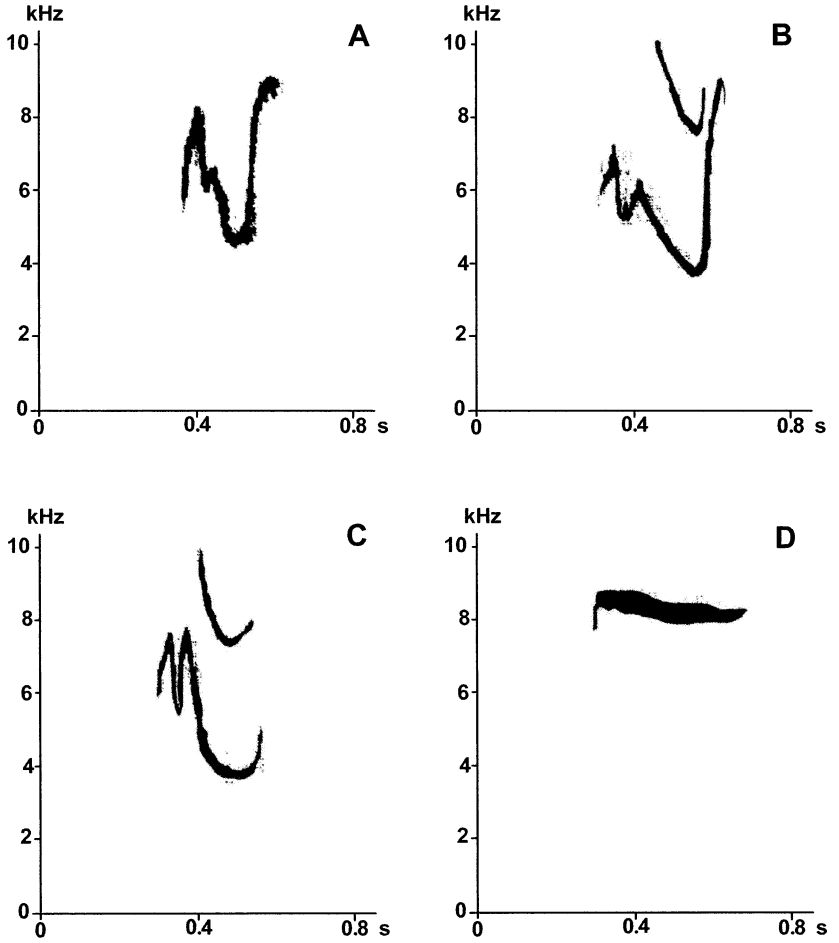


FIG. 4. Sonograms of the advertisement calls (A–C, from males on territories 5, 1, and 14, respectively, shown in Fig. 1), and (D) high-pitched whistle, all emitted by Swallow-tailed Hummingbirds (*Eupetomena macroura*) on the lek. Recordings were made by WRS during February 1992 on the campus of Univ. Estadual de Campinas, São Paulo state, southeastern Brazil. Sonograms were produced with a Uniscan II sonograph.

ritories on the lek is common among lekking hummingbirds (Stiles and Wolf 1979) and caused the rearrangement on the lek area we observed. For an unknown reason, a disproportionate number of new territories were established on the lek area during July 1991. It is possible that these territories were held by young birds attempting to establish themselves on the lek. The behavior of such newcomers was similar to that of young individuals of other hummingbird species trying to establish lekking territories (Snow 1974, Stiles and Wolf 1979, Harger and Lyon 1980), and is exemplified by male 23, first recorded on the lek in April 1991. This male engaged in many chases and frequently was absent from its territory. As a consequence, it had the shortest calling time among all the males we observed. Man-made changes (e.g., gardening) that periodically took place in the lek area also may have contributed to its spatial rearrangement.

The lek behavior of *E. macroura* revealed many similarities and some important differences with respect to other lekking hummingbirds studied to date. One such difference was the year round nature of lek attendance by *E. macroura*. For almost all hummingbird species for which lekking seasonality is known, male attendance at leks is not continuous but

suffers interruptions throughout the year, usually during the nonbreeding or dry seasons (Stiles and Wolf 1979). In *E. macroura* the lek is active throughout the year, suggesting an extended period of reproduction. In fact, we found active nests around the lek area from November to May, but nesting also may occur from August to October and in June in São Paulo state (del Hoyo et al. 1999, Oniki and Willis 2000), resulting in an eleven-month reproductive period. Stouffer and Bierregaard (1996) also reported that *Phaethornis superciliosus* leks throughout the year in an Amazonian forest near Manaus, Brazil, and that reproduction spans the whole year. Since reproduction in birds usually is closely linked to food availability (Snow 1974, Stiles 1985, Fleming 1992), the year round lekking period of *E. macroura* may be a consequence of the unnatural, abundant availability of nectar from ornamental flowers in the gardens that surround the lek area. To clarify this point, studies on the lek behavior and nesting cycle of *E. macroura* under different ecological conditions, preferably away from urban areas, are needed.

The trait that makes the lek of *E. macroura* particularly unusual compared to other hummingbird species is the short daily period of lekking activity just before sunrise. The only other hummingbird known to systematically lek for such a short daily period is the Rufous-tailed Hummingbird (*Amazilia tzacatl*) which, according to Skutch (1981:43) sings ''from the dim early dawn until a little before or shortly after sunrise.'' Two questions immediately arise: why such a short lekking period, and why does it happen before sunrise and not during any other time of the day? Mace (1987) presented seven functional hypotheses to answer the question why some passerines sing at dawn (the dawn chorus). Among these, three hypotheses (good acoustic conditions, low foraging profitability, and honest advertisement) could be applied plausibly to the dawn lek of *E. macroura*. A fourth, which we call the low predation risk hypothesis (discussed below), also could have acted as a proximate cause for the evolution of the unusual lekking period of *E. macroura*.

Although predation on lekking birds rarely has been observed, the concentration of birds in a restricted, predictable area, and the production of advertisement songs, could attract the attention of predators (Trail 1987). Hummingbirds are victims of a variety of predators, including diurnal and nocturnal raptors, passerines, and bats (Miller and Gass 1985, Sick 1993, Martuscelli 1995). By lekking during a brief time window at dawn, *E. macroura* may reduce the risk of predation both by diurnal predators, possibly not fully active at that time, and nocturnal ones, which already may have retired to their diurnal roosts. The suggestion that predation risk may exert an important influence on the timing of lekking activities is not novel (Hartzler 1974, Benalcazar and Benalcazar 1982, Andersson et al. 1998). As Endler and Théry (1996) pointed out, the light environment may have an important effect on the evolution of lek behavior in birds, which may display under conditions that minimize predation risk. For *E. macroura*, it is tempting to hypothesize that the combination of the dark body coloration and the twilight conditions that prevail during the lekking period is suited precisely to this purpose. Obviously, all the hypotheses cited above may have acted synergistically to adaptively restrict the lekking time of *E. macroura* to the very first minutes of the day and not later.

The answer to the question of why the lekking period is so short seems to be more straightforward. Males engaged in lekking activities have passed a night of no energy intake; thus, energy replenishment may urge the attendance at nectar sources. Moreover, early establishment at feeding territories may be important to maintain its exclusiveness (Kuban and Neill 1980).

For most lekking hummingbirds studied to date, the establishment and maintenance of feeding territories and the attendance at leks, two time-consuming activities, are incompatible tasks. These species rely upon a nonterritorial foraging strategy, making several brief visits to their food sources throughout the day (traplining; Stiles and Wolf 1979). Over its evolutionary history, *E. macroura* apparently has resolved this conflict in a different way. By adjusting the lek activities to a short period of the day prior to the arrival at feeding territories, males are able to engage in both lekking and feeding territoriality. As both males and females probably defend feeding territo-

ries throughout the day (Rojas and Ribon 1997, Rocca-de-Andrade 2001), a male that cheats and stays longer on the lek would gain no net benefit because it probably would not be visited by any female. Thus, we hypothesize that the unusual lek behavior of *E. macroura* here described represents a trade-off between the conflicting demands of feeding and mating. Supporting this hypothesis is the observation that *Amazilia tzacatl*, the only other hummingbird known to lek at dawn, also defends feeding territories (Skutch 1981). To test the generality of our findings, as well as the hypotheses presented here, studies should be conducted on other populations of *E. macroura*, especially those inhabiting the *cerrados* and forest borders, where a more natural availability of food resources is found.

At present, we can not rule out the possibility that *E. macroura* males adopt a dual mating strategy of displaying at dawn leks and also seeking mating opportunities on their feeding territories as many hummingbird species do. It would be informative to observe feeding territories carefully to determine if singing and/or flight displays, such as the tail-flashing display, take place.

Finally, although lekking is known for only 28 of 320 hummingbird species (Atwood et al. 1991, Höglund and Alatalo 1995), the mating systems of the other 292 or so are poorly known. Therefore, lekking may be more common among hummingbirds than we currently think. Researchers should confirm that a hummingbird species is not lekking at any time of the day and, given the behavioral flexibility of hummingbirds (Stiles 1973), under different food availability conditions, before concluding that it does not adopt lekking as its mating system.

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