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LEK CHARACTERISTICS AND THE STATIC MALE SONG OF THE GREEN VIOLET-EAR (*COLIBRI THALASSINUS*) DURING A 3-YEAR STUDY IN A TEMPERATE FOREST OF CENTRAL MEXICO

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Resumen. – Características de los leks y el canto estático de los machos del Colibrí oreji violeta-verde (*Colibri thalassinus*) durante un estudio de 3 años en un bosque templado del centro de México. – Aun cuando los colibríes son el segundo grupo de aves más diverso, el conocimiento sobre la conducta de formación de leks es limitado. Las características del establecimiento de 11 leks del Colibrí oreji violeta-verde (*Colibri thalassinus*) fueron analizadas en un bosque templado del centro de México, desde el año 2009 al 2011. En cada lek contamos el número de machos que lo conformaba, el tipo de percha utilizada para los despliegues vocales, y medimos la distancia entre las perchas adyacentes. Asimismo, verificamos la permanencia espacial y temporal de cada lek. Los cantos de despliegue de los machos fueron registrados para obtener el repertorio vocal. Nuestros resultados mostraron que los machos de *C. thalassinus* forman leks en ambientes espacialmente variables y con requerimientos específicos de las características del hábitat. Los leks fueron establecidos en zonas de vegetación secundaria, la cual generalmente estuvo bordeada por bosque de pino y campos de cultivo. Los machos frecuentemente usan pinos para establecer sus perchas de canto y las distancias entre estos territorios vocales individuales (8ñ15 m) define a estos leks como “explosivos”. La información registrada durante los tres años del estudio, indican que algunos de estos leks fueron establecidos en sitios previamente ocupados, incluyendo el uso de las mismas perchas de canto entre años. Finalmente, presentamos la primer descripción del repertorio vocal desplegado en los leks, incluyendo el número de notas emitidas. Son necesarios más estudios enfocados en la descripción de los requerimientos ambientales para el establecimiento de los leks.

Abstract. **–** In spite of the fact that hummingbirds are the second most diverse group of birds, knowledge of lekking behavior in this family is limited. The characteristics of 11 established leks of Green Violet-ear (*Colibri thalassinus)* were analyzed in a temperate forest of central Mexico from 2009–2011. In each lek, we counted the number of males attending the lek area, type of perch used for the vocal displays, and measured the distance between adjacent perches. In addition, we verified the spatial and temporal permanence of each lek, and the male display songs were recorded to obtain the vocal repertoire. Our results show that males of *C. thalassinus* form leks in variable spatial environments with specific requirements regarding habitat characteristics. The leks were established in secondary vegetation zones, which generally bordered pine forest and cornfields. The males frequently used pine trees to establish their singing perches and the distance between these individual singing territories (8–15 m apart) define these leks as “explosive.” Recorded information during the 3-year study period indicate that some leks were established in previously occupied sites including the use of the same singing perches in consecutive years. Finally, we provide the first description of the vocal repertoire of static vocal displays at the leks including the number of notes emitted. Further studies are needed focusing on the description of the environmental requirements for lek establishment. *Accepted 13 August 2013.*

Key words: *Colibri thalassinus*, Trochilidae, habitat, lek behavior, vegetation composition, vocal repertoire, Mexico.

INTRODUCTION

A lek is a gathering of males occupying and defending the same small territories on a mating display arena (Payne 1984, Höglund & Alatalo 1995, MacDougall-Shackleton & Harbison 1998, Almeida & Macedo 2001). These display territories do not function to defend resources required by females but are defended by males for display to females (Pizo & Silva 2001). Birds are one of the most studied groups in the formation of lek arenas. For instance, aggregations of male display territories have been reported in over 130 species from six families (Cotingidae, Paradisaeidae, Pipridae, Ptilonorhynchidae, Pycnonotidae, and Tyrannidae). In spite of the fact that hummingbirds (Trochilidae) are the second most diverse group of birds in the New World, knowledge of lekking behavior in this family is limited (Bleiweiss 1997, 1998; Hayes 2002). In reviewing the existing literature, we found reports of 49 different species of hummingbirds that suggest the formation of leks (Table 1). Four of these reports provide a brief description of leks, five include a spatial and temporal description of the mating system, and the rest only mention that leks are formed during the mating season without providing more details. Also, the vocal repertoire displayed by males in these arenas is rarely described. Clearly further studies are necessary to generate more basic information about leks in hummingbirds.

Since the first description of its natural history by Wagner (1945) in Mexico, the Green Violet-ear (*Colibri thalassinus*) has been considered a lekking species. Later studies performed in Costa Rica confirmed these observations (Feinsinger 1977, Gaunt *et al.* 1994, Barrantes *et al.* 2008). The information gathered from these studies reveal that Green Violet-ears are highly flexible to the environmental conditions they use to form their aggregations and to perch during singing displays. Nevertheless, specific data about the characteristics of the vegetation and possible variation in location and time the leks sites are established require further exploration. Furthermore, although there is information on the song of this species (Gaunt *et al.* 1994, Barrantes *et al.* 2008), the vocal repertoire displayed by males forming leks has not been described.

The objective of our study is to describe the characteristics of leks formed by Green Violet-ears in a temperate forest in central Mexico based on measurements and observations over a 3-year study. In addition, our study presents the first description of the repertoire of vocal displays for this species during lek formation.

METHODS

Study site. The fieldwork was carried out during three reproductive seasons of Green Violet-ears, from June to October 2009–2011 in the "La Malinche" National Park (MNP), Tlaxcala, Mexico (Fig. 1). The MNP forms part of the Trans-Mexican Volcanic Belt. It has an area of 46,093 ha, being located at 19°14'N, 98°14'W, with an altitude ranging from 2300 to 4461 m a.s.l. (López-Domínguez & Acosta Pérez 2005). The vegetation is mainly a mosaic of pine forest (dominated by *Pinus montezuma*, *P. pseudostrobus*, *P. leiophylla*, and *P. hartwegii*) and second growth vegetation (Villers *et al.* 2006).

Study species. Colibri thalassinus (Swainson 1827) is a medium-sized, sexually monochromatic species. Both sexes are iridescent green in

TABLE 1. Hummingbird species with evidence in forming leks. Some species have shown a description of leks, and details of the spatial and temporal variation of thereof, but most only documents the formation of leks without offering details. References referring to indices: [1]Wagner 1945, [2]Skutch 1958, [3]Wiley 1971, [4]Barash 1972, [5]Snow 1974, [6]Feinsinger 1977, [7]Stiles & Wolf 1979, [8]Payne 1984, [9]Armstrong 1987, [10]Tamm *et al.* 1989, [11]Atwood *et al.* 1991, [12]Bleiweiss 1997, [13]Dastagir *et al.* 1997, [14]Johnsgard 1997, [15]Bleiweiss 1998, [16]MacDougall & Harbison 1998, [17]Pizo & Silva 2001, [18]Ornelas *et al.* 2002, [19]Boughman & Moss 2003, [20]González & Ornelas 2009, [21]del Hoyo *et al.* 1999, [21]Ramjohn *et al.* 2003, [22]Pizo 2012, [23]Hayes 2002.

Species	Description	Reference
Band-tailed Barbthroat *Threnetes ruckeri*	Lek formation (3–5 individuals) during the breeding season. There is no description of the system.	7, 11, 12, 15
Pale-tailed Barbthroat *Threnetes leucurus* (*niger*)	Lek formation during the breeding season. There is no description of the system.	7, 12
Green Hermit *Phaethornis g. guy*	Lek formation during peak activity (12–15 individuals). In the lek, the members are separated by less than 10 m without visual contact. Males consistently sang from one perch within these vocal territories.	6, 7, 11, 12, 14, 16, 20
Green Hermit *Phaethornis guy coruscans*	Lek formation during the breeding season. There is no description of the system.	12
Long-tailed Hermit *Phaethornis superciliosus*	Formation of "explosive" leks (20–25 individuals), with an area of approximately 1 km^2. Distance between individuals ranging from 20 to 500 m. If environmental conditions are favorable the leks are formed throughout the year.	7, 11, 12, 13, 14, 17, 20
Little Hermit *Phaethornis longuemareus*	Leks are established in areas with tall trees of 27–30 m. The height of the song perches was 22 to 45 cm, and these were located in the deep shade near the forest floor. In the lek, the members are separated by less than 10 meters and without visual contact.	3, 5, 7, 11, 12, 14, 20
Straight-billed Hermit *Phaethornis bourcieri*	Lek formation during the breeding season. There is no description of the system.	12
Reddish Hermit *Phaethornis ruber*	Lek formation during the breeding season. There is no description of the system.	7, 8, 12, 14
Tawny-bellied Hermit *Phaethornis syrmatophorus*	Lek formation during the breeding season. There is no description of the system.	12
Grey-chinned Hermit *Phaethornis griseogularis*	Lek formation during the breeding season. There is no description of the system.	12
White-whiskered Hermit *Phaethornis yaruqui*	Lek formation during the breeding season. There is no description of the system.	7, 12
White-bearded Hermit *Phaethornis hispidus*	Lek formation during the breeding season. There is no description of the system.	12
Minute Hermit *Phaethornis idaliae*	Lek formation during the breeding season. There is not a description of the system.	7, 12
Sooty-capped Hermit *Phaethornis augusti*	Lek (6 individuals) observed in February (Venezuela). Males displayed from an average of 2.5 perches per male located 1.10–2.25 m above ground on understory plant stems 2.5–4.0 cm thick.	21
White-tipped Sicklebill *Eutoxeres aquila*	Leks (3–4 individuals) established from December to February.	7, 8, 11, 12, 14, 15

TABLE 1. Continuation.

Species	Description	Reference
Tooth-billed Hummingbird *Androdon aequatorialis*	Lek formation during the breeding season. There is no description of the system.	15
Scaly-breasted Hummingbird *Phaeochroa cuvierii*	During the breeding season (Guatemala: May–Dec; Costa Rica: May–Jan) males form leks (of up to 8 individuals) in canopy of second growth or low mangrove, or at forest edge. In the lek, the members are separated by 38 m and without visual contact. The height of the song perches ranges from 6 to 12 m.	11, 12, 21, 22
Wedge-tailed Sabrewing *Campylopterus curvipennis*	Up to 15 individuals form a lek. The size of individual vocal territories ranges from 10 to 20 m. Song perches are established at 2–5 m high.	18, 20, 21, 22
White-tailed Sabrewing *Campylopterus ensipennis*	Leks are composed by 2–4 individuals. The height of the song perches ranges from 2 to 10 m.	22, 23
Long-tailed Sabrewing *Campylopterus excellens*	Leks are composed by 2–3 individuals.	22
Rufous Sabrewing *Campylopterus rufus*	Small leks composed by 2 individuals. Breeding season in Oaxaca, Mexico (Apr–May). The height of the song perches ranges from 3 to 3.6 m.	11, 12, 21, 22
Violet Sabrewing *Campylopterus hemileucurus*	During the breeding season (S Mexico: Jun–Sep; Costa Rica: May–Oct; El Salvador: Jul) males form leks (8 to 10 individuals), usually near rich food sources. In the lek, the members are separated by 38 m. In the lek, the members are separated by more than 15 m and without visual contact.	6, 11, 12, 18, 21
Grey-breasted Sabrewing *Campylopterus largipennis*	Leks are composed by 2–4 individuals.	12, 22
Swallow-tailed Hummingbird *Eupetomena macroura*	Formation of "explosive" leks from March to December. In the lek, the distance between individuals is 24 to 120 m and without visual contact. The height of the song perches ranges from 0.3 to 4.2 m. If environmental conditions are favorable the leks are formed throughout the year.	17, 20
Brown Violet-ear *Colibri delphinae*	Lek formation during the breeding season. There is not a description of the system.	11, 12
Green Violet-ear *Colibri thalassinus*	Leks of three to five males occupy a limited area, usually only 8 to 15 meters apart, so that they could hear and see each other. At these sites, the males call continually in the breeding territory to attract the attention of the females. Males sing in exposed perches (high cypress trees) and food resource withdrawals. Leks are established during breeding season (C Mexico: Jul–Nov; Guatemala: Sep–Mar; El Salvador: Sep–Jan; Costa Rica: Oct–Mar; Colombia: Mar–Aug).	1, 12, 18, 21
Green-breasted Mango *Anthracothorax prevostii*	Lek formation during the breeding season. There is no description of the system.	8, 11
Violet-headed Hummingbird *Klais guimeti*	Leks are composed up to 10 individuals, spaced at more than 15 m and without visual contact. Leks are established during breeding season (Costa Rica: Jan–May). The height of the song perches ranges from 6 to 18 m.	2, 7, 8, 11, 21

TABLE 1. Continuation.

Species	Description	Reference
Plovercrest *Stephanoxis lalandi*	Leks are established during breeding season (Oct–Mar), and are composed by 2–7 individuals in small areas ranging from 9–25 m^2. the distance between individuals was 9–25 m, the height of the per. The height of the song perches ranges from 0.8 to 3.5 m.	21, 22
Blue-throated Goldentail *Hylocharis eliciae*	Leks are composed up to 10 individuals, spaced at more than 30 m and without visual contact. Leks are established during breeding season (Dec–Apr). The height of the song perches ranges from 5 to 13 m. Males display songs of variable phrases of 5–8 notes from parches on horizontal twigs in upper understory or lower canopy.	11, 14, 21, 22
White-eared Hummingbird *Hylocharis leucotis*	Leks where members are spaced up to 15 m and without visual contact.	11, 14
Golden-tailed Sapphire *Chrysuronia oenone*	Leks are established during breeding season (E Colombia: Jun–Nov), and are composed by 5–10 individuals.	21
White-bellied Emerald *Amazilia candida*	Leks (3–6 individuals) are established in open areas. The distance between leks reaches into 0.5 km. Within the lek, individuals defend territories of approximately 450 m^2. The branches or lianas that extended into relatively open portions of the mid–canopy, were used as song perches, and they were 10–15 m above ground level.	11, 12, 18, 22
Blue-chested Hummingbird *Amazilia amabilis*	The leks are composed by 5 members, the distance between individual territories is 15–30 m, and the height of the song perches is 2.4–6 m.	7, 11, 12, 18, 22
Rufous-tailed Hummingbird *Amazilia tzacatl*	The leks (2–4 individuals) are established early in the morning. The distance between the individual territories is 15–22 m, and the height of the song perches is 2–6 m. During the day individuals spend more time defending their territory than singing.	11, 12, 15, 17, 22
Cinnamon Hummingbird *Amazilia rutila*	Lek formation during the breeding season. There is no description of the system.	11, 12
Charming Hummingbird *Amazilia decora*	Lek formation during the breeding season. There is no description of the system.	11, 12, 18
White-tailed Emerald *Elvira chionura*	Although often solitary during the breeding season (Jun–Nov) males form small leks of 2–5 members.	11, 21
Coppery-headed Emerald *Elvira cupreiceps*	During the breeding season (Oct–Mar) males form leks of 3–6 members.	11, 21
Black-bellied Hummingbird *Eupherusa nigriventris*	Males form leks (up to 5 individuals) during the breeding season (Costa Rica: Aug, Oct–Mar). Song perches are established in tall shrubs or subcanopy along edges of forest gaps.	21
Snowcap *Microchera albocoronata*	During breeding season (Costa Rica: Jan–May) males form leks (3–6 individuals) and sing a soft warble from exposed up twigs 4–8 m in forest edge.	11, 21
Amethyst-throated Hummingbird *Lampornis amethystinus*	This species form leks during the breeding season. The singing was more prevalent early in the morning, with a second peak in the evening. Males were perched on exposed twigs 1–3 m high.	11, 14, 18

TABLE 1. Continuation.

Species	Description	Reference
Green-crowned Brilliant *Heliodoxa jacula*	Lek formation during the breeding season. There is no description of the system.	15
Anna's Hummingbird *Calypte anna*	Males form "explosive" leks, where members sing at a distance at which they can listen to each other. The individual territories vary in size from 0.9 ha to 1.3 ha.	9, 19
Calliope Hummingbird *Stellula calliope*	Males established "explosive" leks (Apr–Jul), where members are spaced up to 100 m. The leks are usually near where the females lay their nests.	9, 10
Broad-tailed Hummingbird *Selasphorus platycercus*	Males form leks (June) of up to 3 individuals with an average distance between them of 7 m. These vocal assemblies are kept up to four consecutive days.	4, 22
Rufous Hummingbird *Selasphorus rufus*	Lek formation during the breeding season. There is no description of the system.	8, 14
Crimson Topaz *Topaza pella*	Leks are formed by 2–20 individuals, the height of the song perches is 10.5 m.	8, 22

color and present a large blue mark on the chest and a bluish-violet mark on the auricular area). The tail-feathers are metallic blue with a subterminal wide, black band (Howell & Webb 1995, Johnsgard 1997). Its geographic distribution is widespread from the northern to the central Neotropics, comprising central Mexico to Guatemala, El Salvador, Costa Rica, Colombia, Ecuador, and Peru. The species is found at altitudes from 1200 to 3000 m a.s.l. (Howell & Webb 1995, Johnsgard 1997, Lara 2006). Preliminary observations in the study site demonstrate that this species forms leks in the MNP.

Capturing and color-marking of hummingbirds. To evaluate the spatial and temporal variation in habitat characteristics associated with the establishment of leks, we captured and color marked the majority of individuals of this species once the reproductive season began in the study area. Several weeks prior to and during the initial stages of lek formation, hummingbirds were captured in different areas of the MNP in which abundant patches of flowering *Bouvardia ternifolia* (Rubiaceae) and *Penstemon roseus* (Scrophulariaceae) were observed. For captures, we used 10–12 mist nets that were 3, 6, and 12 m long placed from 07:00–15:00 h.

We mist-netted and color-marked individuals visiting the lek areas every year according to González & Ornelas (2009). Briefly, marks consisted of small colored circles made of foam sheets, attached with nontoxic, fast-drying hard glue (Kola Loka, E. I. du Pont de Nemours and Company, Edo. de México), to the back of the Green Violet-ears. This marking technique has demonstrated to be an efficient alternative (with respect to the use of rings) for the visual identification of individuals in the field (González & Ornelas 2009). Initial tests demonstrate that these markings last between two and three months until the back feathers are replaced by molt. Caught individuals were handled gently and were not harmed during mist netting and color marking. Marked individuals were observed defending territories over several weeks after manipulation; none of these birds disappeared or was found dead in the course of this study. Each individual carried an exclusive

color combination for further identification. We were able to locate, identify, and record the songs of color-marked territorial males. Because banding the hummingbirds was not feasible, and color marks are not permanent, it was not possible to know if the same individuals occupied the same territories in consecutive years. Field research reported here was performed with minimal bird manipulation and the approval of the Graduate Studies Committe of the Universidad Autónoma de Tlaxcala, and followed the Guidelines for the Use of Wild Birds in Research by the North American Ornithological Council.

Spatial and temporal distribution of the leks. In addition to the capturing and marking of individuals, field observations were conducted in different areas of the MNP to detect the presence of leks. We defined a lek area when a group of individuals were vocalizing at a constant rate (up to 20 consecutive min) on permanent perches, and daily monitored for about a week the areas where individuals were not vocalizing constantly. The observations ceased if the establishment of a lek was not confirmed in these areas. Once the establishment of a lek was settled, the spatial distribution of each singing individual within the arena was recorded using a GPS (Garmin model Oregon 300). In order to confirm the temporal permanence of the lekking area, subsequent observations at 3 d intervals were conducted until lek establishment was confirmed for the whole breeding season, and every new individual joining the lek was recorded.

Characteristics of the perches. After determining that a lek has been established, the spatial location of each individual attending the lek and the characteristics of the singing perches were daily recorded from 08:00 to 17:00 h until lek disintegration. These characteristics included: (1) the species of tree or shrub where singing perches were located, (2) the number of perches used per individual, and (3) the height (m) of the perches with respect to the ground measured with a clinometer (Suunto model PM5/36 PC).

Vegetation within the lek areas. Within the area of each established lek, we recorded the vegetation type present and collected plant material for further identification. Plant species identification was aided using field guides (Rzedowski & Rzedowski 2001, 2003; Villers *et al.* 2006) and determination of plant material done at the Laboratorio de Sistemática del Centro de Investigación en Ciencias Biológicas de la Universidad Autónoma de Tlaxcala (CICB–UAT).

To determine the possible differences among lek areas in plant species composition, the Sorensen similarity index was calculated (Moreno 2001). After creating a list containing all plant species recorded at leks throughout the study, we created a data matrix with presence/absence of plant species in each lek site using the Multivariate Statistical Package (Kovach Computing Services 1985–2000).

Vocal repertoire and associated lekking behaviors. To obtain the vocal repertoire and associated courtship behaviors at the leks, the vocalizations of the individuals that joined the leks were recorded. Each recording was analyzed to generate a spectrogram and identify the number of different notes. Vocalizations of marked territorial males were tape recorded approximately twice per wk with a digital Tascam DA-P1 tape recorder, two digital SONY PCM-M10 recorders, a Sennheiser MKH-70 shotgun microphone, and headphones. Spectrograms of recordings of all individuals were generated with Raven Pro 1.3 (Charif *et al.* 2008). Recordings were digitized at a sampling rate of 44,100 Hz and stored as 16-bit samples. Spectrograms were produced with a

349.7-Hz filter bandwidth and a frame length of 512 points (= 11.6 ms). The temporal and frequency-grid resolution of the spectrograms were 64 points (= 1.45 ms) and 2.69 Hz, respectively. For analyses, we used 600 songs (149 in 2004, 107 in 2005, 146 in 2006, and 198 in 2007). In most cases, we obtained 15 full songs per individual (range 5–20). The largest number of recordings possible was performed for each individual in different times throughout the day, trying to obtain all of the recordings of one individual within the same day. In order to obtain the vocal repertoire, each spectrogram was displayed for the visual identification (with letters) and the quantification of the types of notes and syllables present in the song. The vocal repertoire was defined as the total number of distinct notes for each of the individuals recorded in the leks.

During the audio recording process, some additional observations and videotaping of the individuals were performed to describe the behaviors of males within leks.

RESULTS

The spatial and temporal organizations of the leks. During the three reproductive seasons of our study, a total of 114 Green Violet-Ear individuals were captured and color marked, although many were presumably recaptured and remarked during subsequent seasons. Eighty-eight of these individuals were confirmed to establish vocal territories and belonged to 11 different leks distributed into seven different areas of the MNP: (1) Ixtenco, (2) Cabañas, (3) Caseta 5, (4) km 78, (5) km 73, (6) km 69, and (7) Albergue (Fig. 1).

In 2009, only one lek was established (Caseta 5), three leks (km 78, km 69, and Albergue) in 2010, and seven leks in 2011 in the aforementioned sites, all of which varied in the number of members that belong to the lek (Fig. 2, Table 2). These sites typically contained flowering patches of *Bouvardia ternifolia* and *Penstemon roseus* and were the feeding territories with the greatest abundance of hummingbirds.

The 11 leks we recorded were established in the edges of the MNP, in areas close to the perimeter of the MNP. These sites are composed of recovering pine forest (*Pinus hartwegii*, *P. leiophylla*, *P. montezumae*, and *P. pseudostrobus*) with open spaces. The leks were established in an altitudinal strip ranging from 2060–2800 m a.s.l. From the time of its formation, the average (± SE) lek lasted 30 active days (± 9.52 d), ranging from 10–50 d, with a constant turnover of individuals in each lek.

The average distance between neighboring leks was 2.39 km (± 0.9 km; range = 0.54–9.65 km), while the average distance between perches of singing individuals within a given lek was 99.72 m (± 4.95 m; range = 28.75–715.98 m), and between perches of one individual the average distance was 23.13 m (± 1.54 m; range = 4.68–68.88 m). These data indicate that individuals were quite dispersed and too far out of sight to maintain visual contact, but they were able to maintain vocal contact among each other.

Characteristics of the perches. The 88 recorded birds that formed all of the described leks sang from one, two, or three different perches. These perches were typically branches found on the periphery of the tree or shrub. Thirty-one percent of the individuals used only one branch to sing, 60% chose two perches, and 9% sang from three perches. The use of more than one perch always implied the use of more than one tree or shrub inside the lek. A total of 119 perching sites were mostly located on 11 tree species including pine species (*P. hartwegii*, *P. leiophylla*, *P. montezumae*, and *P. pseudostrobus*; 76 recorded), *Buddleia parviflora* (19 recorded), oaks (*Quercus crassipes*, *Q. disophylla*, *Q.*

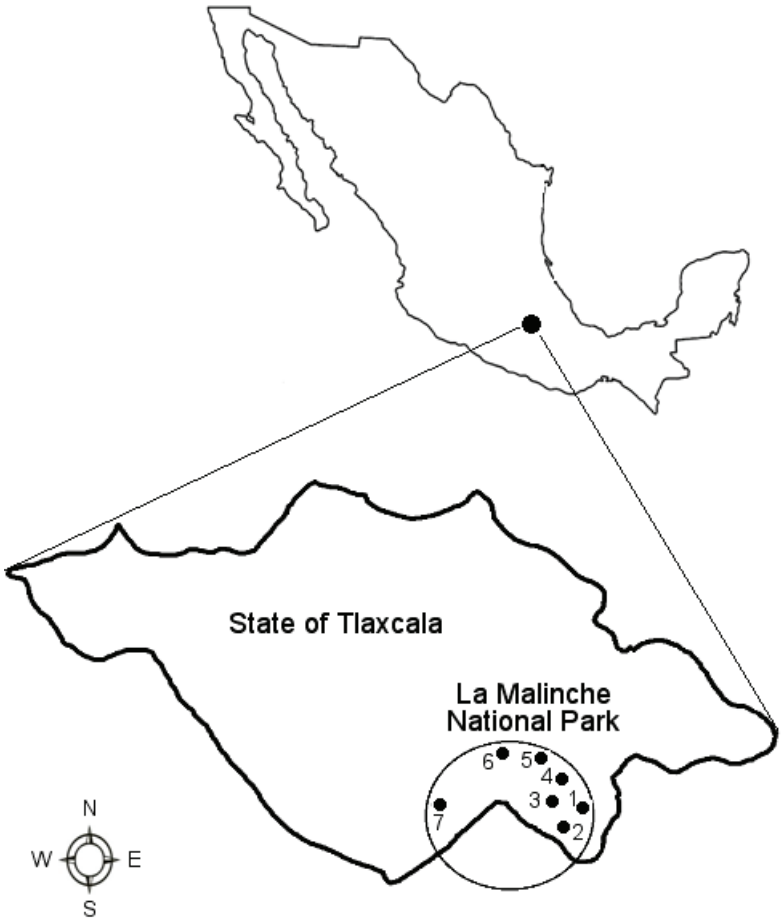

FIG. 1. Geographical location of National Park La Malinche (MNP) in the state of Tlaxcala, Mexico. Dark circles indicate the location of the leks studied.

glabrescens, and *Q. laurina*; 14 recorded), *Alnus acuminata* (11 recorded), and *Prunus serotina* (seven recorded). Additionally, there were six perch records on branches of *Barkleyanthus salicifolius* and 16 records on branches of dead trees whose identification could not be determined. The average height estimated of the recorded perches was 10.96 m (± 0.51 m). In spite of the aforementioned information, there was variation among leks in the preference of the species of tree for perches as well as the height of these perches (Fig. 3).

Vegetation in lek areas. During the first field observations performed at established lek sites, we began recording the present plant species. We obtained a list of 54 species of plants belonging to 25 families. Four species of plants were recorded in all the established lek sites: *Braccharis conferta* (Asteraceae), *Buddleia parviflora* (Loganiaceae), *Lupinus montanus* (Fabaceae), and *Muhlenbergia macroura* (Poaceae). According to the Sorensen similarity index, the seven sites had a similarity index of 0.44 with the highest similarity index between

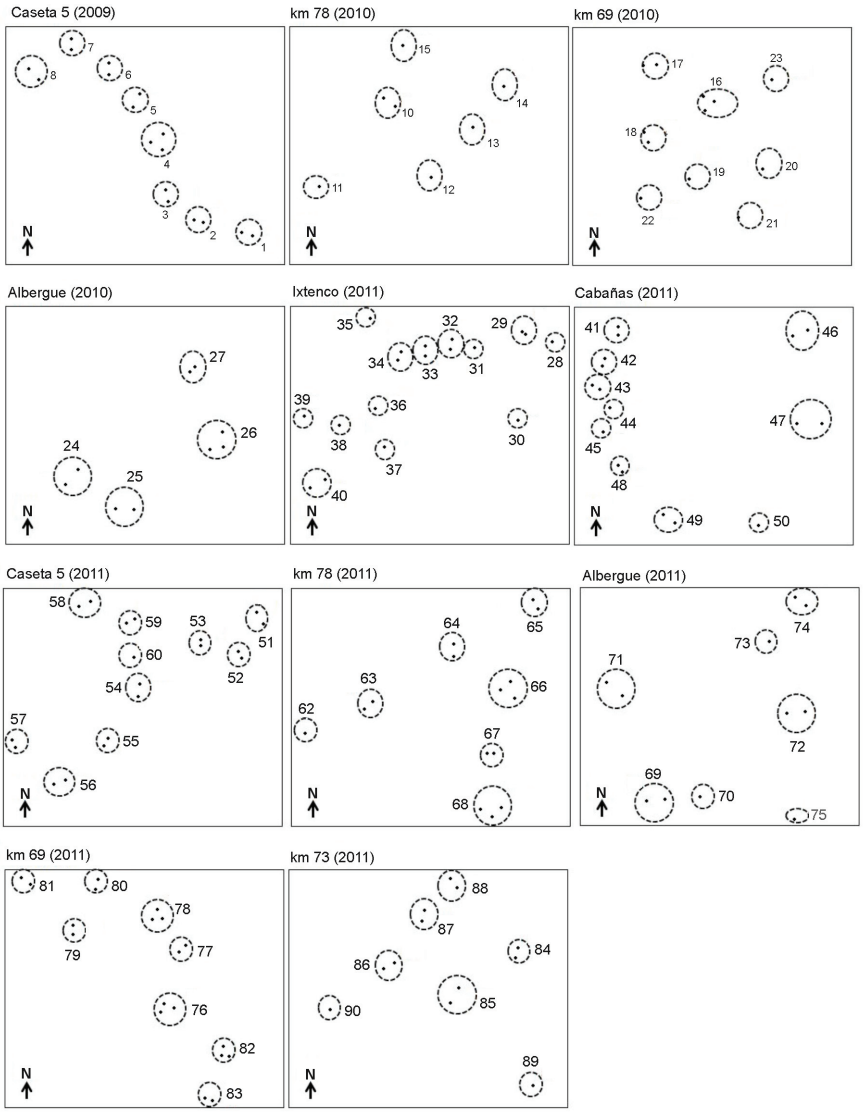

FIG. 2. Spatial location of each individual vocal areas (circles with dotted lines) as and perches (black dots), in each lek studied during 2009–2011.

the km 78, km 69, and km 73 sites located spatially close to one another (Fig. 4).

Vocal repertoire and associated behavior at the leks. The individuals that form part of the lek begun singing on their perches at sunrise and continued doing so during the whole day with a decrease in activity in the afternoon. When the weather was cold with rain or fog, some individuals decreased their activity and others completely stopped singing, as noted by Wagner (1945). Throughout the study we

TABLE 2. General characteristics of the 11 leks studied in 2009-2011 in the La Malinche National Park (MNP), Tlaxcala.

Lek	Year	Location		Altitude	Duration		Members
		N	W	(m a.s.l.)	Starting	Ending	
Caseta 5	2009	19°14', 29.27"	97°58', 43.86"	2836–3060	28 Aug	29 Sep	8
	2011				3 Aug	7 Sep	10
km 78	2010	19°15', 17.51"	97°58', 37.41"	2961–3002	4 Sep	17 Sep	6
	2011				16 Aug	30 Sep	7
km 69	2010	19°16', 23.16"	97°59', 12.55"	2914–2953	15 Aug	8 Sep	8
	2011				3 Sep	29 Sep	8
Albergue	2010	19°16', 17.51"	98°3', 12.88"	2929–3045	16 Sep	4 Oct	4
					25 Aug	28 Sep	7
Ixtenco	2011	19°14', 31.33"	97°58', 12.64"	2867–2985	14 Jul	3 Sep	13
Cabañas	2011	19°58', 12.34"	97°58', 39.89"	2939–2968	6 Aug	29 Aug	10
km 73	2011	19°15', 58.00"	97°59', 5.07"	2977–3002	2 Sep	28 Sep	7

obtained recordings of the vocal repertoire of 69 of the 88 individuals, who formed the leks. For each of the individuals, five recordings were obtained at different times throughout the day. Using spectrograms and based on our observations, two types of singing were identified: (1) the singing vocal repertoire at leks, and (2) the singing display when foraging. The singing that made up the vocal repertoire of the lek consisted of 40 different notes that were sung only when the individuals were perched (Figs 5a–b). The second foraging singing type is a single note (absent form the vocal repertoire of the lek) repeated in phrases from 2–12 consecutive notes (Fig. 5c).

Starting with the focused observations of the 88 individuals who formed part of a lek, four exhibited behaviors used only within a lek were typically recorded during the vocalizations while perched (Fig. 6). These four behaviors were defined as: (1) swerving the head, which is when the individuals turn their head from the left to the right repeatedly; this behavior is repeated while they are singing from their perches; (2) flapping the wings, where the individuals extend their wings, and turn left and right while lowering the wings; (3) complete turn, done when the individuals land then extend the wings, rise, turn 180°, land and lower the wings, and (4) fanning the tail, where the individuals extend and retract rectrices in the form of a fan one to three times and retract the rectrices until they are together like a closed fan. Flapping the wings, the complete turn and fanning the tail are behaviors that are done with the least frequency while singing on the braches.

DISCUSSION

This study provides information about the characteristics of the habitat used by *Colibri thalassinus* in the establishment of leks in a temperate forest in central Mexico. Additionally, we show the repertoire of vocal displays in these courtship arenas.

Based on data on the spatial distribution of the 88 individuals inside of the 11 studied leks, we determined that *C. thalassinus* forms leks characterized by individuals dispersed very far apart who possibly lose visual contact but maintain vocal interactions. Gaunt *et al.* (1994) observed that this species forms scattered leks in Costa Rica. This spatial organization, called "explosive leks", has already been

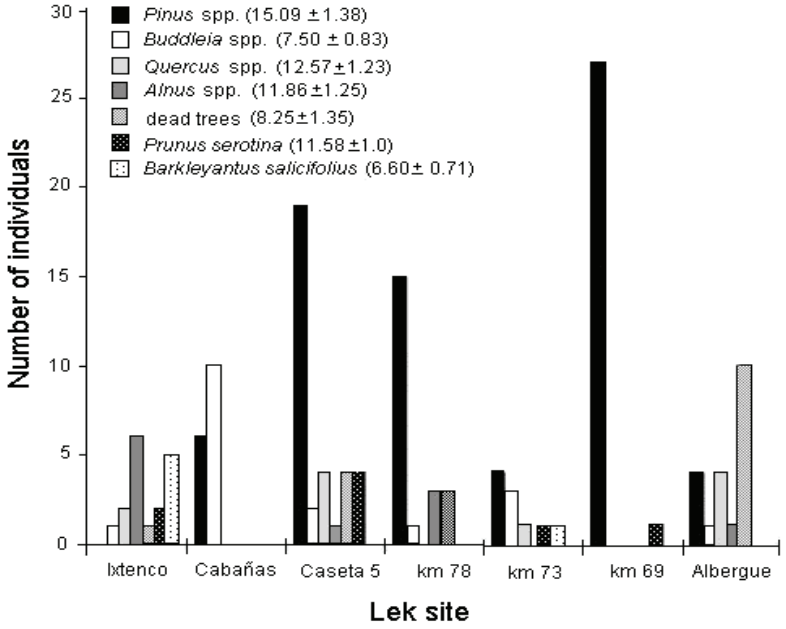

FIG. 3. Frequency of species of trees and shrubs used as perches on each lek, including mean height (m ± standard error).

reported in other species of hummingbird, such as *Amazilia candida* (Atwood *et al.* 1991), *Eupetomena macroura* (Pizo & Silva 2001), *Calypte anna* (Powers 1987), and *Stellula calliope* (Tamm *et al.* 1989). Furthermore, distances as large as 15 m between individuals who make up a lek have been reported in other species, for example in *Campylopterus hemileucurus* (Skutch 1972), *C. curvipennis* (González & Ornelas 2009), *Amazilia amabilis* (Skutch 1972), *A. tzacatl* (Skutch 1981), *Hylocharis eliciae* (Skutch 1972), *H. leucotis* (Skutch 1972), *Phaeochroa cuvierii* (Skutch 1964), and *Klais guimeti* (Skutch 1958). On the contrary, other studies have determined distances between 10 m or less in leks of *Phaethornis superciliosus* (Stiles & Wolf 1979), *P. longuemareus* (Wiley 1971), *P. guy* (Snow 1974, MacDougall-Shackleton & Harbison 1998), and *Selasphorus platycercus* (Barash 1972).

Even though these studies do not mention the type of lek that forms, they point out that in spite of the short distances between them, the individuals loose sight of one another due to the presence of dense vegetation (Atwood *et al.* 1991). As far as the spatial distribution of the individuals inside of the lek, *C. thalassinus* does not present any type of pattern (Fig. 2). In this sense, some studies done in leks of *P. longuemareus* (Wiley 1971), *P. guy* (MacDougall-Shackleton & Harbison 1998), *E. macroura* (Pizo & Silva 2001), and *C. curvipennis* (González & Ornelas 2009) – species for which a spatial description has been given – also do not mention any type of spatial pattern between the members of the leks. In other groups of birds, which form leks such as the grouse (*Lyrurus tetrix*), it has been demonstrated that the spatial agreement between the males that join a lek can be related to hierarchal levels. In these leks, males compete for positions in the centre of the arena, where the success rate of copulation is the greatest (Hovi *et al.* 1994). This

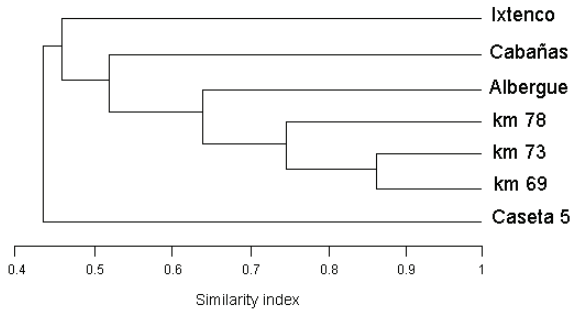

FIG. 4. Similarity index according to Sorensen coefficient for the vegetation in seven sites where leks were established.

type of spatial pattern in leks formed by hummingbird continues to be unexplored and requires further studies in order to be fully understood.

The *C. thalassinus* leks can remain active between 10–50 d from the beginning of their formation to their complete disintegration. In general they last for 30 active d, and the peak of their activity with the greatest number of members occurs between 10–20 d. These characteristics denote a great dynamism in these types of assemblies. The only previous study that shows the changes in a lek throughout time is the study of Pizo & Silva (2001) with *E. macroura,* in which territorial locations are shown for March, July, and October 1990, and February 1991. According to these authors, the duration of a lek can be defined by a reproductive period and by the availability of food. The leks in *E. macroura* were formed on the campus of a state university, a site in which the leks had food resources for the whole year. In *C. thalassinus*, the duration of the leks might be determined by the migratory movement of the females. According to Wagner (1945), females and the young individuals migrate while the male adults stay in the same sites waiting for the next reproductive season, which occurs from August–November in Mexico. In our study site, we observed that this period extends for about a month, sometime between July and October, coinciding with the flowering period of *P. roseus* (Lara 2006) growing in large patches close to the sites of the leks. Therefore, current data suggest that lek duration among hummingbirds is possibly determined by the reproductive period and availability of flowers.

The repeated use of a given site to form a lek attended by the same individuals has been relatively unexplored in hummingbirds. In our study, three of the leks followed this pattern. The lek established in Caseta 5 was located in the same site in 2009 and 2011 with same perches being used presumably by the same two individuals in both years. The same occurred with the km 78 lek in 2010 and 2011. The lek established in Albergue had the same location in 2010 and 2011 with presumably the same six individuals using the same perch as in the previous year. Even though the repeated use of perches between years seemed evident, the color-marking technique adopted here impeded us from confirming whether they are the same individuals. Further detailed studies are needed to determine site fidelity of individuals participating in the leks over the years.

Our results show that the singing perches used by the males to sing within leks were preferably dried branches of pine, tepozan,

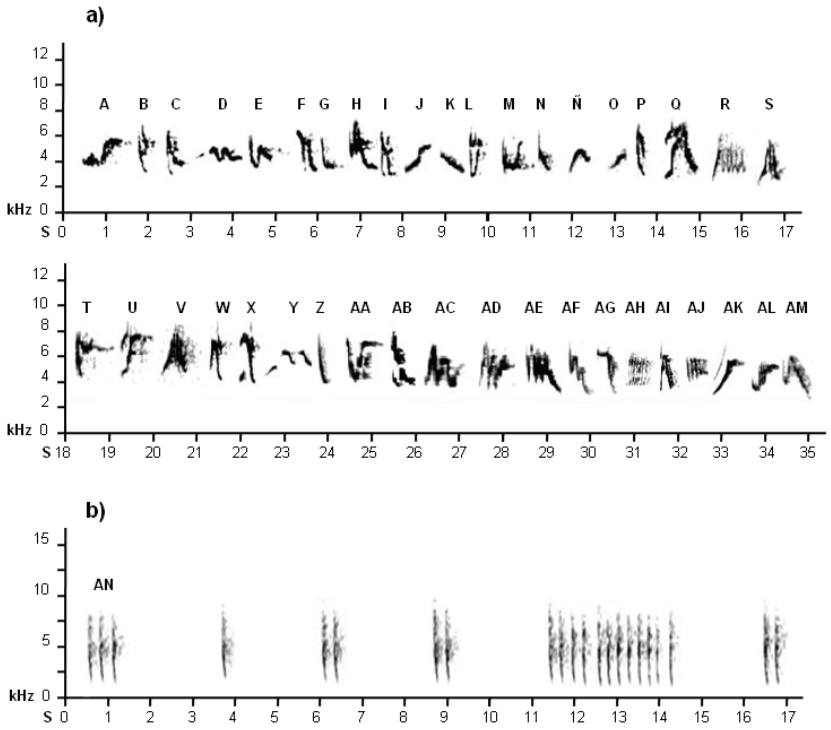

FIG. 5. Vocal repertoire of Green Violet-ear Hummingbird (*Colibri thalassinus*) at La Malinche, Tlaxcala, Mexico, under different behavioral contexts: (a) male song displayed in a lek, and (b) feeding call. Letters indicate the type of note or syllable.

oak, and completely dead trees. Also, in the leks located in sites with the most tree covering (Cabañas, Caseta 5, km 78, and km 69), the heights of the perches were higher than in the more open sites (such was the case in Ixtenco, km 73, and Albergue). The same tendency was found with respect to the species of tree present in the leks. Wagner (1945) observed that Green Violet-ears used dried branches as perches in firs (*Abies religiosa*) and oaks (*Q. crassipes*, *Q. nitens*) in areas near Mexico City. Alternatively, Barrantes *et al.* (2008) observed that this species uses oak trees as perches 8–25 m high in Costa Rica, and the individuals are found separated by 20–100 m. Results from both studies concur with our data with respect to the use of oak tress. Nevertheless, it is clear that in our study site the pine trees are preferentially used by the males when singing in the leks.

The number of perches used by individuals evaluated in our study was preferably two. The use of multiple perches in the species was previously suggested by Wagner (1945), who notes that the males present in one territory move from one perch to another, emitting its calls from both. The importance of having various perches inside of a lek has not been previously evaluated in hummingbirds and its possible relationship with courtship displays needs to be further explored. Intuitively, having few perches implies a small territory inside of the lek and this could represent the possibility of a better broadcasting

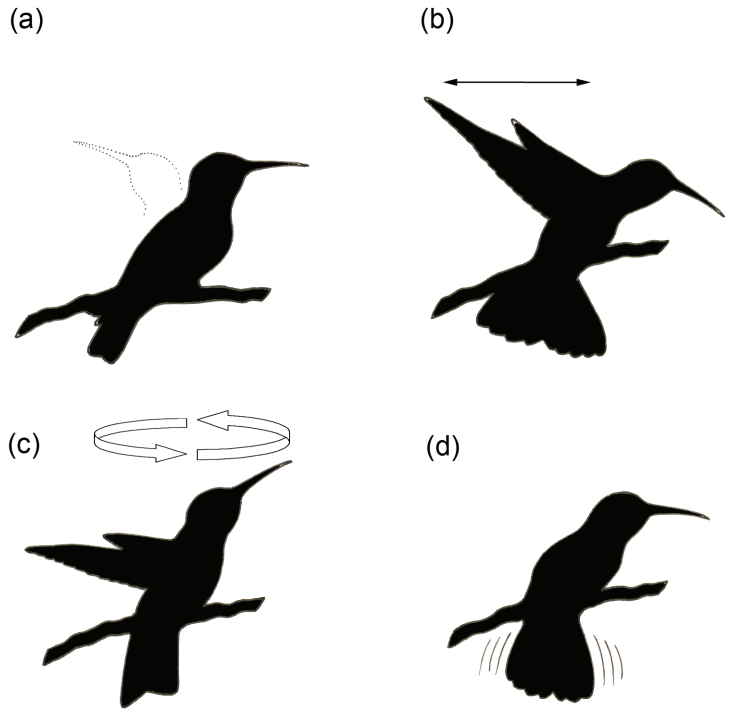

FIG. 6. Behaviors exhibited by males in leks and displayed during the vocalizations while perched. These four behaviors were: (a) swerving the head, (2) flapping the wings, (3) complete turn, and (4) fanning the tail (drawings by E. Saavedra).

location to sing to the females. This has been previously suggested in *P. longuemareus* by Wiley (1971).

The location of the recorded leks throughout the study coincided with the line of the road known as the "perimetral," which marks the limits of the MNP. This path includes a strip of a recovering pine forest found between a small wooded area and areas used for cultivation. The altitude of the strip goes from 2800–2060 m a.s.l., and in this area different vegetation strata and open spaces can be observed. Our data suggest that this type of environment is preferred by *C. thalassinus* to establish leks. In these sites, during this study, the abundant presence of patches of de *P. roseus* (Scrophulariaceae) was common. This plant species is used as a food resource, and the leks are typically established in areas close to these plants.

As suggested by Wagner (1945), our data also suggest that *C. thalassinus* males establish their leks in areas with secondary vegetation, particularly in areas between the forest and areas of cultivation. These sites are open areas with the presence of tall trees (< 15 m). These characteristics may facilitate the males broadcasting a loud vocalization and the females may more easily identify the location of the singer. The lack of information about this topic is evident as the few descriptions of leks in hummingbirds only include the type of vegetation or the organizational characteristics of established leks.

During the time that the evaluated leks remained active, the individuals who formed the leks sang from three to five different notes, accumulating a vocal repertoire of 24 notes inside the leks (static singing) and one note in the singing displayed when foraging. According to Wagner (1945), *C. thalassinus* makes short, monotonous calls that repeat continually. These calls are presented in three forms of expression: the first is done when standing on an exposed branch, *huit ti titatia*; *huit tita, tetahuit tetahuit,* and *teta tetuit tetahuit,* continually and with little intensity. The second, with greater intensity and force, *ahuit ahuit ta ta* and *huit ti ta huit ti ta,* is done when moving the head from one side to another. In the third type, *huita huita,* is repeated continually while turning the head from one side to another and at the same time raising the feathers of the head and the back. Another call that is not mentioned in these three forms of expression is the flight call that is a repetitive *itta itaa* or a *huita huita* (Wagner 1945). This can be the singing of the foraging that was recorded in the MNP. Two previous studies on vocal variation in *C. thalassinus* (Gaunt *et al.* 1994, Barrantes *et al.* 2008) noted that this species presents a song with complexity in its composition of notes even though it had not been detailed for any site how many notes formed this repertoire. Our study documents the complexity of different notes in the static singing complex. Variations of vocalizations between *C. thalassinus* males displaying in lek neighborhoods (González & Ornelas 2009) at the centre of the MNP area compared to lek neighborhoods located in the peripheries (Martínez-García, Lara & Ornelas unpubl. data), could be an indication of song learning (see Baptista & Schuchmann 1989, González & Ornelas 2009).

In summary, our study demonstrates that males of *C. thalassinus* form leks in varying spatial and temporal conditions, with specific requirements for the habitat characteristics where leks are established. Additionally, we have demonstrated that leks of this species can be established in previously occupied sites, including the use of the same perch during successive years. Finally, we provide the first description of the repertoire of vocal displays in the leks considering the number of notes emitted. Further studies are still necessary to elucidate the environmental requirements necessary for the establishment of leks in hummingbirds. The information generated here will help to prove basic concepts in this field of study.

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