NICHE PARTITIONING AMONG HUMMINGBIRDS FORAGING ON *PENSTEMON ROSEUS* (PLANTAGINACEAE) IN CENTRAL MEXICO

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Resumen. – **Repartición de nicho entre colibríes forrajeando en *Penstemon roseus* (Plantaginaceae) en el centro de México. –** En la Malinche Tlaxcala, México, *Penstemon roseus* florece cuando otros recursos florales son escasos y cuando las ocho especies de colibríes registradas en la región están presentes, sugiriendo una alta posibilidad de competencia por néctar. Investigamos la repartición espacial y temporal de colibríes forrajeando en esta planta a lo largo de su periodo de floración. Midiendo en diferentes horarios la disponibilidad de néctar y producción de azúcar en diferentes parches florales de *Penstemon*, y cuantificando su número de flores y plantas, registramos el tiempo de llegada de los colibríes a las plantas del parche. Asimismo, registramos la posición de la flor visitada en la planta y la posición de la planta dentro del parche. Encontramos segregación temporal entre colibríes de acuerdo a su peso corporal y conducta territorial durante los horarios de mayor producción de néctar. Las especies de colibríes difieren en sus horarios de visita, y encontramos diferencias a nivel especie y sexo en la posición de las flores visitadas en las plantas, donde las especies subordinadas y las hembras visitan más las flores en la parte inferior de las plantas, y las especies dominantes y los machos visitan más las flores en la parte superior de las plantas. La segregación especial y temporal entre colibríes es interpretada como una forma para reducir el riesgo de daño. Esto puede facilitar la coexistencia y llevar a los colibríes a satisfacer sus demandas energéticas a corto plazo.

Abstract. – In La Malinche Tlaxcala, México, *Penstemon roseus* flowers when other floral re are scarce and when all eight hummingbird species recorded on the region are present, suggesting a high possibility of direct interspecific competition for the nectar resources. We investigated temporal and spatial partitioning of hummingbirds foraging on this plant species over the flowering period. By measuring the availability and quality of nectar in several patches of *Penstemon* at different times, and counting the number of plants and flowers of each patch, we recorded the time until a hummingbird visited a plant within each patch. Likewise, we recorded the position of the visited flower on the plant as well as the position of the visited plant within the patch. We found temporal segregation among hummingbirds according to body size and territorial behavior during the most nectar-limited time. Hummingbird species differed in the times of day they visited flowers on this plant species, and both species and sexes differed in the location of flowers visited on plants. Subdominant species and females visited more flowers on the bottom of plants while dominant species and males preferred flowers on the tops of plants. Temporal and spatial segregation among hummingbirds is interpreted as adaptations to reduce risk of aggressive encounters. These behaviors may facilitate coexistence and allow hummingbirds to meet their short-term energy demands. *Accepted 18 December 2008*.

Key words: Hummingbirds, México, nectarivory, niche partitioning, *Penstemon roseus*.

INTRODUCTION

The study of the factors influencing the distribution and abundance of animals has long been fundamental to ecology (Andrewartha & Birch 1954). Resource partitioning among species in time and space has often been used to ascertain the influence of conspecifics and heterospecifics on the behavior of a variety of animals (Davies 1978). Behavioral responses such as spatial separation, temporal avoidance and dietary differences have been suggested as ways to minimize competition of foraging species. However, studies exploring niche separation along all three axes are scarce in the literature (but see Ben-David *et al.* 1996, Kronfeld-Schor *et al.* 2001, Steward *et al.* 2002).

Behavioral dominance has been proposed as a mechanism by which communities of nectarivores composed of insects, hummingbirds, passerine birds, and bats sharing patchy and ephemeral floral resources over time, are structured (Lyon & Chadek 1971, Primack & Howe 1975, Boyden 1978, Carpenter 1979, Schaffer *et al.* 1979, Kodric-Brown & Brown 1979, Gill *et al.* 1982, Martínez del Rio & Eguiarte 1987, Westerkamp 1990, Sazima & Buzato 1994, Fleming *et al.* 1996, Symes *et al.* 2008). Likewise, it has been suggested that access to nectar resources by mixed-species assemblages is often determined by inter-specific aggression in which larger species dominate the smaller ones (Ford &Paton 1982, Camfield 2006). However, direct interference among nectarivorous taxa is not the only way to access nectar resources. For example, it has been suggested that hummingbirds can show temporal and spatial segregation while foraging on a limited floral resource, thus allowing the coexistence of species (Ornelas *et al.* 2002). Such a phenomenon may result from temporal and spatial heterogeneities in resource distribution following environmental processes that act independently of the consumers (Cheson & Warner 1981), but can be reinforced by the behavior of the foragers. Temporal and spatial partitioning of foraging potentially promotes coexistence (Carothers & Jaksic, 1984), and may reduce resource overlap or negative interactions that occur during co-feeding (Richards 2002). For example, by studying niche partitioning of nectarivores at *Agave marmorata* inflorescences in Tehuacán, México, Ornelas *et al.* (2002) found evidence of coexistence by temporal and spatial segregation among insects, hummingbirds, and perching birds during the most nectar-limited time.

In this paper, we present data from an assemblage of hummingbirds (Trochilidae) feeding on *Penstemon roseus* when other floral resources are scarce in a temperate forest in La Malinche, México. We investigated feeding behavior of hummingbirds throughout the day in order to identify temporal and spatial niche partitioning that may assist in the reduction of direct interference between hummingbirds foraging in this floral resource. This study is a pioneer work to generate hypotheses about the behavioral processes affecting the structure of this community of hummingbirds.

METHODS

Study time and site. The study was carried out from September to November 2005, in the National Park "La Malinche", Tlaxcala (19°14'N, 98°58'W, 2900 m a.s.l.). This protected area (45,711 ha of pine, oak, and sacred fir forest) is located 80 km from Tlaxcala City, Tlaxcala, Mexico. The vegetation is pristine and dominated by *Pinus montezumae, P. pseudostrobus, Abies religiosa* (Pinaceae), *Quercus laurin*, and *Q. crassipe* (Fagaceae).

Study species. A recent investigation at the study site yielded eight ornithophilous plant species

as year-round potential food sources for hummingbirds (Lara 2006). In the middle of the year (May to July), plant species such as *Salvia elegans* (Lamiaceae) and *Bouvardia ternifolia* (Rubiaceae) help to maintain resident species such as White-eared Hummingbird (*Hylocharis leucotis*) and Magnificent Hummingbird (*Eugenes fulgens*), and altitudinal migrant species such as Green Violetear (*Colibri thalassinus*), Blue-throated Hummingbird (*Lampornis clemenciae*), and Ruby-throated Hummingbird (*Archilochus colubris*) (Lara 2006). However, during our study (September-November), the plant species with the greatest flower production was *Penstemon roseus* (hereafter *Penstemon*), a perennial herb (~ 1.2 m high) endemic to Mexico, commonly found in fir, pine, oak and cloud forests (2250–3900 m a.s.l.) from Sinaloa and Chihuahua to Oaxaca (Calderón & Rzedowski 2001). Individuals of *Penstemon* bear 1020 paniculate inflorescences, each with 2-4 pendant flowers open per day from terminal branching stems, and 80 floral buds may eventually reach the flower stage during the blooming season (three months), which extends from August to November in the region. The bright red tubular flowers are protandrous (corolla length, mean ± SE = 22.7 ± 0.22 mm; corolla-entrance width = 6.8 ± 0.11 mm, N = 60; Lara & Ornelas 2008) and last 24 days. Each flower passes through a 12 day male phase (staminate), followed by a 12 day female phase (pistillate), with no significant differences in the production of nectar in both phases (C. Lara unpubl.). Flowers with four pollen-bearing anthers (Dieringer & Cabrera 2002) are visited by nectar-robbing bumblebees; they are pollinated mostly by hummingbirds.

The peak flowering period of *Penstemon* (late September) coincided with the arrival of latitudinal migrant hummingbirds to the area such as Broad-tailed Hummingbird (*Selasphorus platycercus*), Rufous Hummingbird (*S. rufus*), and Allens Hummingbird (*S. sasin*). We were able to observe all hummingbird species recorded at La Malinche that visit this plant species. Alternate scarce nectar resources during this time of year include hummingbird-pollinated *Castilleja tenuiflora* and *C. scorzonerifolia* (Scrophulariaceae), but the floral abundance and the amount of nectar offered per flower is minimal (0–1.2 μl per flowers; Lara 2006). Therefore, the nectar offered by *Penstemon* between August–November was the primary nectar food source for visiting hummingbirds, and the plant-bird interactions can be used as a model system to explore their foraging and behavioral strategies.

Temporal segregation. We selected 15 flowering *Penstemon* patches (each containing a range between 31 and 553 plants) as they appearing at the study area (~100 ha) to observe floral visitors over the course of a day. To be selected, a patch had to have > 30 plants, be visited by hummingbirds, and be in an area where visibility was not interfered with the surrounding vegetation. Although the number of plants varied between patches, patches with few plants and a distance > 1 m between individuals covered a similar circular area (~113 m^2) to patches with many plants and growing close together (< 50 cm between individuals). Each patch was divided into a central portion (plants covering a radius of 2 m from the center of the patch) and a peripheral portion (all plants around the central zone). The flowers on this plant species are distributed evenly throughout the plant, allowing us to explore the hummingbird's spatial use of individual plants. For this purpose, we visually divided plants into halves "upper area" and "lower area" respectively. To be able to identify with better accuracy if a visit was made in the center or periphery of a patch, and in the upper or lower area of a plant, we used a level rod (3 m) placed in the center and in the periphery of each selected patch. Each month, three different patches were simultaneously recorded

for a day. Prior to that, a 3-day observational period (from 07:00 to 19:00 h, a total of 36 h) was conducted to establish when hummingbirds were more actively foraging. Based on the observational results, we recorded every foraging event in each patch throughout three observation periods (08:00–10:00, 12:00–14:00, and 16:00–18:00 h; 96 h of sampling effort), and noted the hummingbird species, sex, time of day, number of flowers and plants visited, position of flowers visited in the plant (upper vs. lower), position of plants in the patch (center vs. periphery) and aggressive interactions defined as displays of territorial proclamation and intimidation of conspecifics or heterospecifics. Because we do not mark birds during the observations, some of them may be repetitions of the same individuals. Observers were located ~3 m away from the focal patch. Approach and avoidance behavior by birds in apparent response to observers was not detected during observations. Throughout the study 10 individuals of each hummingbird species were captured by using mist nets to obtain morphological measurements, e.g., body length and body mass. Body mass measures were used to classify hummingbird species into three categories of body size: 1) small (3–3.5 g), 2) medium (3.6–6 g), and (3) large (6.4–8.4 g).

We conducted an ANOVA blocked for time of day to analyze the frequency of hummingbird visits to *Penstemon*, followed with multiple comparison procedures of Tukey (Zar 1999). Data were arcsine transformed to fit assumptions of parametric tests. Normality of the obtained data was tested by using a Kolmogorov-Smirnov goodness of fit test. At the end of each observation periods, we counted the number of plants and open flowers in the patch. The nectar volume encountered by a hummingbird can vary within a plant over time and this may influence subsequent foraging events. To account for this we measured nectar volume in the flowers.

Throughout the study, we numbered all open flowers in a patch and randomly selected 20 open flowers per period and patch (from ~10 plants, including individuals from the periphery and center of the patch, as well as flowers at the upper and lowers area of the plants). Nectar volume was measured by standing crop following standard procedures (Kearns & Inouye 1993). Nectar volume per flower was estimated using calibrated micropipettes (5 μl) and a ruler. Nectar concentration according to the Brix scale was estimated using a digital manual refractometer (Atago, Japan), and the amount of sugar was expressed in milligrams (Kearns & Inouye 1993). We then correlated these characteristics (Spearman Rank Correlation) with the number of visits, and used them as covariates to explore spatial segregation. A previous data exploration using a three-way ANOVA to search for possible differences in the production and concentration of nectar with respect to the position of the plants in the patch and the position of flowers in the plant through time intervals, demonstrated that there was no significant effect of the position of plants (three-way ANOVA, nectar volume: $F_{1,888} = 2.70$, $P = 0.128$, nectar production $F_{1,888} = 4.13$, $P = 0.98$) and flowers (three-way ANOVA, nectar volume: $F_{1,888} = 0.78$, $P = 0.501$, nectar production $F_{1,14} = 0.67$, $P = 0.438$) . Therefore, the position factor was eliminated and variation in nectar volumes and concentrations over time were analyzed by using one-way ANOVAs (Zar 1999). Differences in the number of hummingbird visits to upper and lower flowers and to central and periphery plants in a patch were assessed by two-way ANOVAs.

RESULTS

Temporal segregation. We observed eight hummingbird species feeding on *Penstemon* flowers. A total of 765 foraging events (visits to a
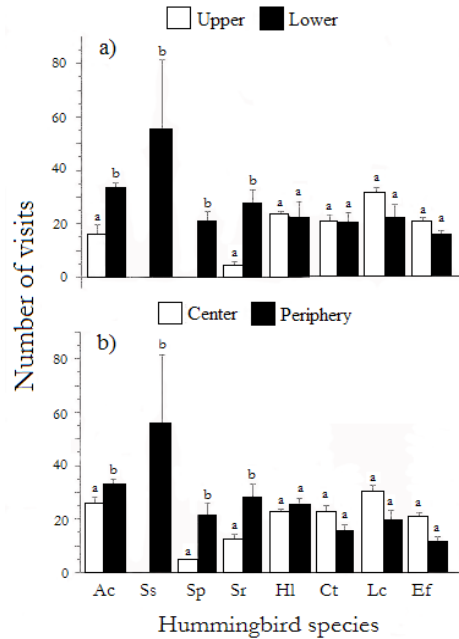
FIG. 1. Variation among hummingbird species in (a) the number of visits (mean ± SE) to upper and lower flowers in a plant, and (b) the number (mean ± SE) of central and periphery plants visited in a patch. Bars with the same superscript letter are not significantly different groups ($P > 0.05$). Abbreviations: Ac = *Archilochus colubris*, Ss = *Selasphorus sasin*, Sp = *S. platycercus*, Sr = *S. rufus*, Hl = *Hylocharis leucotis*, Ct = *Colibri thalassinus*, Lc = *Lampornis clemenciae*, Ef = *Eugenes fulgens*.

patch) were registered during our study (Ruby-throated Hummingbird = 200, Green-Violetear = 115, Magnificent Hummingbird = 89, White-eared Hummingbird = 197, Blue-throated Hummingbird = 108, Rufous Hummingbird = 24, Broad-tailed Hummingbird = 18, Allens Hummingbird = 14). We observed 7.9 ± 0.5 (mean ± SE) bird visits per patch and hour (Fig. 1). The frequency of hummingbird visitation throughout the day showed significant variation among hummingbird species (one-way blocked ANOVA, $F_{2,14} = 2.78$, $P = 0.038$, Table 1). Hummingbirds were more active in the morning (12.2 ± 0.2 birds per patch and hour) than later in the day. We recorded significant differences between species with respect to their body size (mass) (one-way ANOVA, $F_{7,72} = 452.21$,

$P < 0.0001$). The post hoc Tukey test showed two groups: the small and large size hummingbirds. White-eared Hummingbird and Green Violetear differed from the other groups compared. Thus both species were arbitrarily grouped together to form the medium size hummingbird group (Table 1). Small species, such as Ruby-throated Hummingbird and *Selaphorus* spp., visited the *Penstemon* patches more frequently early in the morning while larger species, e.g., Blue-throated Hummingbird and Magnificent Hummingbird, visited the patches in the afternoon. However, territorial medium-sized hummingbirds, e.g., Green Violetear and White-eared Hummingbird were observed defending and visiting *Penstemon* patches throughout the day (Table 1).

TABLE 1. Relative frequency of hummingbird visitors over time in *Penstemon roseus*, and data for their body size. Data (n = 10 for each species) with the same superscript letters are not significantly different between groups (*P* > 0.05).

Hummingbird species	Time intervals (h)			Body size
	08:00–12:00	12:00–14:00	16:00–18:00	(mass in g ± SE)
Archilochus colubris	0.27[a]	0.15[b]	0.14[b]	3.03 ± 0.02[a]
Selasphorus sasin	0.10[a]	0.06[a]	0.05[a]	3.09 ± 0.04[a]
Selasphorus platycercus	0.11[a]	0.07[b]	0.07[b]	3.16 ± 0.02[a]
Selasphorus rufus	0.11[a]	0.05[b]	0.04[b]	3.17 ± 0.03[a]
Hylocharis leucotis	0.17[a]	0.21[a]	0.19[a]	3.62 ± 0.02[b]
Colibri thalassinus	0.15[a]	0.15[a]	0.16[a]	5.11 ± 0.07[c]
Lampornis clemenciae	0.06[a]	0.15[b]	0.20[b]	6.83 ± 0.01[d]
Eugenes fulgens	0.03[a]	0.16[b]	0.15[b]	7.03 ± 0.04[d]

TABLE 2. Nectar volumes and concentrations (mean ± SE) measured by standing crops over time in flowers of *Penstemon roseus*. Data with the same superscript letters are not significantly different between groups (*P* > 0.05).

	Time intervals		
	08:00–12:00	12:00–14:00	16:00–18:00
Volume (μl)	7.43 ± 0.51[a]	4.21 ± 0.72[b]	3.82 ± 0.90[b]
Concentration (mg/ml)	0.21 ± 0.02[a]	0.18 ± 0.07[b]	0.17 ± 0.08[b]

To determine whether temporal segregation was explained by patch and plant characteristics ,e.g., the number of plants and open flowers in a patch, and the nectar volume and concentration in flowers of a plant, we looked at the variation in the number of visits as a function of these variables. The number of plants in a *Penstemon* patch ranged from 31 to 553 (mean ± SE = 198.4 ± 42.25), and the number of open flowers in a patch from 99 to 5076 (mean ± SE = 1442.06 ± 326.20), however the number of visits recorded were not positively correlated with these characteristics ($r^2 = 0.36$, *P* = 0.15, and $r^2 = 0.26$, *P* = 0.33 respectively). We found significant differences between interspecific schedules with respect to volumes (one-way ANOVA, $F_{2,897} = 22.43$, *P* < 0.01) and concentrations measured in the sampled flower (one-way ANOVA, $F_{2,897} =$ 19.09, *P* < 0.01). Nectar volume and concentration were highest early in the morning and declined throughout the day (Table 2). Nectar volumes ranged from 0–23 μl and sugar production from 0.23 mg × ml[1]. Nectar volume was positively correlated with the number of hummingbird visits ($r^2 = 0.78$, *P* = 0.03), but no correlation was found for sugar production ($r^2 = 0.29$, *P* = 0.28).

Spatial segregation. The mode of plant and patch exploitation varied among species. Small hummingbirds (Ruby-throated Hummingbird and *Selasphorus* spp.) foraged mostly on lower flowers on peripheral plants, while medium- and large-sized hummingbirds visited upper and lower flowers equally but fed less frequently from plants located in the center of a patch (Table 3, Fig. 2). Likewise,

TABLE 3. Summary of two-way ANOVAs on the effect of A) position of flowers in the plant and B) position of plants in the patch on the number of visits recorded by hummingbird species and for sex.

	df		F		P	
Position	A	B	A	B	A	B
Hummingbird species	7	7	1.86	3.27	0.073	0.002
Position	1	1	1.26	0.28	0.258	0.591
Hummingbird species × Position	7	7	2.99	1.98	0.011	0.050
Error	705	705				
Sex	1	1	3.20	3.58	0.071	0.060
Position	1	1	4.25	0.25	0.039	0.617
Sex × Position	1	1	7.44	1.53	0.006	0.215
Error	705	705				

when we grouped all species and analyzed differences between sexes (a total of 332 females and 423 males), females were found to visit lower flowers in a plant more often than males, but both sexes visited plants from the periphery and center of a patch with equal frequencies (Table 3). During our observations, interspecific chases were observed (n = 61 events). White-eared Hummingbird and Green Violetear aggressively excluded smaller species (Ruby-throated Hummingbird and *Selasphorus* spp.) from *Penstemon*. Most commonly, intraspecific aggressive encounters were observed (Ruby-throated Hummingbird = 20, Green Violetear = 32, Magnificent Hummingbird = 31, White-eared Hummingbird = 42, Blue-throated Hummingbird = 33, *Selasphorus* spp. = 12).

DISCUSSION

In this study, spatial and temporal segregation between hummingbird species and sexes visiting *Penstemon roseus* at La Malinche, Tlaxcala, México, was examined. We found that different species and sexes visited different areas within a patch and fed on flowers from different parts of a plant. However, because we did not evaluate possible differences in produc-

tion of nectar and sugar considering the position of the plants within the patch, we can not know whether these differences are a reflection of different variables concerning microclimate in the patch. Additional analysis is required to evaluate this possibility. Likewise, visitation periods varied among the hummingbird species. Small hummingbirds, e.g., *Selasphorus* species, tend to visit lower flowers in a plant and plants located on the periphery of patches. This foraging strategy may either help to avoid aggressive encounters of small hummingbirds with larger and more territorial species, or reflects a preference by the latter to lower flowers (cf. Lyon 1976 for *Rigidella orthantha*).

Another interesting finding in our study was sexual differences in foraging modes. In addition to segregation by species, we found that females of all hummingbird species carry out more visits to flowers in lower areas of a plant. Typically, females foraging in these flowers feed with impunity in the territories defended by dominant species such as White-eared Hummingbird (C. Lara pers. obs.). Since females were immediately driven away by territorial individuals when foraging at upper flowers, we interpreted this behavior as a way to reduce the risk of aggressive encounters.
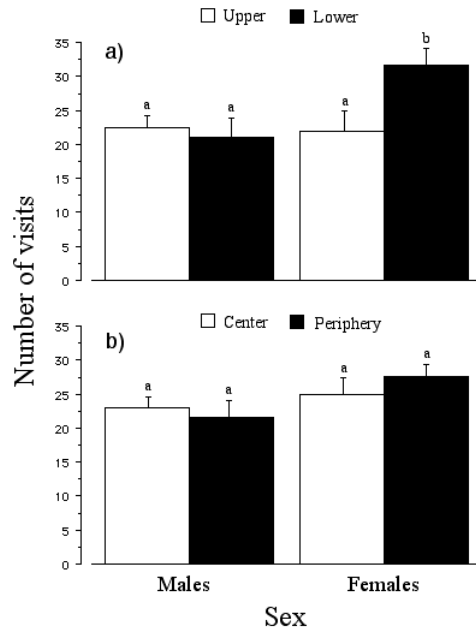
FIG. 2. Differences between sexes (including all hummingbird species) in the number (mean ± SE) of visits to upper and lower flowers in a plant, and (b) the number (mean ± SE) of central and periphery plants visited in a patch. Bars with the same superscript letter are not significantly different groups ($P > 0.05$).

Sexual segregation in hummingbirds has been previously reported by Stiles (1972) for Annas Hummingbird and Des Granges (1979) for White-eared Hummingbird, and requires further research.

Our results suggest that temporal segregation is determined by differences in size, where small hummingbird species, e.g., Ruby-throated Hummingbird (*Calypte anna*) and *Selasphorus* spp., use *Penstemon* flowers earlier in the day than larger species. For example, Magnificent Hummingbird and Blue-throated Hummingbird may use alternative food sources in the early morning (0700-0900 h) when they were mostly observed capturing insects by gleaning and fly-catching in zones of secondary vegetation, and only sporadically seen foraging in small patches of *Castilleja* spp. This behavior may suggest that the energy requirements of both species are satisfied

mostly by catching insects during this period of the day, while their foraging later focused on *Penstemon* flowers.

Temporal segregation mediated by size can be interpreted as a strategy to reduce the risk of aggressive encounters, by reducing the frequency of encounters with territorial and more aggressive hummingbirds such as Green Violetear. Most studies on the use of resources in animal communities report spatial segregation and only rarely temporal segregation (Schoener 1986). In theory there is no advantage to temporal segregation, because no energy can be gained when not feeding. For example, Cotton (1994) described the interactions of four species of tropical hummingbirds which defended the same territory at different stages in the flowering period and at different times of the day. He found that hummingbirds started defend-

ing territories as soon as there were sufficient resources, until they were either displaced by a larger species or replaced by a smaller one as the value of the territory changed. Consequently, temporal segregation should only occur if the risk of damage is higher relative to the need for energy, and this may have occurred in our study.

Behavioral dominance has been proposed as a mechanism by which communities of nectarivores are structured. Most of the aggressive encounters we observed were between conspecifics. In a study of a nectarivorous community visiting *Agave salmiana* (Agavaceae) in the Tehuacan Valley, Puebla, México, Martinez del Rio & Eguiarte (1987) documented that competition between diverse taxa (insects, passerine birds and hummingbirds) was common. However, within a similar system Ornelas *et al.* (2002) showed differences at *Agave marmorata* in the arrival times of floral visitors and the spatial location of the inflorescences visited, suggesting that these patterns minimize competitive interactions between species and facilitate coexistence. This result is similar to that found in our study.

Access to nectar resources in mixed species assemblages is often determined by interspecific encounters where large species dominate smaller species (Ford & Paton 1982, Cotton 1998, Camfield 2006). During our study, interactions between individuals of different species were common. When interactions occurred, the visitors moved to a different area within the patch in relation to the area occupied by a territorial hummingbird. Aggressive encounters between individuals of territorial species, e.g., White-eared Hummingbird or Green Violetear, were the most common interactions observed. Because the establishment of feeding territories is closely related to the distribution of nectar resources, territorial species can play a greater role in determining the composition and

structure in hummingbird assemblages (Wolf *et al.* 1976, Feinsinger 1976, Carpenter 1979, Des Granges 1979, Schuchmann 1999). In our study, White-eared Hummingbird aggressively excluded smaller-sized species foraging on *Penstemon* (Ruby-throated Hummingbird and *Selasphorus* spp.). It has been suggested that the losers in interspecfic interactions can disperse, visit low reward flowers and / or adopt opportunistic behaviors (for example traplining) when a patch is aggressively defended (Feinsinger 1976, Carpenter 1979). Moreover, there was no evidence that the availability of *Penstemon* nectar was limited to hummingbirds, allowing the coexistence of a mixed hummingbird assemblage at the study site.

The evidence of a dominance hierarchy based on the size of the interacting species has been described in competitive interactions of nectarivorous birds and insect pollinators (Gill & Wolf 1979, Kodric-Brown & Brown 1979, Schaffer *et al.* 1979, Martinez del Rio & Eguiarte 1987). Some studies show that birds adversely affect the availability of nectar for insects (Lyon & Chadek 1971, Primack & Howe 1975, Boyden 1978, Carpenter 1979), but other studies suggests that insects can affect birds because of their size and number (Kodric-Brown & Brown 1979, Schaffer *et al.* 1979, Gill *et al.* 1982). In the case of competition between nectar-feeding birds occupying the same habitat, access to nectar can often be determined by interspecific aggression, where large species dominate smaller ones (Collins 1985, Camfield 2006). In our study, territorial hummingbirds such as Green Violetear, varied from 55.9 g, whereas generalists, such as *Selasphorus* spp., from 33.2 g (Jonhsgard 1997). Thus, the aggressive interspecific interactions recorded suggest that the dominance hierarchy depends on size (Brown *et al.* 1978). However, large hummingbird species (6.87 g) such as Magnificent Hummingbird and Blue throated Hummingbird were seldom seen

attacking other species of hummingbirds, possibly because they behave like routers when they visit the flowers of *Penstemon.*

In summary, we found evidence that hummingbirds foraging in *Penstemon roseus* patches at La Malinche, showed spatial and temporal segregation during their visits. Our results suggest that niche partitioning on both scales can be interpreted as a way of reducing the risk of aggressive encounters in hummingbirds. In particular, small-sized species may benefit from a strategy that allows them to fill their energetic short-term demands in coexistence with larger, territorial hummingbirds. However, for future studies about niche partitioning in hummingbirds it will be necessary to consider factors, such as residence status, abundance, age of the birds, or nectar production differences, in different parts of the plants due to microclimatic shifts.

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