

Temporal-spatial segregation among hummingbirds foraging on honeydew in a temperate forest in Mexico

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Abstract Spatial and temporal variation in interactions between hummingbirds and plants have often been examined, and hummingbirds and insects are known to indirectly interact in networks of nectar plants. In a highland temperate forest in Hidalgo, Mexico some oak trees were heavily infested by honeydew-producing insects (family Margarodidae, tribe Xylococcini, genus *Strigmacoccus*) and the honeydew was consumed by hummingbirds. Here using survival analysis we investigate how the honeydew produced by dense populations of these margarodids is temporally and spatially partitioned by hummingbirds. We also measured the availability and quality of honeydew exudates, and then we recorded the time until a bird visited and used such resources. Four hummingbird species consumed this resource (*Atthis eloisa*, *Hylocharis leucotis*, *Colibri thalassinus* and *Eugenes fulgens*). Data from 294 hours of observation on seven focal trees suggested temporal and spatial segregation among visiting birds according to body size and territorial behavior during the most honeydew-limited time. Hummingbird species differed in the daily times they foraged, as well as in the location where honeydew-producing insects were visited on the trees. Temporal and spatial segregation among hummingbird species is interpreted as an adaptation to reduce the risk of aggressive encounters. This may facilitate multispecies coexistence and allow these birds to exploit honeydew more effectively [*Current Zoology* 57 (1): 56–62, 2011].

Key words Honeydew, Hummingbirds, México, Nectarivory, Niche partitioning

Spatial and temporal variation in interactions between hummingbirds and their nectar plants have often been documented, both in mainland and insular environments (e.g. Feinsinger, 1976; Cotton, 1998; Lara, 2006; Lara et al., 2009; Ortiz-Pulido and Vargas-Licona, 2008; Dalsgaard et al., 2009). Behavioral dominance is one mechanism by which communities of hummingbirds sharing patchy and ephemeral floral resources are structured (Lyon and Chadek, 1971; Primack and Howe, 1975; Feinsinger, 1976; Wolf et al., 1976; Boyden, 1978; Carpenter, 1979; Gill et al., 1982; Sazima and Buzato, 1994; Fleming et al., 1996). It has been suggested that access to nectar resources may be determined by inter-specific aggression in which larger hummingbird species dominate smaller species (Camfield, 2006). However, direct interference among hummingbirds is not the only way to access nectar resources. Behavioral responses such as spatial separation, temporal avoidance and dietary differences can minimize competition for

food. For example, it has been suggested that hummingbirds show temporal and spatial segregation while foraging on a limited floral resource, thus allowing species coexistence (Ornelas et al., 2002; Lara et al., 2009). Such segregation may result from temporal and spatial heterogeneity in resource distribution following environmental processes that act independently of the consumers (Cheson and Warner, 1981) and may also be reinforced by the behavior of foragers.

Honeydew is a sugary exudation from sap-sucking insects such as scale insects (Hemiptera: Margarodidae), and is an important food resource for many bird species in Australia (Paton, 1980), New Zealand (Beggs and Wardle, 2006), Costa Rica (Jiron and Salas, 1975), Colombia (Koster and Stoewesand, 1973), Brazil (Reichholf and Reichholf, 1973) and the Dominican Republic (Latta et al., 2001). These interactions between birds and honeydew-producing scale insects have been suggested to differ at large spatial scales.

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Since the first report by Edwards (1982) in Mexico, research on the use of honeydew by birds has been lacking. However, Greenberg et al. (1993), established honeydew as an important resource in high elevation oak communities near San Cristobal de las Casas, Chiapas, and quantified the dynamics between different passerine species in terms of aggressive dominance of this resource. Also, they proposed a biogeographical pattern and ecological mechanism (release from competition from ants) to explain why honeydew use is rare in warm temperate climates and what explains its occurrence. Latta et al. (2001) later expanded on the biogeographic aspect of this relationship to include island environments. In a recent study, Gamper & Koptur (2010) reported bird use of honeydew in tropical montane forests near Chiconquiaco, Veracruz and uncovered patterns in honeydew foraging.

Here, we present a study in contrast to previous ones, because we report a site where honeydew is used by hummingbirds only, and no other bird species. We recently found in a temperate forest remnant in Hidalgo, Mexico, honeydew-producing scale insects bearing a long filamentous anal tube (family Margarodidae, tribe Xylococcini, genus *Stigmacoccus*; Hodgson et al. 2007). Our observations indicated that these insects infested some oak trees and hummingbirds fed on the honeydew. These observations led us to investigate whether there was evidence for temporal and spatial niche partitioning among hummingbird species feeding on honeydew. Such niche partitioning may reduce direct interference between hummingbirds, and thereby allow several hummingbird species to coexist. Our study is pioneering in terms of producing evidence of how a non-floral rich-sugar resource may structure a hummingbird community.

1 Materials and Methods

1.1 Study area

Fieldwork was carried out during June 2008 in a 2 ha remnant of oak forest *Quercus Mexicana* located in Tlahuiltepa, Hidalgo, Mexico (20°55'N, 98°56'O; 2100 m a. s. l.). The study area is dominated by *Q. mexicana* and other *Quercus* spp. (Fagaceae), *Cedrela mexicana* (Meliceae) and *Cupressus lusitanica* (Cupressaceae). Most rain occurs during summer with an average annual rainfall of 900 mm. Annual mean temperature is 17°C and this area commonly freezes. Avifauna in the region have not been described, but the presence of several hummingbird species has been noted (Martínez-Morales et al., 2007). Besides hummingbirds, we observed for

example acorn woodpeckers *Melanerpes formicivorus*, crescent-chested warblers *Vermivora superciliosa*, rufous-capped brushfinches *Atlapetes pileatus*, cinnamon-bellied flowerpiercers *Diglossa baritula*, Audubon's orioles *Icterus graduacauda* and yellow-eyed juncos *Junco phaeonotus*.

Few hummingbird-pollinated flowering plants were found in the study area (~30 *Hamelia patens* plants). Therefore, the sugar solution that was offered by scale insects in this highland area between late April and early July represents a major sugar resource to hummingbirds. Whether this phenomenon is constant throughout the year remains unknown.

Seven of 21 oak trees *Q. Mexicana* located in the forest remnant were infested (ca. 1000–3000 scale insects per tree). Our target trees were similar in height (mean \pm SE: 19.25 \pm 0.26 m) and trunk diameter (88.85 \pm 1.85 cm). The anal tubes where honeydew was continuously secreted by scale insects covered most of the trunk and branches.

1.2 Spatial and temporal patterns of visitation

For seven infested oak trees in the study area, we observed and recorded hummingbird visitors over the course of eight days. The anal tubes where honeydew was secreted were distributed roughly evenly throughout the tree, allowing us to explore the hummingbird's spatial use of each infested tree. For this purpose, we visually divided oak trees in a horizontal plane into "central area" (trunk) and "peripheral area" (all branches in the tree), and three areas in the vertical plane of each tree into "lower area" (from the base of the trunk to 5 m), "medium area" (<5–10 m), and "upper area" (>10 m). From June 11–18 2008, focal trees were simultaneously recorded for each day. Prior to this period, a one day observational period (from 07:00–19:00 h, a total of 12 h) was conducted to establish when hummingbirds were more actively foraging. Based on the observational results we recorded every foraging event (hummingbird probing an anal tube) on each infested tree throughout two observation periods (07:30–1030 h and 16:30–19:30 h; 294 h of sampling effort), and recorded the hummingbird species, time of day, number of anal tubes probed by visit, the location where honeydew-producing insects were visited on the trees (in each horizontal and vertical plane), and aggressive interactions (defined as displays of territorial proclamation and intimidation of con-specifics or hetero-specifics). Since we did not mark birds during our observations, individuals may have been observed more than once. Observers were located approximately 5 m

away from the focal tree and on the ground. Approach and avoidance behavior by birds as an apparent response to observers was not detected.

We used survival analysis (“time failure analysis”) to explore temporal segregation among hummingbirds. One of the advantages of this analysis is that allows for the estimation of the probability of visits by hummingbirds at one known time (uncensored data). This feature is apt to field biology (Muenchow, 1986), where the observation period may be too brief for all possible events to occur. Thus, we recorded the beginning of our observations as time zero and subsequent foraging events as minutes from start time. The event for each monitored tree was the visit of all possible hummingbirds to the various parts of the tree and that were recorded during both observation periods (morning and afternoon). If an event occurred for a given infested tree, then it became uncensored data, and if it never occurred, then it became censored data. The monitored trees were evaluated simultaneously by different observers. We then used the Kaplan-Meier product limit non-parametric method for the computation of functions among variables and the log-rank Mantel-Cox statistic to test for differences among hummingbird species. In our case, “survivorship” was the probability that a species had not yet visited an infested tree a given number of minutes after the start of observation.

Differences in the number of hummingbird visits to the recorded areas in an infested tree were assessed using One-Way ANOVA.

1.3 Honeydew characteristics

The honeydew volume encountered by a hummingbird can vary over time (Greenberg et al., 1993) and may influence subsequent foraging events. To account for this, the pattern of honeydew production was studied by monitoring its production from 1030 to 1930 h on June 16. Every three hours 10 different scale insects were randomly selected and the droplets ejected from their anal tubes were collected in capillary tubes (5 μ l). The volume of such collection was measured and the sugar concentration was estimated according to the Brix scale using an optical refractometer (Atago, Japan). Variation in honeydew volume and concentration over time was analyzed using one-way ANOVA (Zar, 1999).

2 Results

2.1 Temporal segregation

We observed four hummingbird species feeding on honeydew. A total of 2124 foraging events (visits to an

anal tube) were observed (bumblebee hummingbird: *Atthis eloisa* = 136, green-violet ear hummingbird: *Colibri thalassinus* = 220, white-eared hummingbird: *Hylocharis leucotis* = 883, and magnificent hummingbird: *Eugenes fulgens* = 885). The relative frequency of hummingbirds to consume honeydew was different throughout the observational periods (Figure 1). Based on the body size (mass) reported for hummingbird species (see Lara et al., 2009) we established three groups: small, medium and large size hummingbirds. Clearly, medium- (white-eared hummingbirds: 3.62 g; and green-violet ear hummingbirds: 5.11 g) and large-sized hummingbirds (magnificent hummingbirds: 7.03 g), exploited honeydew more frequently in the morning, while small species such as bumblebee hummingbird (2.1 g) visited anal tubes preferentially in the afternoon (Fig. 1).

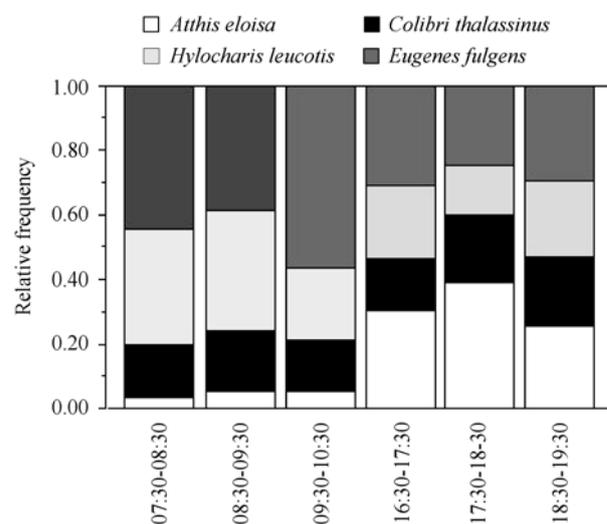


Fig. 1 Relative frequency of hummingbird visitors over time to consume honeydew

Survivorship curves were significantly different between hummingbird species foraging on honeydew in the morning ($\chi^2 = 9.19$, $df = 3$, $P = 0.026$), suggesting that the time until medium and large-sized hummingbird species arrived to an infested tree is shorter (~80 min) than the time of small-sized hummingbirds (~130 min). However, in the afternoon we did not find differences in their arrival times ($\chi^2 = 1.09$, $df = 3$, $P = 0.779$).

To determine whether temporal segregation was explained by honeydew characteristics such as secretion volume and sugar concentration, we examined variation in the number of visits as a function of these variables. We found significant differences between inter-specific schedules with respect to volume (One-Way ANOVA, $F_{2, 42} = 119.8$, $P < 0.001$) and concentration (One-Way

ANOVA, $F_{2,42}=49.71$, $P < 0.001$). This way, honeydew volume and concentration were highest at early hours and declined throughout the day (Table 1). Volumes ranged from 0–2 μl and sugar production from 35–50 mg/ml. Both honeydew volume ($r^2=0.84$, $P = 0.01$) and concentration ($r^2=0.73$, $P = 0.04$) were positively correlated with the number of hummingbird visits.

2.2 Spatial segregation

The spatial mode of honeydew exploitation varied among hummingbird species (One-Way ANOVA, $F_{2,42} = 119.8$, $P < 0.001$). Small hummingbirds (bumblebee) foraged mostly on lower and peripheral areas from infested trees, while medium- (white-eared and green-violet ear) and large-sized hummingbirds (magnificent) fed on honeydew located in medium, higher and central areas (Table 2).

Early in the morning, honeydew from lower ($\chi^2 = 39.67$, $df = 3$, $P < 0.001$; Fig. 2A) and peripheral areas ($\chi^2 = 28.43$, $df = 3$, $P < 0.001$; Fig. 2B) was exploited sooner by medium- and large-sized hummingbirds. At this time, these hummingbird species defended territories against small-sized hummingbirds. In contrast, later

in the day small hummingbirds visited sooner both areas (lower area: $\chi^2 = 27.82$, $df = 3$, $P < 0.001$; peripheral area: $\chi^2 = 31.04$, $df = 3$, $P < 0.001$; Fig. 2C,D), but without evidence of aggressive encounters from medium- and large-sized hummingbirds. During both observation periods, arrival times to medium (morning: $\chi^2 = 1.09$, $df = 3$, $P = 0.779$; afternoon: $\chi^2 = 1.09$, $df = 3$, $P = 0.779$), higher (morning: $\chi^2 = 1.09$, $df = 3$, $P = 0.779$; afternoon: $\chi^2 = 1.09$, $df = 3$, $P = 0.779$) and central areas (morning: $\chi^2 = 1.09$, $df = 3$, $P = 0.779$; afternoon: $\chi^2 = 1.09$, $df = 3$, $P = 0.779$) of infested trees were not statistically different amongst hummingbird species.

Inter-specific chases were observed ($n = 31$ events). Typically, magnificent hummingbirds aggressively chased away medium-sized species such as green-violet ear hummingbirds from infested trees (15 events), while smaller bumblebee hummingbirds were actively excluded by white-eared hummingbirds (16 events). Further, intra-specific aggressive encounters were commonly observed (white-eared hummingbird = 26, magnificent hummingbird = 17, green-violet ear hummingbird = 13, bumblebee hummingbird = 9).

Table 1 Honeydew volume and concentration (means \pm SE) measured by standing crops over time (10 measures per time interval)

	Time intervals			
	10:30	13:30	16:30	19:30
Volume (μl)	1.92 \pm 0.05 ^a	0.78 \pm 0.01 ^b	0.69 \pm 0.11 ^b	0.61 \pm 0.14 ^b
Concentration (mg/ml)	47.5 \pm 0.01 ^a	38.3 \pm 0.01 ^b	36.1 \pm 0.11 ^b	34.5 \pm 0.15 ^b

Data with the same superscript letters are not significantly different between groups ($P < 0.05$).

Table 2 Difference between hummingbird species in the number (mean \pm SE) of visits to anal tubes secreting honeydew and location on different areas of a tree

	Hummingbird species			
	Bumblebee	Green-violet ear	White-eared	Magnificent
Horizontal areas				
Central	1.92 \pm 0.05 ^a	53.7 \pm 0.01 ^b	50.9 \pm 0.11 ^b	54.1 \pm 0.14 ^b
Peripheral	45.8 \pm 0.01 ^a	23.3 \pm 0.01 ^b	21.8 \pm 0.11 ^b	24.9 \pm 0.15 ^b
Vertical areas				
Lower	40.4 \pm 0.02 ^a	12.7 \pm 0.01 ^b	10.6 \pm 0.11 ^b	11.1 \pm 0.14 ^b
medium	7.92 \pm 0.05 ^a	55.8 \pm 0.01 ^b	57.0 \pm 0.11 ^b	54.6 \pm 0.14 ^b
Upper	5.92 \pm 0.05 ^a	61.7 \pm 0.01 ^b	59.9 \pm 0.11 ^b	62.1 \pm 0.14 ^b

Data with the same superscript letters are not significantly different ($P < 0.05$).

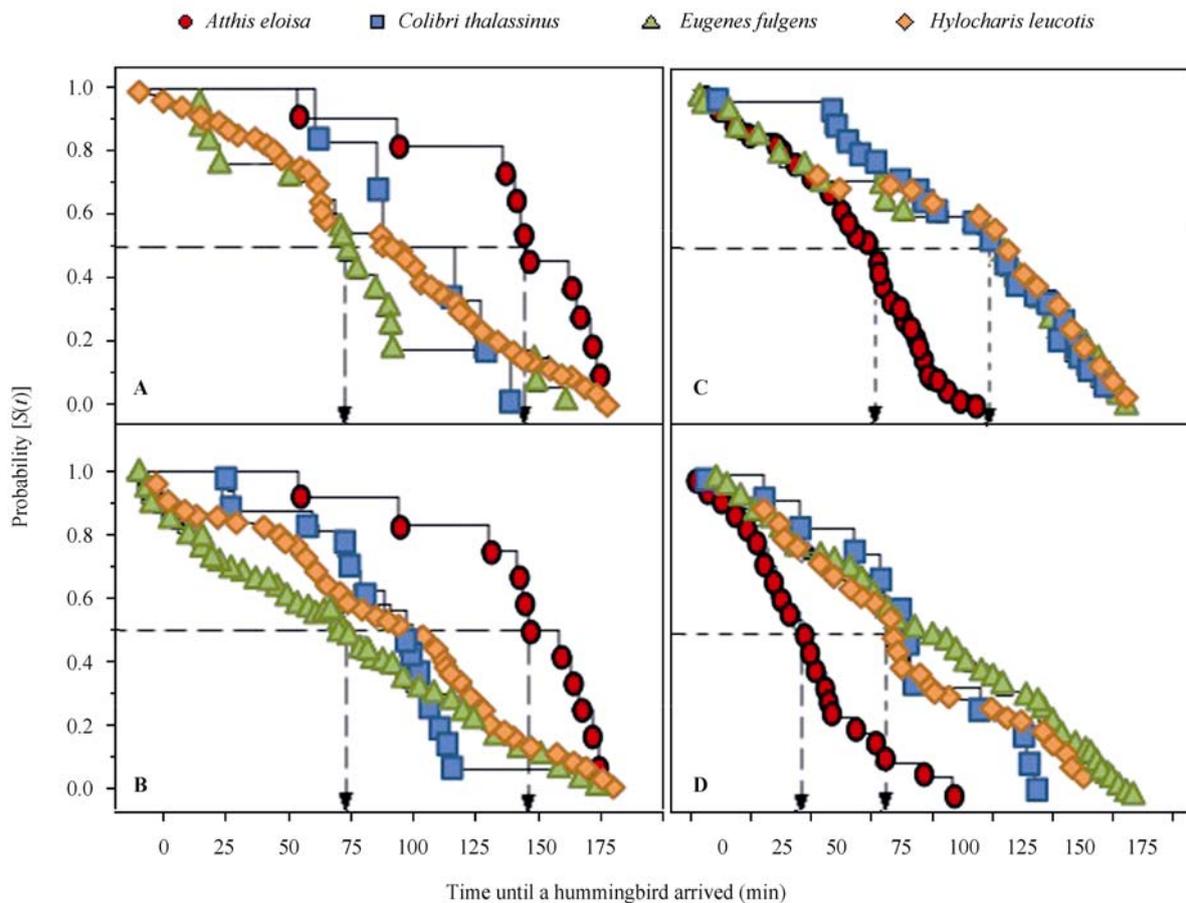


Fig. 2 Nonparametric survival functions showing hummingbird visitation in the morning (left) and afternoon (right) when consuming honeydew in lower (A, C) and peripheral (B, D) areas of a tree

Note during the afternoon anal tubes located in both areas of a tree are visited sooner by *Atthis eloisia*.

3 Discussion

Spatial and temporal variation in interactions between hummingbirds and plants have often been examined (Feinsinger, 1976; Cotton, 1998; Lara, 2006; Ortiz-Pulido and Vargas-Licona, 2008; Lara et al., 2009; Dalsgaard et al., 2009), and hummingbirds and insects are known to indirectly interact in this biotic network (e.g. Dalsgaard et al., 2008). Interestingly, all studies in Mexico (El Cielo, Tamaulipas, Edwards 1982; Tlahuítelpa, Hidalgo, this study; Chiconquiaco, Veracruz, Gamper and Koptur 2010; San Cristobal de las Casas, Chiapas, Greenberg et al. 1993) have been conducted in oak forests at 2000 m above sea level where fog is frequent, the trees infected are *Quercus* spp., and no ants present. This suggests that honeydew consumption by migrant passerines and resident hummingbirds is an eastern phenomenon in Mexico.

Here, we examined spatial and temporal segregation between hummingbird species exploiting honeydew in

Tlahuítelpa, Hidalgo, Mexico. Our findings on the differences between hummingbird species in the foraging times and the location of honeydew-producing insects visited are suggestive of niche partitioning. However, because we did not evaluate differences in volume and sugar of honeydew relative to the position of scale-insects within a tree we do not know whether these differences reflect different variables of microclimate affecting scale-insects. Additional analysis is thus required to evaluate this possibility.

Spatial areas and temporal periods to exploit honeydew varied among species. Small hummingbirds such as bumblebee hummingbird, tended to collect honeydew on lower areas and the periphery of trees mainly in the afternoon. This spatial segregation may reduce the likelihood of aggressive encounters with larger and more territorial species, as occurs when they forage on plants (cf. Lara et al., 2009 for *Penstemon roseus*). In addition, our results suggest that spatial and temporal segregation is determined by differences in humming-

bird size, where medium- and large-sized species (e.g. white-eared and magnificent hummingbirds), use honeydew early in the day compared to small species (bumblebee hummingbird). In this way, temporal and spatial segregation mediated by size may be a strategy to reduce the risk and inherent costs of aggressive encounters by reducing the frequency of encounters with territorial and more aggressive species, such as white-eared hummingbirds.

Many studies on the use of food resources in animal communities have found spatial segregation but only rarely temporal segregation (Kronfeld-Schor and Dayan, 2003). This is presumably because there is no advantage for temporal segregation, as no energy can be gained when not feeding. Consequently, temporal segregation should only occur if the risk of corporal damage is higher relative to the need for energy. Although our results suggest that the smaller *A. eloisia*, was dominated (i.e. chased) by the bigger hummingbird species, we have no evidence that the availability of honeydew was a limiting factor to hummingbirds, allowing the coexistence of a mixed hummingbird assemblage at the study site.

Evidence of a dominance hierarchy based on the size of the interacting species has been described in competitive interactions of nectarivorous birds occupying the same habitat, and access to nectar can often be determined by interspecific aggression, where large species dominate smaller species (Camfield, 2006; Lara et al., 2009). In our study, the weight of territorial hummingbirds such as the magnificent hummingbird varies from 7 to 7.5 g; whereas generalists, such as the bumblebee hummingbird can weigh from 2 to 2.3 g. The aggressive interspecific interactions recorded here suggest that the dominance hierarchy could depend on size (Lara et al., 2009).

In summary, we found evidence that hummingbirds foraging on honeydew 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 meet their short-term energetic demands in coexistence with larger and territorial hummingbirds. Future studies regarding niche partitioning in hummingbird foraging on honeydew should consider factors such as abundance, sex and the age of hummingbirds, and honeydew variation across different sections of infested trees due to microclimatic shifts.

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