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INTERFERENCE BETWEEN WASPS AND HUMMINGBIRDS AT A FEEDER

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Resumen

Observamos la respuesta de alimentación del colibrí (*Lampornis amethystinus*) en presencia de dos especies de avispas (*Polistes* sp. y *Eumenes* sp.) sobre un bebedero artificial colocado en condiciones naturales. El objeto fue examinar la influencia de las avispas sobre el consumo de "néctar" e investigar si la interacción bebedero-colibrí-avispa es un buen modelo para analizar los efectos indirectos y modificadores de interacciones mutualistas de un visitante floral no polinizador en la interacción mutualista planta-colibrí. La avispa *Eumenes* no influyó el comportamiento de alimentación de los colibríes, mientras que la avispa *Polistes* provocó que *L. amethystinus* no se alimentara en el 72% de las visitas registradas al bebedero. En ausencia de *Polistes*, los colibríes se alimentaron en el 91% de los casos. La posición y movimientos de *Polistes* actúan como un estímulo que desencadena un determinado patrón de comportamiento en los colibríes (intentar comer, alimentarse, huir, etc.). Sugerimos que una alta densidad de *Polistes* puede modificar indirectamente el resultado de la interacción directa planta-colibrí, ya que es posible que la presencia de *Polistes* represente un efecto negativo en el éxito reproductivo de las plantas que dependen de los colibríes para su polinización.

Abstract

We observed hummingbirds (*Lampornis amethystinus*) and two species of wasps (*Polistes* sp. and *Eumenes* sp.) foraging at sugar water feeder located under natural condition. Our objectives were to explore how wasps influence the hummingbirds' "nectar" consumption, and whether the feeder-hummingbird-wasp interaction is a good system to investigate the indirect effects and the mutualistic interaction modifiers of a nonpollinating floral visitor onto the plant-hummingbird mutualistic interaction. Hummingbird's feeding behavior was not affected by the presence of *Eumenes* wasps, while the presence of *Polistes* wasps impeded hummingbirds from feeding on 72% of the observed visits to the feeder. When *Polistes* was not at the feeder, hummingbirds fed on 91% of visits. The position and movements of the *Polistes* wings seems to influence the hummingbirds' behavior such as escape or drinking. We suggest that a high density of *Polistes* wasps may indirectly modify the outcome of a direct plant-hummingbird interaction, since the presence of these wasps may represent a negative effect to the reproduction of plants that depend on hummingbirds to be pollinated.

Key words: Foraging behavior, hummingbirds, indirect effects, *Lampornis amethystinus*, nectar thieves, *Polistes*, wasps.

Introduction

Hummingbird-pollinated plants are commonly visited by an array of species that establish, from mutualistic to antagonist relationships, a continuum of plant-animal interactions (Bronstein, 1994). The outcome of these interactions is conditioned by the morphology of the interacting species and the ecological and evolutionary context (e.g., Bronstein, *op. cit.* and Thompson 1982, 1994). It also depends on the ability of each visitor to pollinate the plant (e.g., McDade and Kinsman, 1980, Thompson and Pellmyr, 1992 and Arizmendi *et al.*, 1996), the response of a visiting species to other members of the array (e.g., Soberón and Martínez del Río,

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1985, Cushman and Beattie, 1991), and the density of each of the members of the array (Soberón and Martínez del Río, 1985, Thompson and Pellmyr, 1992). Although most studies ignore this, plants pollinated by hummingbirds engage in multiple interactions with other floral visitors (e.g., Arizmendi *et al., op. cit.*).

Hummingbirds influence one another's choice of flowers, which results in partitioning of flowers among different species and may have evolutionary consequences (Feinsinger, 1983), but also their behaviors are influenced presumably by the whole array of floral visitors. Such array composed mainly by pollinators and other floral visitors, and nectar-robbing species play a role on molding these multiple interactions. In particular, the interactions between floral visitors such as hummingbirds and insects (Lyon and Chadek, 1971, Primack and Howe, 1975; Boyden, 1978, McDade and Kinsman, 1980 and Roubik, 1982), and the outcomes of these presumably competitive interactions are scarce (Primack and Howe, 1975, Gill *et al.,* 1982).

Field observations suggest that insects may negatively affect hummingbird foraging behavior. Hummingbirds increased their foraging efficiencies when *Trigona* bees were excluded from the flowers (Gill *et al., op. cit.*), and hummingbirds has being attacked by *Trigona ferricauda* bees (Roubik, 1982). We observed *Polistes* wasps visiting hummingbird feeders, (1) to explore how *Polistes* wasps influence the hummingbirds' (*Lampornis amethystinus*) nectar consumption, and (2) then asked whether the plant-hummingbird-wasp interaction is a good system to investigate the indirect effects of a nonpollinating floral visitor onto the plant-hummingbird mutualistic interaction.

Materials and methods

Study site.- Our study was conducted 6 km S of Xalapa City in the state of Veracruz, Mexico (19°30'30'' N, 96°50'42'' W). The landscape at the site include pastures and agricultural fields with remnant patches of Acacia sp. and coffee plants growing under the shade of *Inga* sp., bananas and citrus.

Field observations.- A hummingbird feeder was built using a glass container with a red plastic flower. It was hung three months before the field observations started at a shady place with a roof that allowed the birds to drink from it until they got used to it. We added a sugar-water solution (3:1) with two spoons of honey produced by bee and boiled for one minute to delay the fermentation process. The feeder was refilled as visitors emptied it.

A total of 58 observation hours were accumulated from September to December 1995 and then on March 1996. Observations were made between 6:30 to 11:00 horas and 16:00 to 18:30 horas. We removed the feeder during the winter months (January and February 1996), in the course of this time, *Polistes* wasp colonies were also abandoned. The feeder was replaced for hummingbirds, to use as a control, while *Polistes* wasps were no longer around.

We registered each hummingbird (*Lampornis amethystinus*) visit to the nectar feeder as one behavioral event (foraging bout). A hummingbird flew towards the nectar feeder and by hovering in front of it (at a distance of ca. 15 centimeters), it reached the plastic flower with rapid movements. After inserting its bill into the flower and drink, the hummingbird immediately flew back. This behavior (bill insertion) would be repeated several times before the hummingbird left the feeder. By using binoculars (Swift 6x30), the presence of *Polistes* and *Eumenes* wasps, as well as any other insect (flies and butterflies), was registered during each of the hummingbird visits and the response of the hummingbirds to the presence of insects at the feeder.

Data analyses.- We used Chi square tests with Yates correction for continuity to compare hummingbird responses to the presence and absence of wasps. We used a Wilcoxon unpaired *Z* test to compare the average of consecutive bill insertions to the red flower within each hummingbird visit, with and without *Polistes* wasps (Zar, 1984).

Results

As soon as we put the nectar feeder out, it was frequently visited by insects (*Polistes* and *Eumenes* wasps, and unidentified flies and butterflies) and hummingbirds (*Lampornis amethystinus*). We registered a total of 287 hummingbird visits to the nectar feeder. During our observational periods, 33.1% of the visits were made when one or more *Polistes* wasps were sitting on the flower, and 66.9% without these wasps. The hummingbirds did not insert their bills into the flower when *Polistes* wasps were present at the feeder in 71.6% of the visits. However, hummingbirds fed in 91.2% of the times when the wasps were not present (X^2 =

79.76, df= 1, P<0.001; Table 1). We found a highly and negative significant relationship between the wasp presence and the hummingbird feeding behavior (X^2= 116.96, df= 1, P<0.001; table 1). On many occasions (25/76) there were *Eumenes* wasps or other insects on the flower and the hummingbirds did not react to their presence. Hummingbirds stopped drinking from the nectar feeder and flew backward (ca. 20 cm from the feeder) when any flying insect approached (wasps or other insects). When the visitor was a *Eumenes* wasp or another insect, the hummingbird resumed feeding; however, when it was a *Polistes* wasp, hummingbirds always flew away. During our observations in March, there were no *Polistes* wasps around, and hummingbirds inserted its bills in all observed visits (n = 49 visits).

Table 1. Observations made at nectar feeder showing the effect of *Polistes* wasp on hummingbird feeding behavior. There is a highly significant relationship between the presence of wasps presence and the hummingbirds behavior.

	Hummingbirds behavior		**Total**
	Feeding	**Not feeding**	
With wasps	27	68	95
Without wasps	175	17	192
Total	202	85	287

The position of the wings and movements by *Polistes* at the flower seems to influence the hummingbirds' behavior (leave, bill insertion or drinking). Once the hummingbird has inserted its bill into the flower, the wasp is practically ignored, as long as it remains immobile with its wings folded. Every time the hummingbird fed in the presence of *Polistes* wasps, the bird would approach the flower up to three times, before it decided to insert its bill. Sometimes a hummingbird touched the wasp with its bill. If the wasp stayed motionless, hummingbirds feed, but upon the first wasp motion, the hummingbird immediately retreated.

Often *Polistes* wasps were very aggressive towards hummingbirds. That is, when a hummingbird hovered in front of the feeder and a *Polistes* wasp was sitting near by, the wasp flew directly to the hummingbird's face and forced it to leave. *Polistes* wasps also attacked *Eumenes* wasps, flies, and even other cospecifics in the same way. However, by comparing the average of consecutive bill insertions within each hummingbird visit, with and without *Polistes* wasps, we did not find differences (Unpaired test, Z= -0.067, P>0.05).

Discussion

Interactions between hummingbirds and insects may be more frequent in nature than is commonly thought, since hummingbird-pollinated plants secrete nectar that can be attractive to a suite of floral visitors, including those insects that can potentially pollinate plants (Feinsinger, 1983; Handel, 1983 and Heithaus, 1979), to non-pollinating insects that act as parasites, or nectar thieves (Lyon and Chadek, 1971, McDade and Kinsman, 1980; Roubik 1982, Irwin and Brody, 1998), competitors (Colwell *et al*., 1974), or predators of floral visitors (Domínguez *et al.*, 1989). Also, secondary nectar robbers such as *Apis*, *Lasloglosum*, and *Bombus* (Lyon and Chadek, *op. cit.*) extract floral nectar otherwise unavailable to them taking advantage of corolla perforations made by primary nectar robbers such as *Trigona* bees (McDade and Kinsman, *op. cit.*), flower piercers *Diglossa plumbea* (Lyon and Chadek, *op. cit.*; Colwell *et al.,* 1974 and Arizmendi *et al.*, 1996), and hummingbirds (Ornelas, 1994).

Although some of the hummingbirds defended actively the nectar feeder against other hummingbirds, insects that visited it were not attacked by hummingbirds as it has been observed in natural settings (Primack and Howe, 1975 and Boyden, 1978). In this study, we showed that *Lampornis amethystinus* undoubtedly avoids the interaction with *Polistes* wasps. One can argue that such interactions between *Polistes* and hummingbirds are not very common in nature because hummingbirds mostly visit long-tubed flowers. However, tubular and non-tubular flowers mainly pollinated by hummingbirds are visited by wasps in search of nectar rewards, oviposition sites, and/or prey items (Heithaus, 1979 and Domínguez *et al.,* 1989), which may result in frequent encounters with hummingbirds.

Our study showed that hummingbirds visited the feeder fewer times in the presence of wasps. This suggests that hummingbirds consider encounters with wasps as a negative experience (Eibl-Eibesfeldt, 1979). If so, one outcome of hummingbirds avoiding flowers with wasps could be that plants receiving fewer visits from hummingbirds would suffer reduced reproductive success (Gill *et at.,* 1982; Irwin and Brody, 1998). Nectar-robbing bees, *Trigona ferricauda,* from Panama attacked Long-tailed hermits *Phaethornis superciliosus*, forcing them to move to a different portion of the floral patch, and although they rarely were ejected from patch, they reduced by half the number of flowers visited. Also, a floral patch with a high density of *T. ferricauda* was not visited by hummingbirds as frequently as were those with a low density. (Roubik, 1982).

We showed with complementary observations made in March 1996 that hummingbirds foraged continuously in the absence of *Polistes*, suggesting that a high density of these wasps can indirectly modify the outcome of a direct plant-hummingbird interaction (Wilson, 1986; Roubik, *op. cit.*; Strauss 1991; Wootton, 1993 and Irwin and Brody, 1998).

The effects that antagonistic species have on mutualistic interactions such as those between plants and their pollinators, have been investigated as independent chain of interactions (e.g., Wootton *op. cit.*), commonly by looking at one of the components of the mutualistic interaction (Colwell *et al.,* 1974; McDade and Kinsman, 1980; Stiles, 1985, Feinsinger, 1987 and Arizmendi *et al.,* 1996). This approach has impeded the understanding of the role of antagonistic species in molding the ecology and evolution of these multiple interactions (Arizmendi *et al., op. cit.*). For instance, the abundance of one species in a given community not only affects those species to which interacts directly, but also it may modify indirectly the abundance of other species as a result of its direct interactions (e.g., Wilson, 1986; Strauss, 1991, and Wootton, 1993). Researchers have rarely analyzed how antagonistic floral visitors, such as nectar thieves, indirectly affect the dynamics of a given mutualistic plant-pollinator interaction. Instead, they have estimated the effect on the plant reproductive success (e.g., Hawkins, 1961; Heinrich and Raven, 1972; McDade and Kinsman, 1980; Roubik, 1982 and Roubik *et al.*, 1985) and pollinator's foraging efficiency (Koeman-Kwak, 1973, Cushman and Beattie, 1991). The evolution of plant-hummingbird interactions could be influenced by the indirect effect of the interaction between hummingbirds and other species that interfering with their activities (as *Polistes* and *Trigona* wasps).

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