

# Resources foraged by Euglossa atroveneta (Apidae: Euglossinae) at Union Juárez, Chiapas, Mexico. A palynological study of larval feeding

Elia Ramírez Arriaga, Enrique Martínez Hernández

### ► To cite this version:

Elia Ramírez Arriaga, Enrique Martínez Hernández. Resources foraged by Euglossa atroveneta (Apidae: Euglossinae) at Union Juárez, Chiapas, Mexico. A palynological study of larval feeding. Apidologie, 1998, 29 (4), pp.347-359. hal-00891500

## HAL Id: hal-00891500 https://hal.science/hal-00891500

Submitted on 11 May 2020  $\,$ 

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

### **Original article**

## Resources foraged by *Euglossa atroveneta* (Apidae: Euglossinae) at Unión Juárez, Chiapas, Mexico. A palynological study of larval feeding

Elia Ramírez Arriaga\*, Enrique Martínez Hernández

Instituto de Geología, Dpto. de Paleontología, Lab. de Palinología, Universidad Nacional Autónoma de México, Apartado Postal 70-296, 04510 Coyoacán, Mexico

(Received 25 August 1997; accepted 5 March 1998)

Abstract – Weekly larval feeding samples belonging to 51 nests of *Euglossa atroveneta* were analyzed palynologically at Unión Juárez, Chiapas, Mexico. It was determined that *E. atroveneta* foraged 74 plant species throughout 1 year, from 31 May 1990 to 29 May 1991. The most important resources of larval feeding were classified as: a) polliniferous: *Antirhea* sp., *Cassia* sp., *Combretum* sp., *Commelina* sp., *Cordyline terminalis, Dendropanax* sp., Leguminosae type 4, *Lycianthes* sp., *Saurauia* sp., *Solanum* aff. *tuerckheimii, Tibouchinia longifolia*; and b) nectaropolliniferous: *Drymonia* aff. *strigosa, Kohleria elegans, Lonchocarpus* sp. and *Nautilocalyx* aff. *panamensis*. Through the year *E. atroveneta* displayed a heterogeneous foraging behavior with a diversity index average of 0.83, and little overlap for resources between the solitary and parasocial nests studied. © Inra/DIB/AGIB/Elsevier, Paris

Euglossa atroveneta / larval feeding / palynology / Neotropics / orchid bees / throphic resources

#### **1. INTRODUCTION**

The Euglossinae are neotropical bees. They are solitary, communal and parasocial bee species, and they comprise five genera: *Eulaema, Eufriesea, Euglossa, Exaerete* and *Aglae.* The *Euglossa* genus is the most abundant and diverse in the neotropics [17]. This group of bees is well known because the male bees collect fragrances from orchid flowers and at the same time they carry out the pollination, often with specific pollinizers for each orchid species. These relationships are considered to constitute examples of coevolution [2, 5, 6, 16, 29, 32].

\* Correspondence and reprints

E-mail: elia@servidor.unam.mx

The Euglossinae have a broad flight pattern and sometimes fly as far as 23 km [8]. Due to this capacity to travel for collecting pollen and nectar, they are one of the main agents for cross pollination in tropical rain forest.

These bees visit plants with wide distribution and long flowering periods [1, 8], plants that offer abundant food reward (nectar or pollen), or that provide resin that is used in nest construction. Records related to plant species of feeding importance in Euglossinae have been based exclusively on direct field observations [1, 8, 15, 31]. However, many flowering plants visited by Euglossine bees are unknown to science. It is important to increase knowledge of how the Euglossinae exploit the angiosperms and to find out what taxa are most relevant in their life cycle. In this way, it will be possible to better understand the role of female euglossine bees in tropical ecosystems.

The utilization of floral resources may be assessed by direct observation or by palynological analysis of larval feeding and measuring ecological parameters such as pollen diversity, evenness and overlapping of feeding resources [4, 9, 12–14, 20–22, 28].

For this research, a nesting area was established for *Euglossa atroveneta* in a disturbed zone on the hillside of Tacaná volcano, in Chiapas State. It was possible to assess the annual foraging behavior of female bees through palynological analysis of larval feeding and to complement these data by means of field observations. Finally, the results were compared with those cited for stingless bees (Apidae; Meliponinae) studied in the same area, where the overlap in resource utilization was also determined.

#### 2. MATERIALS AND METHODS

The studied nests of *E. atroveneta* are located at Unión Juárez in Chiapas ( $15^{\circ}5'N$ ,  $92^{\circ}3'W$ ), at an altitude of 1 400 m. In this region, secondary vegetation of tropical rain forest is found in patches and the landscape is dominated by crops of various coffee varieties (*Coffea arabica*).

The larval feeding samples were collected from open cells in 51 nests of *E. atroveneta* maintained in wooden boxes [23], to know which resources were currently being exploited. During 1 year, from 31 May 1990 to 27 May 1991, a total of 143 weekly samples were collected: in solitary nests, one sample per nest and in parasocial nests, from 1 to 5 weekly samples per nest. To remove the larval food a wooden stick was used and each sample was put in individual tubes, sealed carefully and labeled with date, nest and cell number.

All larval feeding samples were acetolyzed, following Erdtman's [7] method, and the slides obtained deposited in the palynological collection of the Institute of Geology, at the National University of Mexico (IGLUNAM).

The pollen grains of each sample were described and identified, consulting palynological reference collections (IGLUNAM) from Chiapas and Los Tuxtlas, Veracruz, and by means of Mexican catalogues of tropical pollen [10, 11, 18, 24] and following floristic lists [3]. For each sample, the frequencies of the plant taxa were based on 1 200 pollen grains counted randomly [30].

The important species were those present in 10% or higher percentages [21]. The flower morphology of important taxa was reviewed. Some field observations of plants visited by the bees were made also.

Based on palynological results, three ecological parameters were calculated monthly: the Shannon-Weaver index [26] (H'), Pielou's formula [19] (J') and the Schöener index [25] (PS').

The Shannon-Weaver Index (H') expresses the palynological diversity of the samples, considering the total number of plant species and the relative frequency of each taxa in the sample

$$H' = -\sum_{i=1}^{n} p_{i} \ln p_{i}$$

where H' is the diversity index, pi is the proportion of each pollen type found in samples of nest in question during the month considered, and in the natural logarithm.

Pielou's formula (J') was used to determine the uniformity of pollen species at each sample. The J' value can vary from 0 to 1, and is a measure of whether a sample is heterogeneous or homogeneous

$$J' = \frac{H'}{H' \max}$$

where J' is the evenness, H' is the diversity index, and H' max is the natural logarithm of the total number of pollen types present in the samples.

Schöener (PS) index was calculated to determine the overlapping of resources among the *E. atroveneta* nests. This index can vary from 0 to 1, when two samples are different or similar, respectively. The overlap in feeding sources was calculated monthly

$$PS = 1 - \frac{1}{\Sigma^{cf}} |ph_i - ph_j|$$

$$2h$$

where PS is the resource overlap,  $ph_j$  the proportion of pollen from species h collected by *E. atroveneta* at nest i, and  $ph_j$  is the respective value for the nest j.

The palynological analysis of larval feeding, the study of the flower morphology and the field observation were used to show the collecting strategies of *E. atroveneta* at Unión Juárez. The ecological parameters employed (pollinic diversity, the evenness and overlapping of feeding resources), are also important tools to evaluate foraging behavior in the Apidae [12–14, 20–22, 27].

#### **3. RESULTS**

During the year of this research, 51 nests of *E. atroveneta* were studied. Through palynological analysis, 67 plant species belonging to 42 families and seven undetermined taxa were registered. Of the total taxa observed, only 22 were of importance ( $\geq 10 \%$ ) in the *E. atroveneta* diet at the Unión Juárez area (*table I*).

The total number of plant species found for each nest varied from 4 to 25. The major number of taxa (from 20 to 25) was registered only in five parasocial nests.

Generally, only a few species were exploited with high intensity in solitary and parasocial nests. The species with low frequencies could be considered as alternative resources (*table I*).

In the case of solitary nests, i.e. nests constructed by only one female (n = 42), from one to six species of importance were registered, with an average of three important taxa per sample. In parasocial nests (n = 9), three to nine important taxa were observed, with an average of five important species per sample.

In this species, some female bees were polylectic (*figure 1*), while some others had an oligolectic behavior (*figure 2*).

The important resources (> = 10 %) for E. atroveneta were exploited during short time periods from 1 to 3 months and consisted of Dendropanax sp., Commelina sp., Kohleria elegans, Cordyline terminalis, Antirhea sp., Rondeletia sp., Solanum aff. torvum, Solanum aff. tuerckheimii, Cassia sp. and four undetermined species. Other resources registered during medium time periods, from 4 to 6 months were Saurauia sp., Begonia biserrata, Combretum sp., Drymonia aff. strigosa, Nautilocalyx aff. panamensis and Leguminosae type 4. The species, visited during long flowering periods from 7 to 11 months, were Lonchocarpus sp., Tibouchinia longifolia and Lycianthes sp.

The monthly analyses showed from nine to 39 plant species, but only from two to ten important species per month were recorded. The major number of taxa was registered in June, July, September, October, January and February (*table I*).

The flower morphology of these taxa was reviewed and nectaropolliniferous species with tubular flowers were detected (*Drymonia* aff. strigosa, Kohleria elegans, Nautilocalyx aff. panamensis, Rondeletia sp.) and a Fabaceae (Lonchocarpus sp.) (figure 3). Also, two genera had been associated with buzz pollination for Euglossinae bees: Cassia and Solanum [15, 31].

The important *polliniferous* species were Saurauia sp., Dendropanax sp., Begonia biserrata, Combretum sp., Commelina sp., Cassia sp., Leguminosae type 4, Cordyline terminalis, Tibouchinia longifolia, Antirhea sp., Lycianthes sp., Solanum aff. torvum, S. aff. tuerckheimii and four undetermined taxa.

Taxa	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	May
ACANTHACEAE	_	_	_	_	-	_	_	_	×	×	×	_
ACTINIDIACEAE												
Saurauia sp.	_	×	×	×		+	+	+	+	×	+	×
AMARANTHACEAE												
Iresine celosia	÷	_	_		_	_	_	_	_	_	_	_
ARALIACEAE												
Dendropanax sp.	_		_	_	_	_	_	_	_	+	×	+
ARECACEAE												
Chamaedorea sp.	_	_	_	_	_	_	_		×	×		_
Coccos nucifera	_	_	×	_	_	_	_	_	_	-	_	_
ASTERACEAE	×	×	×	_	×	×	×	×	×	×	×	_
BALSAMINACEAE												
Impatiens wallerana		_	_			×	_	_	×	×	×	×
BEGONIACEAE												
Begonia biserrata	_	_	_	_	_	+	+	+	+	+	_	×
BETULACEAE										•		
Type 1	×	×	_	_	_	_	_				_	
Alnus sp.	_	_	_	_	×	×	_	×	×	×	×	
BIGNONIACEAE												
Parmentiera aculeata	_	_	_	_	_	_	_	×	_	~	_	_
BOMBACACEAE												
Bombax sp.	_	_	_	_	_		_	_	×		_	_
BORAGINACEAE												
Cordia sp.	_	×		_	_	_	_	_	_	_	_	_
CHENOPODIACEAE-	_	×	_	_	×	×	×	×	×	×	_	_
AMARANTHACEAE		~				~	~	~	~	~		
CLETHRACEAE	_	×	_	_	_	_	_	_	_		_	_
COMBRETACEAE		~										
Combretum sp.	×	+	×	_	_	×	_	_	+	+	+	_
COMMELINACEAE	~		~			^				т	т	
Commelina sp.	_	_	_	_		+	×	_	×	_	_	_
CONVOLVULACEAE					-	т	^		^	_	_	_
Evolvulus sp.	_	×	×	×	×	×	×	×	×	×		
CUCURBITACEAE		^	^	^	^	^	^	^	^	^	-	-
Cionosicys macranthus	;					$\sim$						
CYPERACEAE	× –	_		_	~	×	-	-	-	-	_	_
DIOSCOREACEAE	^	_	_	_	_	_	-	-	_	-	_	_
Dioscorea sp.							$\sim$	~	$\sim$			
EUPHORBIACEAE	_	_	_	_	_	_	×	×	×	_	_	_
Croton sp.												
crown sp.	-	×	_	-	_	_	_	_	_	-	-	

**Table I.** List of pollen types ( $\times$ ) and important plant species (+) with more than 10 % of representativity found in the larval feeding samples of *Euglossa atroveneta*, during 1 year from May (1990) to May (1991).

Таха	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	May
Dalechampia sp.	_	_		_	_	×	_	_	_	_	_	_
Ricinus communis	_	_	_	-	_	×	_	_	_	_	_	_
Type 1	_	_	_		-	_	_	_	_		×	_
GESNERIACEAE												
Drymonia aff. strigosa	+	+	+	×	×	_	-		×	×	_	+
Kohleria elegans		+	×	×	+	+	×	_		_	-	+
Nautilocalyx aff.												
panamensis	+	+	+	+	+	_	_	_	+			+
LABIATAE												
Salvia purpurea	_	_		_	_	_	_	×	×	×		-
LEGUMINOSAE												
<i>Cassia</i> sp.	_	+	+	×	×	+	-	-	×	-	_	
Lonchocarpus sp.	_	_	_		+	+	+	+	+	+	×	+
Mimosa orthocarpa		_	×	_	×	×	_	_	-	-	×	
Mimosa pigra	_	_	_	_	×	×	_	-			-	-
Mimosa pudica	_	×	×	_	×	×	_	-	_	_	×	_
<i>Mimosa</i> sp.	_	×	×	_	×	×	_	-	_	-	-	
Type 4	_	_	_	_	-	-		_	_	-	—	-
Type 5	-		+	_	+	+	+	+		-	-	-
LILIACEAE												
Cordyline terminalis	_	×	+	+	×	-	-	—	_	-	-	
Type 1	_	-	×	_		_	_	_	_	-	-	-
MELASTOMATA												
Tibouchinia longifolia	×	+	+	+	+	+	+	+	+	+	+	+
MELIACEAE	_	_	-	_	-	-	×	-	-			-
MYRTACEAE												
<i>Eugenia</i> sp.	_	×	_	_			_	_	-	_	-	-
OLEACEAE												
Fraxinus sp.		-	-	_	_	-	×	-		-	-	-
ONAGRACEAE												
PAPAVERACEAE	_	_	-	-	-	-	-	-	-	-	-	×
Bocconia sp.		_	_	-	-	_	×	_	×	-	-	_
PIPERACEAE												
Peperomia sp.	×	-	-	_	-	-	-	-			-	-
Piper sp.	_		-	_	×	-	-	-	-		-	-
POACEAE												
Type 1	_	-	-	_	×	×	×	_	×	-	-	-
Zea mays	-		_	-	×	×	-		-	-	-	-
POLYGONACEAE												
Polygonum sp.	×	×	_	-	-	-	-		-	_	-	-
Type 1	×	-	_	-	-	-		-	-	-	-	-

#### E.R. Arriaga, E.M. Hernández

Таха	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	May
RUBIACEAE												
Antirhea sp.	_	+	_	_	_	_	_	_	_	_	_	_
Coffea arabica	_	_	_	_	_	_	_	_	×	×	×	_
Rondeletia sp.	_	_	_	_	_	+	+	×	+	×	_	_
RUTACEAE						•						
Citrus sp.	×	_	_	_	_	×	×	×	×	×	×	×
SOLANACEAE												
Capsicum sp.	_	_	_	_	_	×	_	_	_	×	×	_
Lycianthes sp.	×	+	+	+	+	+	+	×	+	+	_	+
Solanum aff. torvum	_	_	_	_	+	_	_	_	+		_	+
Solanum aff. tuerckheimi	ï _	_	+	_	_	_	_	_	_	-	_	_
TILIACEAE												
Heliocarpus sp.	×	×	×	_	_	×	×	×	_	×	_	_
ULMACEAE												
Celtis sp.	_	_	_	_	_	×	_	_	-	-		_
Trema micrantha	×	×	×	_	×	×	_	_	_		_	×
Chaeptoptelea	_	_	_	_	×	×	_	_	_	_	_	_
mexicana												
Type I	_	×	_	_	_	_	_	_		-	_	
ZINGIBERACEAE												
Costus sp.	×	×	×	_	_	×	_	_	_	_	_	×
Elettaria cardamomum		×	_	_	×	×	_	_	_	_	_	_
Undetermined Taxa												
Type a	×	_	_	_	_		_		_	_	_	_
Type b	_	_	×	_	×	_	_	_	_	_	_	_
Туре с	_	+	_	_	×	-		_	_	_	_	_
Type d	_	_	×	_	_	_	_	_	×	×	_	+
Type e	_	_	_	_	×	×	_	-	_	×	_	×
Type f	_	_	×	_	_	×	_	_	+	-	_	_
Type g	-	×	-	_	-	×	-	_	-	-	-	+
Total and (important)	16	28	24	9	27	39	16	17	27	23	15	18
taxa registered per month		(9)	(8)	(4)	(7)	(10)	(7)	(5)	(9)	(6)	(3)	(9)

The resources of feeding importance were from the secondary vegetation of this area, most of them constituted the arboreal and bushy strata, and few plant species belong to the herbaceous stratum.

Some important plants, such as Begonia biserrata, Commelina sp., Cordyline termi-

nalis, Saurauia sp. and Solanum torvum were within a few meters around *E. atro*veneta nests. Other taxa visited exclusively to collect nectar and which were near the nesting area included *Elettaria cardamo*mum (cultivated species) and Salvia purpurea.

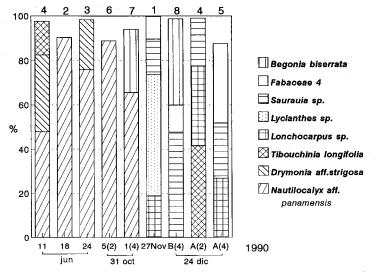


Figure 1. Important plant species registered in a parasocial nest. The numbers that are at the top of each bar refer to taxa represented by less than 10 %.

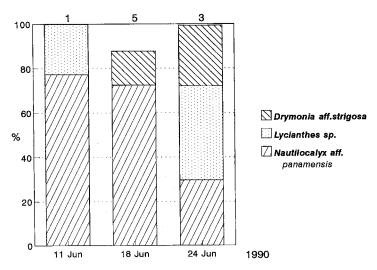


Figure 2. Important plant species registered in a social nest. The numbers that are at the top of each bar refer to taxa represented by less than 10 %.

#### 3.1. Foraging behavior

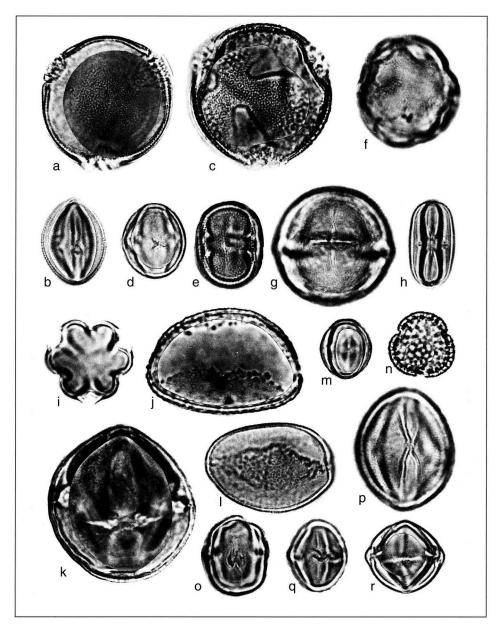
#### 3.1.1. Pollinic diversity (H')

In the population studied, the diversity index by nest (n = 51), varied from 0.12 to 2.04, with a population average of  $1.12 \pm$ 

0.19. However, most of the data were between 0.83 and 1.3 (*figure 4*).

#### 3.1.2. Evenness (J')

Regarding the evenness (n = 51), the values varied from 0.07 to 0.75, with an ave-



**Figure 3.** Nectaropolliniferous plant species. Gesneriaceae (a–c): a) *Drymonia* aff. *strigosa*, b) *Kohleria elegans*, c) *Nautilocalyx* aff. *panamensis*; Leguminosae: d) *Lonchocarpus* sp.; Rubiaceae: e) *Rondeletia* sp. Polliniferous plant species: Actinadiaceae: f) *Saurauia* sp.; Araliaceae: g) *Dendropanax* sp; Begoniaceae: h) *Begonia biserrata*; Combretaceae: i) *Combretum* sp.; Commelinaceae: j) *Commelina* sp.; Leguminosae: k) type 4; Liliaceae: l) *Cordyline terminalis*; Melastomataceae: m) *Tibouchinia longifolia*; Rubiaceae: n) *Anthirhea* sp.; Solanaceae: o) *Lycianthes* sp. Pollliniferous plant species with buzz pollination: Leguminosae: p) *Cassia* sp.; Solanaceae (q–r): q) *Solanum* aff. *tuerckheimii*, r) *Solanum* aff. *torvum*.

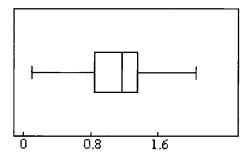


Figure 4. Box diagram showing the distribution of the diversity indexes (H') calculated per nest.

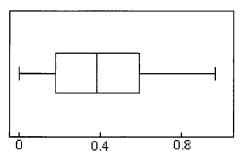


Figure 6. Box diagram showing the the resources overlapping (PS) during the studied year

rage of  $0.48 \pm 0.02$ , which means that *E. atroveneta* had heterogeneous collecting sources (*figure 5*). The major record numbers obtained were registered from 0.4 to 0.6.

#### 3.1.3. Overlapping of feeding resources (PS)

The overlapping values (n = 300) varied from 0.002 to 0.95 with a mean of 0.38  $\pm$  0.06. On the other hand, the main records were grouped in the 0.19–0.57 interval.

In general, when the *E. atroveneta* population was increased, the major number of plants and the major number of high overlapping indexes were registered. These occurred during June, July, September, October, January, February and May (*figure 6*).

The overlapping behavior occurred when *E. atroveneta* females foraged over *Saurauia* sp., *Dendropanax* sp., *Chamaedorea* sp., *Impatiens wallerana*, *Begonia biser*-

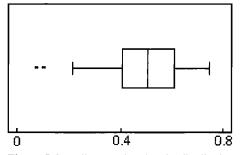


Figure 5. Box diagram showing the distribution of the evenness indexes (J') calculated per nest.

*rata*, *Alnus* sp., Betulaceae type 1, Chenopodiaceae–Amaranthaceae, *Combretum* sp., *Evolvulus* sp., *Dioscorea* sp., *Drimonia* aff. *strigosa, Kohleria elegans, Nautilocalyx* aff. *panamensis*.

#### 4. DISCUSSION

The present study is the first palynological research of larval feeding carried out in solitary and parasocial *E. atroveneta* nests.

The *E. atroveneta* population studied was polylectic. All the plant species with values of importance for *E. atroveneta* were exclusively polliniferous and nectaropolliniferous from the arboreal and herbaceous strata belonging to secondary vegetation. Despite the abundance of *Coffea arabica* in the surroundings, this species was not an important feeding resource.

Some important genera for *E. atroveneta*, such as *Solanum*, *Cassia*, *Drymonia* and *Tibouchinia* had been previously cited for other Euglossinae through field observations.

With respect to resource availability, the important species *Begonia biserrata, Commelina* sp., *Cordyline terminalis, Saurauia* sp. and *Solanum torvum* were near the nests although, these plants were not in abundance. This forage behavior differs from that cited by Janzen [8], who mentioned that Euglossinae moves long distances in the Costa Rican tropical forest, to obtain resources and it can take up to 2 h even for a single trip. It is possible that *Euglossa* at Unión Juárez visited nearby plants that were attractive because their exploitation involved less energy expenditure. It is possible that they do travel long distances during periods of scarcity. This is indicated by pollen collecting times that vary from 5 min to 2 h [23].

The differences in the foraging behavior observed between the Costa Rica Euglossinae and that of *E. atroveneta* at Unión Juárez, Chiapas, could be related to differences in the types of vegetation. Hence, Janzen carried out his observations in an undisturbed tropical rain forest, while the present study was made in a perturbed tropical community. Janzen [8] cited that the important food plants for 'orchid bees' produce a small number of flowers over long periods of time. However, *E. atroveneta* visited not only species with long flowering periods, but also foraged plants that flowered for medium and short time periods.

Female bees that constructed their nests at the same time had similar forage behavior and visited the same taxa, although the intensity of exploitation could change. This was reflected in the frequencies registered in larval feeding samples. There were also differences in female behavior, possibly related to the individual preferences for some flowers. This indicates a level of plasticity in the diet of these bees.

Differences were also observed in foraging behavior between solitary and parasocial nests (i.e. *figures 1* and 2). The differences in the higher number of taxa of importance may reflect that parasocial nests existed for a longer period of time and it is possible that during this interval, the plants registered at the beginning finished flowering and then other plant species started to bloom and were visited by *Euglossa* females. The previous statement could be tested with the following regression analysis with the equation:

#### Y = 7.64 + 0.076 (X)

where Y is the number of plant species (dependent variable), and X the time of nest construction (independent variable).

The result gave a value for R-squared of 35.4, which means that 35.4 % of plant species variation depends on the time of nest construction.

Also, differences between solitary and parasocial nests may be due to the particular preferences of each female bee. In parasocial nests two or more bees cohabited, but there was no communication among them on the location of the important resources, as in social bees. Then, it is possible that each female had different preferences at the same time and thus increased the species richness. This could be proved with a regression where 26.7 % of sample richness is due to the variation of number of female bees in the same nest. The regression equation was:

$$Y = 8.82 + 1.44 (X)$$

where Y is the number of plant species (dependent variable), and X the number of female bees by nest (independent variable).

Comparing the results obtained in the present study with those from other studies for stingless bees (eusocial bees) in the same area, it was observed that *E. atroveneta* visited more plant species than stingless bees. This may be due to *E. atroveneta* displacement ability that permits it to forage over more polliniferous and nectariferous resources in a given time.

In addition, the *E. atroveneta* larval feeding analysis showed that the important trophic species are polliniferous and polliniferous–nectariferous. Similar results were obtained for *Melipona* and Trigonini [12, 14, 22, 27], indicating that both bee groups follow the same patterns for foraging to optimize their resources.

It is worth noting that there were important common taxa visited by *Melipona*, Trigonini and *E. atroveneta* in Unión Juárez which were: *Saurauia* sp., *Commelina* sp., Lonchocarpus sp., Cordyline terminalis, Tibouchinia longifolia, Rondeletia sp. and Solanum sp. [12, 14, 22, 27]. Particular floral preferences were registered in the *E. atro*veneta population, where female bees exploited the following plant species: Dendropanax sp., Begonia biserrata, Combretum sp., Drimonia aff. strigosa, Kohleria elegans, Nautilocalyx aff. panamensis, Cassia sp., Leguminosae type 4, Antirhea sp., Lycianthes sp., Solanum aff. torvum and Solanum aff. tuerckheimii.

So far, it is evident that a resource partition exists among the different Apidae members that had been studied at the same zone. Although there is overlapping in feeding resources, there are differences in interspecific and intraspecific forage strategies.

#### 4.1. Ecological aspects

According to the palynological diversity registered in the samples, the H' values were high throughout the year of study. These results indicated that *E. atroveneta* collected its resources heterogeneously. The heterogeneous foraging in space and time determined that euglossas have different preferences to collect their resources. Nevertheless, they exploited more intensely only a few plants, and even *E. atroveneta* had very specific foraging.

In general, the values of PS show a low amount of overlapping, proving that although *Euglossa* females visited the same blooming resources, these were exploited in a different way. Higher levels of overlapping occurred only during the rainy season and at the beginning of the year, coinciding with an increase in the *E. atroveneta* population [23].

If the H' values of *E. atroveneta* are compared with those cited for maximum and minimum H' and J' values for *Tetragonisca angustula* [27] in the same area, the major diversity in larval feeding samples had been registered in both *Tetragonisca* and *E. atro*- veneta.

With respect to the evenness (J'), the highest index was registered in *T. Angustula* [27], meaning that this bee forages homogeneously for its resources, and *E. atroveneta* follows in importance. In contrast, the lowest evenness data were registered in *E. atroveneta*, indicating that this bee can collect its resources heterogeneously, when it has specific floral preferences.

#### ACKNOWLEDGMENTS

This research was supported by CONACyT (reg. 55888). The authors are grateful to Dr Michener and Dr Dressler for their important taxonomical contributions as well as Magdalena Alcayde for reviewing the English version and to M. en C. Lourdes Flores Delgadillo for her statistical advice.

Résumé – Plantes butinées par Euglossa atroveneta (Apidae : Euglossinae) à Unión Juárez, Chiapas, Mexique. Une étude palynologique de la nourriture larvaire. Des échantillons de nourriture larvaire ont été prélevés chaque semaine durant une année, du 31 mai 1990 au 29 mai 1991, dans 51 nids d'Euglossa atroveneta à Union Juarez, dans le Chiapas (Mexique). Leur analyse palynologique a montré que E. atroveneta butinait 74 espèces de plantes (tableau D. On a observé des différences dans le comportement de butinage entre nids solitaires et nids parasociaux (figures 1 et 2), différences qui sont liés à la période de nidification et aux préférences de chaque femelle. Au cours de l'année E. atroveneta a présenté un indice moyen de diversité de 0,83 (figure 3) et un comportement de butinage hétérogène (J' = 0.45) (figure 4) avec un faible recouvrement des ressources (PS moyen = 0,38) entre les nids solitaires et les nids parasociaux étudiés (figure 5). On a enregistré le plus grand nombre d'espèces butinées et le plus grand indice de recouvrement pour les populations les plus nombreuses. Les res-

sources les plus importantes pour la nourriture larvaire sont au nombre de 22 et ont été classées en : a) espèces pollinifères : quatre taxons indéterminés, Anthirhea sp., Begonia biserrata, Cassia sp., Combretum sp., Commelina sp., Cordvline terminalis, Dendropanax sp., Légumineuses type 4, Lycianthes sp., Rondeletia sp., Saurauia sp., Solanum aff. torvum, Solanum aff. tuerckheimii, Tibouchinia longifolia et b) nectaropollinifères : Drymonia aff. strigosa, Kohleria elegans, Lonchocarpus sp. et Nautilocalyx aff. panamensis et toutes les Gesneriaceae à fleurs tubulaires. Certaines de ces espèces sont associées à la pollinisation vibratile (Cassia et Solanum). © Inra/-**DIB/AGIB/Elsevier**, Paris

#### *Euglossa atroveneta /* ressource alimentaire / nourriture larvaire / analyse pollinique

Zusammenfassung - Nahrungsressourcen von Euglossa atroveneta (Apidae: Euglossinae) in Unión Juárez, Chiapas, Mexiko. Eine palynologische Untersuchung der Larvenernahrung. Bei 51 Nestern von Euglossa atroveneta wurden wöchentlich Proben von der Larvennahrung entnommen und palynologisch untersucht. Es zeigte sich, da $\beta$  *E. atroveneta* im Verlauf eines Jahres, vom 31 Mai (1990) bis zum 29 Mai (1991) 74 Pflanzenarten besammelte, von denen 22 Arten vermehrt beflogen wurden. Dabei wurden Unterschiede im Sammelverhalten zwischen Einzel- und parasozialen Nestern beobachtet (Abb. 1 und 2), die mit der Zeit des Nestbaus und besonders mit individuellen Bevorzugungen einzelner Weibchen zusammenhingen. Während des Jahres zeigte E. atroveneta einen durchschnittlichen Diversitätsindex von 0,83 (Abb. 3) und ein heterogenes (J'= 0,45) Sammelverhalten (Abb. 4). Zwischen den einzelnen und den parasozialen Nestern ergab sich eine durchschnittliche Überschneidung der Nahrungsressourcen von PS = 0.38 (Abb. 5). Bei zunehmender Populationsdichte von E. atroveneta war die

Anzahl der besammelten Arten am größten und der Wert des Überlappungsindex am höchsten. Als für die Larven wichtigste Nahrungsressourcen wurden folgende Arten bestimmt: a) die Pollenerzeuger: Antirhea sp., Begonia biserrata, Cassia sp., Combretum sp., Commelina sp., Cordyline terminalis, Dendropanax sp., der Leguminosen Typ 4, Lycianthes sp., Sauria sp., Solanum aff. torvum, Solanum aff. tuerckheimii, Tibouchinia longifolia, und b) die Nektar- und Pollenerzeuger: Drymonia aff. strigosa, Kohleria elegans, Lonchocarpus sp. and Nautilocalyx aff. panamensis. Alle Gesneriaceae hatten Röhrenblüten. © Inra/-DIB/AGIB/Elsevier, Paris

#### *Euglossa atroveneta /* Larrennahrung / Palynologie / neotropisch / Orchideenbienen / Nahrungsressourcen

#### REFERENCES

- Ackerman J.D., Euglossine bees and their nectar hosts, in: D'Arcy W.G., Correa A.M.D. (Eds), The Botany and Natural History of Panamá, Missouri Botanical Garden, St. Louis, 1985, pp. 225–233.
- [2] Ackerman J.D., Geographic and seasonal variation in fragrance choices and preferences of male Euglossine bees, Biotropica 21 (4) (1989) 340–347.
- [3] Breedlove D.E., Listados Florísticos de México. Flora de Chiapas, Instituto de Biología, IV, Universidad Nacional Autónoma de México, 1986, 246 p.
- [4] Cortopassi-Laurino M., Ramalho M., Pollen harvest by africanized *Apis mellifera* and *Trigona spinipes* in Sao Paulo: botanical and ecological view, Apidologie 19 (1) (1988) 1–24.
- [5] Dressler R.L., The Orchids. Natural History an Classification, MA. Harvard University Press, Cambridge, 1981, 332 p.
- [6] Dressler R.L., Biology of the orchid bees (Euglossini), Annu. Rev. Ecol. Syst. 13 (1982) 373–394.
- [7] Erdtman G., The acetolisis method. A revised description, Svensk Bot. Tidskr. 54 (4) (1960) 561–564
- [8] Janzen D.H., Euglossine bees as long distance pollinators of tropical plants, Science 171 (1971) 203–205.
- [9] Kleinert-Giovannini A., Imperatriz-Fonseca V.L., Aspects of the trophic niche of *Melipona marginata marginata* Lepeletier (Apidae, Meliponinae), Apidologie 18 (1) (1987) 68–100.

- [10] Lozano-García M.S., Martínez-Hernández E., Palinología de los Tuxtlas: especies arbóreas, Instituto de Biología, Publicaciones especiales 3, Universidad Nacional Autónoma de México, 1990, 61 p.
- [11] Martínez-Hernández E., Cuadriello-Aguilar J.I., Ramírez-Arriga E., Medina C.M., Sosa N.M.S., Melchor S.J.E., Atlas de las plantas y el polen utilizados por las cinco especies principales de abejas productoras de miel, en la región del Tacaná, Chiapas, México, Instituto de Geología, Universidad Nacional Autónoma de México, 1993, 105 p.
- [12] Medina C.M., Explotación de recursos florales por Nannotrigona testaceicornis (Apidae) en dos zonas con diferente altitud y vegetación en el Soconusco, Chiapas, Universidad Nacional Autónoma de México, Facultad de Ciencias, Tesis de Licenciatura, 1989, 125 p.
- [13] Medina C.M., Contribución al conocimiento de algunos aspectos ecológicos en relación a la flora apícola explotada por abejas europeas (*Apis mellifera ligustica*, Spinola), abejas africanizadas (*Apis mellifera scutellata*, Lepeletier), e híbridos en el Soconusco, Chiapas. Universidad Nacional Autónoma de México, Facultad de Ciencias, Tesis de Maestría en Biología, 1992, 154 p.
- [14] Melchor S.J.E., Explotación de recursos florales por *Scaptotrigona pachysoma* (Apidae) en dos zonas con diferente altitud y vegetación en el Soconusco, Chiapas, Universidad Nacional Autónoma de México, Facultad de Ciencias, Tesis de Licenciatura, 1991, 231p.
- [15] Michener C.D., An interesting method of pollen collecting by bees from flowers with tubular anthers, Rev. Biol. Trop. 10 (2) (1962) 167–175.
- [16] Michener C.D., The Social Behavior of the Bees. A Comparative Study, Harvard University Press, Cambridge, Massachusetts, 1974, pp. 257–260.
- [17] Michener C.D., Classification of the Apidae (Hymenoptera), Univ. Kans. Sci. Bull. 54 (4) 9 (1990) 75–164.
- [18] Palacios-Chavez R., Ludlow-Wiechers B., Villanueva G.R., Flora palinológica de la reserva de la biosfera de Sian Ka'an, Quintana Roo, México, Centro de Investigaciones de Quintana Roo, Chetumal, 1992, 321 p.
- [19] Pielou E.C., Mathematical Ecology, 2nd ed., Willey-Interscience Publication, John Wiley & Sons, New York, 1977, 385 p.
- [20] Quiroz G.D.L., Patrones Estacionales de utilización de recursos florales por Scaptotrigona hellwegeri en la Estación de Biología Chamela, Jalisco, Universidad Nacional Autónoma de México, Tesis de Maestría en Biología, 1993, 148 p.

- [21] Ramalho M., Imperatriz-Fonseca V.L., Kleinert-Giovannini A., Cortopassi-Laurino M., Exploitation of floral resources by *Plebeia remota* Holmberg (Apidae, Meliponinae), Apidologie 16 (3) (1985) 307–330.
- [22] Ramírez A.E., Explotación de recursos florales por Plebeia sp. (Apidae) en dos zonas con diferente altitud y vegetación en el Soconusco, Chiapas, Universidad Nacional Autónoma de México, Facultad de Ciencias, Tesis de Licenciatura, 1989, 159 p.
- [23] Ramírez A.E., Cuaddriello-Aguilar J.I., Martínez-Hernández E., Nest structure and parasite of *Euglossa atroveneta* Dressler (Apidae: Bombinae: Euglossini) at Unión Juárez, Chiapas, México, J. Kans. Entomol. Soc. 69 (2) (1996) 144–152.
- [24] Roubik D.W., Moreno P.J.E., Pollen and spores of Barro Colorado island, Missouri Bot. Gard., 1991, 268 p.
- [25] Schöener T.W., The Anolis lizards of Bimini: resource partitioning in a complex fauna, Ecology 49 (4) (1968) 704–726.
- [26] Shannon C.E., Weaver W., The Mathematical Theory of Communication, University Of Illinois Press, Urbano, 1949, 117 p.
- [27] Sosa N.M.S., Explotación de recursos florales por Tetragona jaty en dos zonas con diferente altitud y vegetación en el Soconusco, Chis, Universidad Nacional Autónoma de México, Facultad de Ciencias, Tesis de Licenciatura, 1991, 98 p.
- [28] Sosa N.M.S., Martínez-Hernández E., Lozano-García M.S., Cuadriello-Aguilar J.I., Nectaropolliniferous sources used by *Trigona (Tetragonisca) angustula* in Chiapas, southern México, Grana 33 (1993) 225–230.
- [29] van der Pijl L., Dodson C.H., Orchid Flowers: their Pollination and Evolution, University Miami Press, Coral Gables, Florida, 1969.
- [30] Vergeron Ph., Interprétation statistique des résultats en matière d'analyse pollinique des miels, Ann. Abeille 7 (4) (1964) 349–364.
- [31] Wille A., Behavioral adaptations of bees for pollen collecting from Cassia flowers, Rev. Biol. Trop. 11 (2) (1963) 205–206.
- [32] Williams N.H., Whitten W.M., Orchid floral fragances and male euglossine bees: methods and advances in the last sesquidecade, Biol. Bull. 164 (1983) 355–385.