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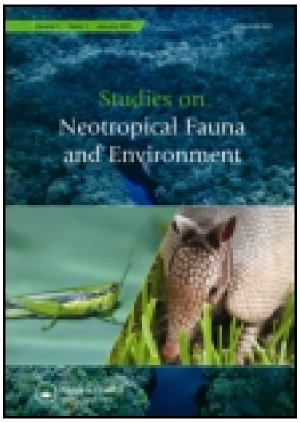

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Pollinating bees and other visitors of Ludwigia elegans (Onagraceae) flowers at a tropical site in Brazil

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Pollinating Bees and Other Visitors of *Ludwigia elegans* (Onagraceae) Flowers at a Tropical Site in Brazil

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ABSTRACT

Flowers of Ludwigia elegans *present a set of generalized characteristics attracting visitors of several insect taxa, however, they strongly depend on bees for pollination. Bees of 32 species were observed visiting* L. elegans *flowers of which* Tetraglossula bigamica *is considered an efficient, oligolectic, and specialized pollinator. This bee has stiff, long and simple hairs on the scopae. The daily and annual activity patterns of* T. bigamica *are synchronized to the flower phenology of* L. elegans. *Other bee species can pollinate the flowers if their body size is large enough to contact the stigma during the harvest.*

KEYWORDS: Tetraglossula bigamica, Ludwigia elegans, *phenology, flower visitors, pollination, coevolution.*

INTRODUCTION

Flowers of Onagraceae produce large pollen grains, usually of 100 µm in diameter, which are glued together by viscin threads forming an adherent mass (Hesse 1984). Only specialized bees can handle this kind of pollen, by means of their stiff, long, and slightly branched bristles on the scopae (Roberts & Vallespir 1978; Gimenes 1991). In addition to these structural adaptations, peculiar behavioural traits like fast body and leg movements enhance the efficiency in pollen harvest (MacSwain *et al* 1973). *Ludwigia elegans* is a relatively common species in tropical and subtropical South America found in swampy areas (Ramamoorthy & Zardini 1987). The genus is considered the oldest and least specialized of the family, because of its open flowers with exposed anthers (Eyde 1982). According to Feinsinger (1983), flowers with these characteristics should attract both oligolectic and polylectic bees. Nevertheless, Estes and Thorp (1974) studying pollination of *Ludwigia peploides* ssp. *glabrescens*, in central USA, recorded only generalist bees visiting the flowers. In the State of São Paulo, Brazil, Sazima and Santos (1982) showed that *Tetrapedia* sp. was an effective pollinator, whereas *Ptilothrix relata* and other rare bees were fortuitous *Ludwigia sericea* pollinators. They considered *Pseudagapostemon* sp. and *Augochlora* sp. as pollen thieves. Martins and Antonini (1994) observed in Minas Gerais, Brazil, that *Diadasina distincta* was an oligolectic bee of *Ludwigia suffruticosa* flowers.

In a survey of bees and plants around Ribeirão Preto, São Paulo, Brazil, Camargo and Mazucato (1984) observed that bees of 36 species visited flowers of *Ludwigia caparosa* (=*elegans*). But only two of them were frequent: *Tetraglossula bigamica* (Col-

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letidae) (probably solitary) and *Pseudagapostemon brasiliensis* (Halictidae) (quasisocial or semisocial, Martins 1993), considered as monolectic and oligolectic, respectively.

In order to determine the effective pollinators of *L. elegans* flowers, the visiting bees and their efficiency in pollen transfer were studied considering behavioural and ecological aspects.

MATERIALS AND METHODS

Study Site

The regional weather conditions correspond to type AW (Köppen classification) defined as tropical climate of altitude with relatively rainy summers and dry winters. Local average temperatures range from 23.8 to 24.5°C during the summer (December to March) and from 18.8 to 20.7°C during the winter (June to September) (Fig. 1). The study period represented an exceptionally rainy year with 2173.9 mm precipitation (Fig. 1), with a normal regional rate of 1416 mm (Oliveira & Prado 1987).

These study sites were located around an artificial lake of the Laureano river (altitude 620–690 m, S 21° 31′, W 47° 30′). Observations were done weekly from April 1986 to October 1986 and every two weeks from November 1986 to March 1987. The bees' behaviour was observed on flowers of 15 individual plants.

Two study sites were chosen. Site A was shadowed by dense vegetation, whereas at site B only a few trees and shrubs were present. At site A, 44 specimens of *L. elegans* were found 7 of which, with numerous flowers, were used for the observations. At site B 8 out of 11 plants were correspondingly selected.

Times of anthesis and dehiscence were registered. For most abundant visitors, *P. brasiliensis* and *T. bigamica*, the frequency of bees on flowers was recorded hourly for 10 min, from dawn until the flowers withered. ♂♂ and ♀♀ of *T. bigamica* were marked with nitrocellulose dye (Dakar colour). Total body length (between median ocellus and apex of the abdomen) and mesoscutum width (across tegulas) of the bees were measured.

To analyse the conditions of seed formation in *L. elegans*, buds were bagged the day before anthesis. Seed production was checked in 140 fruits of 15 plants after spontaneous autopollination (autogamy), conducted autopollination (autogamy), cross pollination (xenogamy or geitonogamy), in emasculated flowers, and after emasculation without bagging. By using reagents like Sudan III and glycerinated or oxygenated water which react with the exudations of receptive stigmas (M. Sazima, pers. commun.),

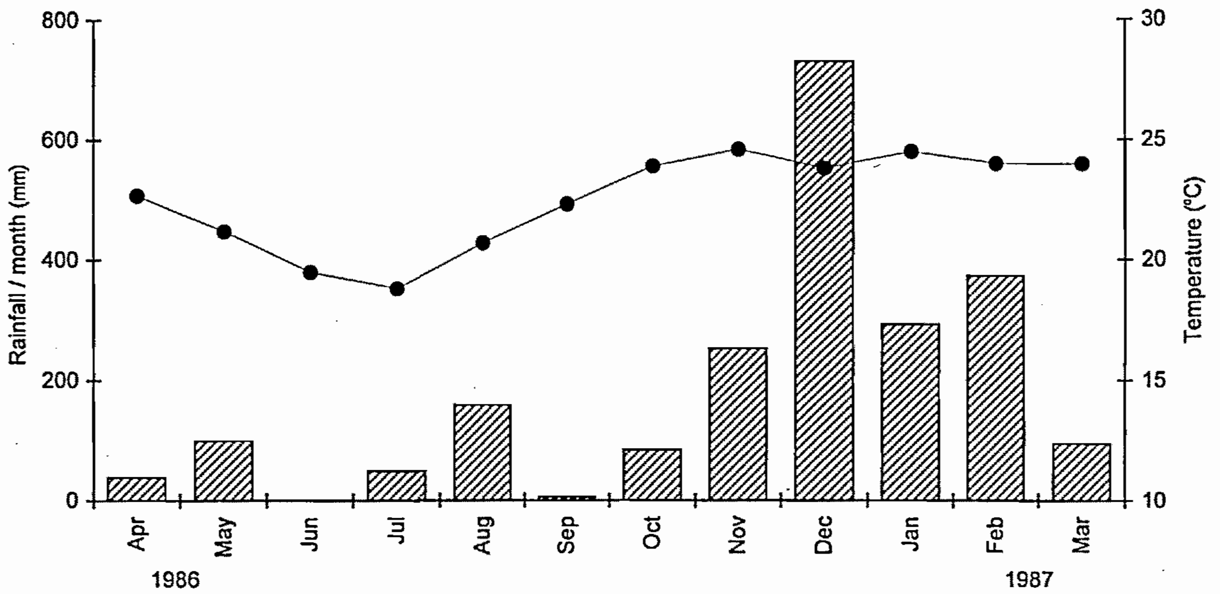

Fig. 1. Meteorological data for Ribeirão Preto during the observations.

the reproductive state of individual flowers was tested.

Weather data were obtained from the Agricultural Climatology Department at Ribeirão Preto. Local temperature and relative humidity were registered every 30 min during each observation.

L. elegans material was deposited at the UEC Herbarium, Campinas State University, under the numbers 20078 and 20079. Voucher specimens of the bees were deposited in the collection at the Faculdade de Filosofia, Ciências e Letras, University of São Paulo, Ribeirão Preto.

RESULTS

Phenology

L. elegans blossomed throughout the year with peaks in March (Fig. 2). Only a few flowers were observed from September to December. There was a difference in blooming rates at the two study sites (Fig. 2).

Flowers opened only at temperatures over 20°C. Anthesis occurred between 6:30 and 9:30 h, and in June and July, between 10:00 and 12:30 h (Fig. 3). Usually, anthers did not open along with petals, but 50 to 90 min later. During the summer flowers lasted only one day, from 15:30 to 17:30 h. In winter flowers withered at sunset or lasted until the next day.

Stigma exudate appeared just after opening as shining droplets which later on fully covered the stigma's surface. Tests showed that only stigmas with exudation reacted to oxygenated water or Sudan III.

The flowers were auto-compatible, however, only a few seeds were produced after autopollination, which is partially prevented by the anther's extroverted opening. The highest numbers of seeds were produced after crosspollination. No seeds resulted from unfertilized ovules (apomixy) (Table 1).

Visitors

The most frequent visitors of *L. elegans* flowers were bees (Table 2), followed by butterflies, beetles, flies, ants and wasps all of which collected nectar. Only bees of a few species collected or tried to collect pollen. Body size of visiting bees ranged from 3.83 mm (*Plebeia droryana*) to 19.66 mm (*Bombus atratus*), the width of the mesoscutum varied between 1.00 mm (*Pereirapis rhizophila*) and 5.58 mm (*Bombus atratus*). Bees of the species *Tetraglossula bigamica* and *Pseudagapostemon brasiliensis* were most frequently observed.

Tetraglossula bigamica

Both ♀♀ and ♂♂ of this species visited flowers of *L.elegans* December through May, with peaks of activity in February and March.

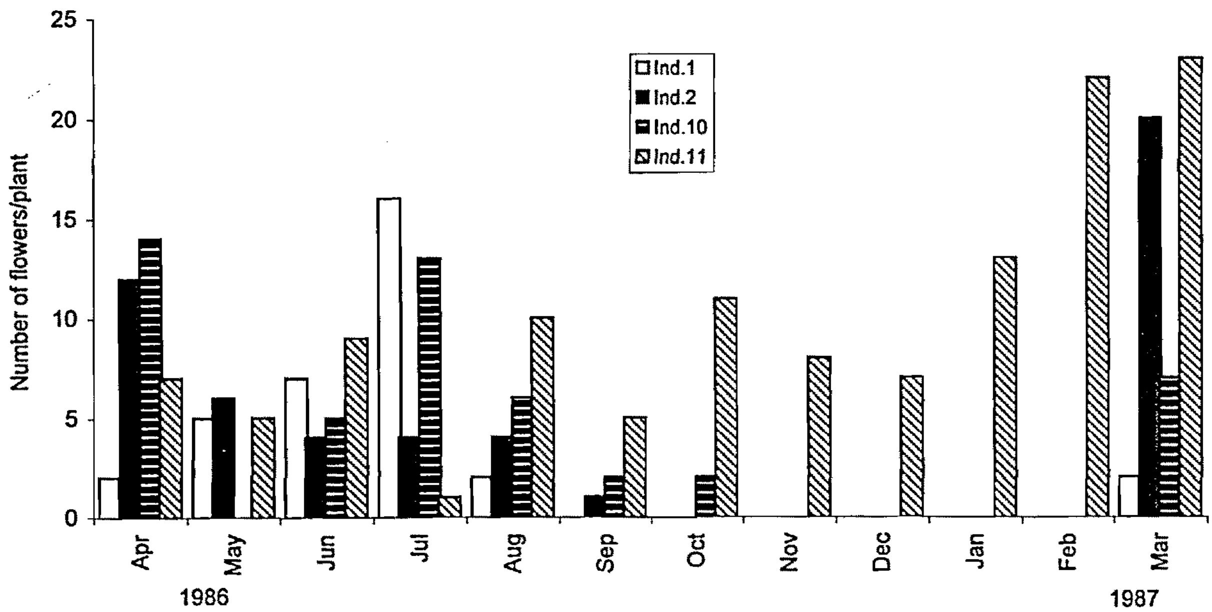

Fig. 2. Flowering periods of 4 individual plants of *Ludwigia elegans* (nos. 1, 2 and 10 at site A and no. 11 at site B) during the observations.

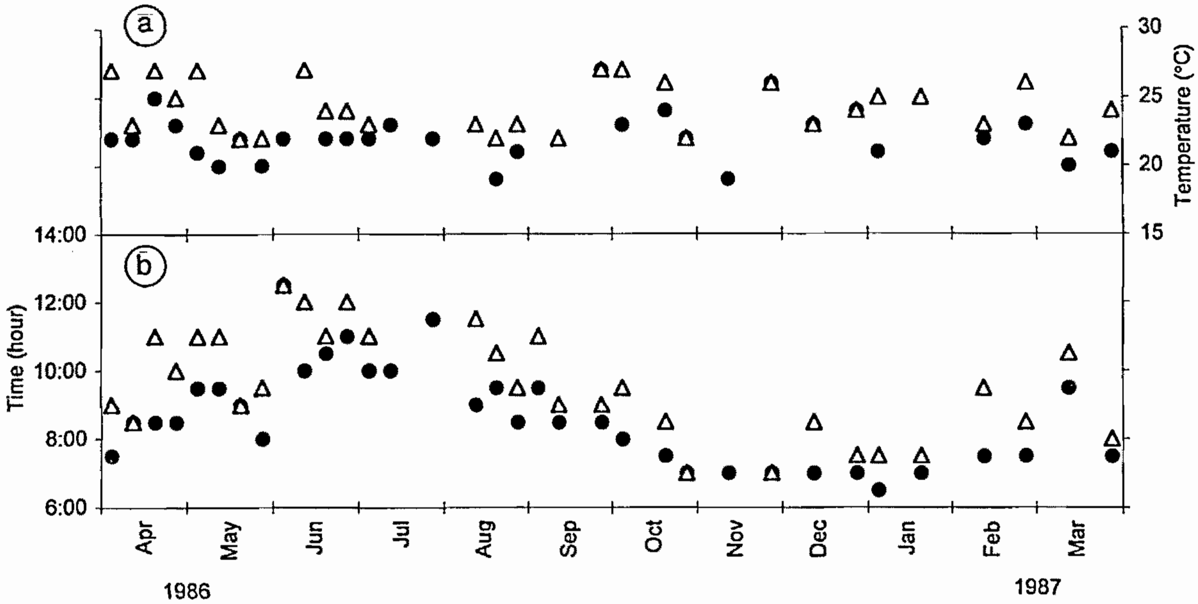

Fig. 3. Ambient temperature (a) triggers the beginning of anthesis (b) in *Ludwigia elegans*. • opening of the flowers, Δ opening of anthers.

♀♀ landed on petals or anthers and collected nectar or pollen usually during the same visit. Still closed anthers were opened with the mandibles, the pollen was removed with the front and middle legs and then transferred to the scopae at the abdominal sterna. When anthers were open and still full, bees collected large amounts of pollen by rubbing the abdomen against the anthers, thus loading the pollen directly into the scopae. While moving on the flower, they touched the stigma and deposited pollen on it.

When the amount of available pollen decreased, visits became more frequent. The bees then landed on more flowers of the same plant. Marked females needed less than 30 s for 2 consecutive visits.

Flowers may also be auto-pollinated during nectar uptake. ♀♀ and ♂♂ moved between nectaries, holding the anthers or the stigma with their hind legs (Fig. 4A).

♂♂ patrolled and frequently inspected the flower patches (ca. 45 inspections of 5 flowers in 5 min). They always returned to the same flower to rest or to collect nectar. ♂♂ attacked any insects approaching the flowers. They tried to mate with ♀♀ that landed in the flowers next to them, but most of the attempts were unsuccessful.

Pseudagapostemon brasiliensis

♂♂ and ♀♀ of this species visited *L. elegans* flowers all over the year, more frequently August through January and rarely in June, July and March.

♀♀ also opened the anthers with their mandibles, collected pollen with their front legs, and transferred

Table 1. Pollination efficiency in *Ludwigia elegans*.

Experiments	Flowers (*n*)	Fruits (*n*)	Success (%)
Spontaneous autopollination	60	10	17
Induced autopollination	39	29	74
Xenogamy	12	12	100
Geitonogamy	06	05	84
Apomixy	12	0	0
Pollination by insects	09	09	100

Table 2. List of bees visiting *L. elegans* flowers. F=♀♀, M=♂♂, W=workers, P=pollen, N=nectar.

Species	Sex or caste	Collected resource	Body length (mm)	Thorax width (mm)
Tetraglossula bigamica	F	PN	8.94	2.06
	M	N	8.94	1.92
Pseudagapostemon brasiliensis	F	PN	7.15	1.62
	M	N	5.76	1.23
Augochloropsis aurifluens	F	N	7.33	1.83
A. aphrodite	F	N	9.16	2.17
	M	N	9.12	2.21
A. melanochaeta	M	N	7.50	1.75
A. illustris	M	N	7.95	1.71
A. brachycephala	F	N	6.25	1.50
A. argentina	F	N	6.58	1.67
Augochloropsis sp	M	N	5.75	1.50
Augochlora esox	F	N	7.66	1.75
	M	N	6.33	1.50
A. (Oxystoglossella) thalia	F	N	6.25	1.33
A. amphitrite	F	N	7.41	1.67
Augochlorella sp	F	N	5.54	1.28
Pereirapis rhizophila	M	N	4.83	1.00
Chloralictus opacus	F	N	4.58	1.00
Megachile (Ptilosaurus) sp	M	N	7.57	2.46
M. (Neomegachile) sp A	M	N	7.41	2.17
M. (Chrysosaurus) sp	M	N	7.83	2.17
M. (Leptorachis) paulistana	M	N	7.16	2.67
Coelioxys sp B	M	N	7.83	2.25
Tetrapedia rugulosa	F	PN	7.35	2.00
	M	N		
Monoeca alblanei	F	N	9.25	2.58
Exomalopsis sp	M	N	4.66	1.25
Melissoptila sp	F	N	8.08	2.33
	M	N	7.00	1.80
Melissodes nigroaenia	M	N	9.66	2.83
Florilegus (Euflorilegus) festivus	F	N	11.24	3.08
F. (Euflorilegus) atropus	F	PN	11.00	2.75
Melissoptila (Comeptila) paraguayensis	F	N	12.49	2.83
	M	N	10.25	2.75
Plebeia droryana	W	N	3.83	1.42
Partamona helleri	W	N	5.66	1.75
Apis mellifera	W	PN	9.16	2.75
Bombus (Fervidobombus) atratus	W	N	19.66	5.58

it to the scopae at the hind legs seldomly touching the stigma. Pollen collection in a single flower could last for up to 3 min, especially in the morning when pollen was plentiful. To collect nectar, ♂♂ and ♀♀ moved around the base of the stamen (Fig. 4B).

♂♂ tried to mate with ♀♀ actively collecting, but most attempts were unsuccessful. They seemed not to set routes or territories, although other flower visitors were occasionally attacked.

Bees of other species found on L. elegans *flowers*
Workers of the Africanized honeybee *A. mellifera*, mainly foraged. To collect pollen, they used the fore-legs, holding the anthers with the hind legs. Then they tried to store the pollen in the corbiculae by rubbing the hind legs. However, they rarely succeeded because of the viscin threads. The pollen grains remained stuck to their body and could be easily transferred to the stigma. *A. mellifera* workers were relatively frequent on the flowers during seasons when *P. brasiliensis* and *T. bigamica* bees were rare or absent, and in the hot afternoon when bees of native species disappeared from the field.

Tetrapedia rugulosa bees were seen on the flowers only in September and after 12:00 h. They remained for a short time collecting nectar and pollen and quickly switched between flowers of the same plant. Bees of *Florilegus (Euflorilegus) atropus* collected pollen and nectar and of *F. (E.) festivus* collected only nectar.

It is noteworthy that large bees (7.4–19.6 mm) like *A. mellifera, T. rugulosa, F. (Euflorilegus) at-*

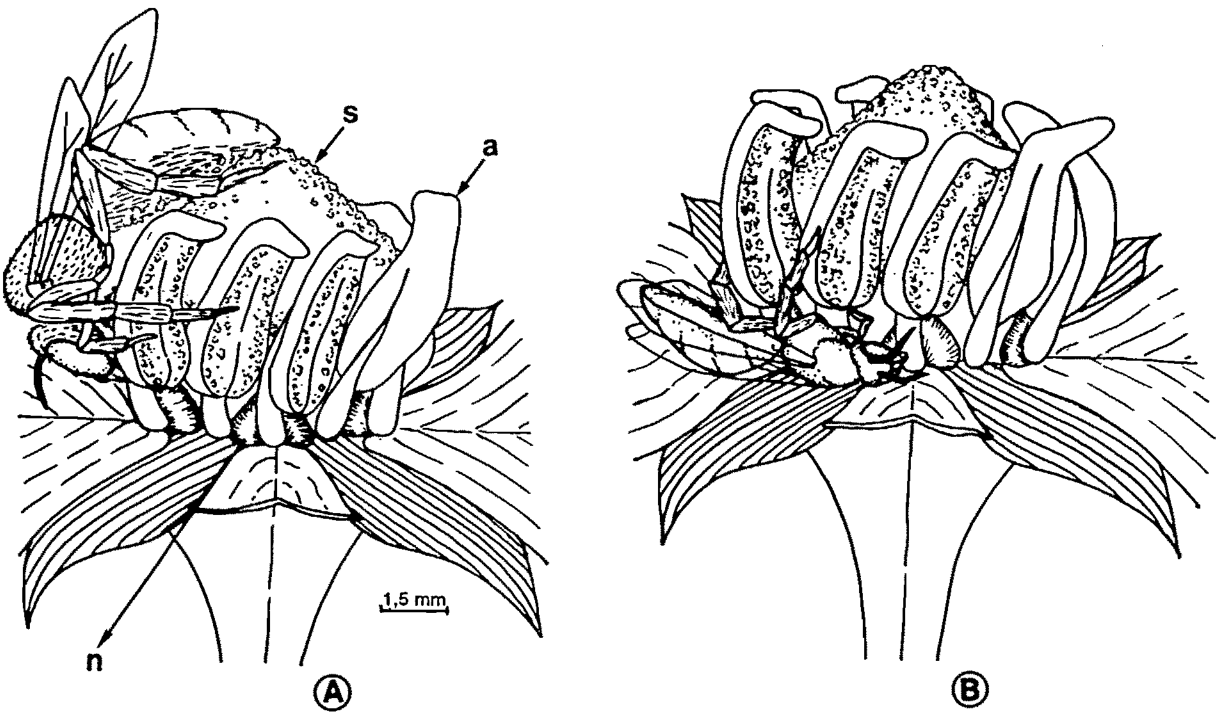

Fig. 4. Females of *Tetraglossula bigamica* (A) and *Pseudagapostemon brasiliensis* (B) collecting nectar from a flower of *Ludwigia elegans*. a = anther, s = stigma, n = nectary.

ropus, F. (Euflorilegus) festivus, Augochloropsis sp., *Megachile* sp. and *Melissoptila* sp. (Table 2) touched the stigma during nectar collection more frequently than small bees (3.8–7.2 mm) such as *Plebeia droryana, Chloralictus opacus, Augochlora* sp., *Augochlorella* sp. Therefore, large bees seem to be better pollinators of *L. elegans*.

DISCUSSION

Flowering of *L. elegans* is evidently controlled by the light/dark regime, since anthesis starts at dawn and was never observed during the night, and depends on ambient temperature, since flowers did not open below 19°C (Gimenes *et al* 1993). The latter condition may explain that at the study sites the plants have blossomed all the year long, because in Ribeirão Preto the mild winter may provide more appropriate flowering conditions than the summer when temperatures are relatively high.

Among the recorded visitors, *T. bigamica* bees are regarded efficient pollen and nectar collectors, and also the most important pollinators. In addition, the territorial ♂♂ safeguard food sources for conspecific ♀♀ which also guarantees pollination as the flowers are visited mainly by its most effective pollinator (Eickwort & Ginsberg 1980).

Both *T. bigamica* and *L. elegans* are distributed in southern Brazil and considered ancient species (Michener 1944, 1979; Eyde 1981), exhibiting primitive characters such as a short bilobate tongue which fits into the shallow *Ludwigia* nectaries, besides derived structures such as scopae adapted to handle pollen with viscin threads. Based on the flowers' characteristics, Eyde (1981) predicted a bee species with such properties to be associated with *Ludwigia* flowers. *P. brasiliensis* bees are too small to pollinate flowers of *L. elegans* but may be adapted to forage on the syntopic *L. octovalvis* (Gimenes *et al* 1993). The contribution of *T. rugulosa, F. atropus* and *F. festivus* bees in pollination of *L. elegans* has not been quantified, and the same is true for the Africanized honeybee workers. Anyhow, only bees of the size of *T. bigamica* or larger can effectively transfer pollen to the stigma of *L. elegans* flowers. Apparently there is a sufficient number of pollinating bees available whenever the plants are in blossom at the study sites near Ribeirão Preto.

Similar specialized interdependencies between native bees and flowering plants as a result of coevolution have been detected in several field studies recently carried out in tropical and subtropical regions of Brazil (Rego & Albuquerque 1989; Wittmann *et al* 1990; Gimenes 1991; Houston *et al* 1993; Hawkeswood 1993; Renner & Feil 1993; Aguiar & Martins 1994; Schlindwein & Wittmann 1995). The present study could verify such relations for the bee *Tetraglossula bigamica* and the plant *Ludwigia elegans*. Observations indicate other oligolectic relationships with congeneric plant species which should be analyzed in the future. Up to now only a rather limited knowledge has been accumulated on interorganismic linkages of neotropical angiosperms and their pollinators.

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