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## DIVERSITY OF FRUGIVOROUS FLIES (DIPTERA: TEPHRITIDAE AND LONCHAEIDAE) AND THEIR RELATIONSHIP WITH HOST PLANTS (ANGIOSPERMAE) IN ENVIRONMENTS OF SOUTH PANTANAL REGION, BRAZIL

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### ABSTRACT

Tephritidae and Lonchaeidae (Tephritoidea) are major pests of horticultural crops worldwide. Knowledge of the interactions between these flies and their host plants is needed for rational methods of population control. In the South Pantanal and adjacent areas in Brazil we sampled fruits from 92 plant species (22 orders and 36 families) in natural environments. Fifty-three species of plants were infested, and 39 not infested. Some aspects of the biology and patterns of species diversity, abundance, frequency, pupation period for males and conspecific females, and the interactions among species of frugivorous flies and their host plants were quantified. Twenty-six species of flies from 4 genera and 2 families were reared from the fruits: 17 species of Tephritidae (16 *Anastrepha* spp. and *Ceratitis capitata*), and 9 species of Lonchaeidae, comprising 8 species of *Neosilba* McAlpine, and 1 species of *Lonchaea* Fallén (Lonchaeidae). The lonchaeids infested 48 species of fruits, and the tephritids 30 species. The most polyphagous species were *Neosilba zadolicha* McAlpine & Steyskal (36 hosts), *Neosilba pendula* (Bezzi) (18 hosts), and *Neosilba inesperata* Strikis & Prado (14 hosts) (Lonchaeidae); and *Anastrepha sororcula* Zucchi (10 hosts), *Ceratitis capitata* (Wiedemann) (10 hosts), *Anastrepha obliqua* (Macquart) (7 hosts), and *Anastrepha zenilda* (6 hosts) (Tephritidae). All the males of Tephritidae (16 *Anastrepha* spp. and *C. capitata*) emerged before their conspecific females. Conversely, all females of the 8 species of *Neosilba* emerged in advance of their conspecific males.

Key Words: biodiversity, Cerrado, frugivory, fruit infestation, Neotropics, taxonomy

### RESUMEN

Tephritidae y Lonchaeidae (Tephritoidea) son las principales plagas de la horticultura en todo el mundo. El conocimiento de las interacciones entre estas moscas y sus plantas huéspedes es necesario para el uso de los métodos racionales de control de sus poblaciones. En el Pantanal Sur y zonas adyacentes en Brasil fueron tomadas muestras de frutos de 92 especies de plantas (22 órdenes y 36 familias) en ambientes naturales, y 26 especies frugívoras de Tephritoidea fueron creadas a partir de sus plantas hospederas (17 especies de Tephritidae y nueve especies de Lonchaeidae). Cincuenta y tres especies de plantas estaban infestadas y 39 no estaban infestadas. Fueron investigados algunos patrones biológicos y fue cuantificada la diversidad de especies, abundancia, frecuencia, período de pupación de machos y hembras de las especie, y las interacciones entre las especies de moscas y sus plantas hospederas. Veinte y seis especies de moscas de 4 géneros y 2 familias fueron criados de los frutos: diecisiete especies de Tephritidae (16 *Anastrepha* spp. y *Ceratitis capitata*), y nueve especies de Lonchaeidae, siendo 8 especies de *Neosilba* McAlpine y una de *Lonchaea* Fallén (Lonchaeidae). El lonqueidos colonizaron 48 especies de frutas, y los tefritídios colonizaron 30 especies. Las especies más polifaga fueron: *Neosilba zadolicha* McAlpine & Steyskal (36 hospederos), *Neosilba pendula* (Bezzi) (18 hospederos), y *Neosilba inesperata* Strikis & Prado (14 hospederos) (Lonchaeidae); *Anastrepha sororcula* Zucchi (10 hospederos), *Ceratitis capitata* (Wiedemann) (10 hospederos), y *Anastrepha obliqua* (Macquart) (7 hospederos) (Tephritidae). Los machos de Tephritidae emergieron de las pupas antes que las hembras (16 *Anastrepha* spp. y *C. capitata*). Mientras, todas las hembras de las 8 especies de *Neosilba* emergieron antes que sus machos co-específicos.

Translation provided by the authors.

The polyphagous and oligophagous species of Tephritidae (fruit flies) and Lonchaeidae (lance flies) (Tephritoidea) are the main pests of horticulture in the Neotropical Region. They are the cause of quarantine constraints imposed by many countries to curtail their entry, and they significantly influence commerce inside and outside of the countries producing fruits and vegetables around the world (Uchôa et al. 2002; Uchôa & Nicácio 2010). On the other hand, many stenophagous and monophagous tephritoid species are important as potential biological control agents for invading species of plants (Norrbom & McAlpine 1997), in the decomposition of fruits and cycling of nutrients in the food web, and as alternative hosts for the multiplication of parasitoids, which may reduce the populations of pest flies in orchards.

The Pantanal and Cerrado biomes host important components of Neotropical biodiversity, and the insects are among the taxa most poorly known in both environments (Myers et al. 2000; Junk et al. 2006). Frugivorous Tephritoidea (fruit flies and lance flies) are biodiverse in all Brazilian regions, but their interactions with their host plants are poorly studied, and surveys of the Cerrado and Pantanal biomes are scarce.

The determination of the host plant status for species of fruit flies on commercially important fruits is a controversial topic that frequently causes commercial disputes between countries around the world, and knowledge about the interactions among fruit flies and their host plants is missing for decades. One of the reasons for this delay is a methodological problem (Aluja & Mangan 2008). As pointed out by Aluja & Mangan (2008), first it is necessary to determine if a plant is a natural host, a conditional host (non-natural infestation that occurs when only one species of fruit is offered to a fruit fly species with no option of choice in laboratory conditions), or a non-host (when even in the laboratory under forced conditions the species of fruit fly does not oviposit in the only species of fruit offered as a resource). Some host plant records for fruit flies may be not trustworthy, because inappropriate methodology was applied to study fruit fly and plant interactions.

Aluja & Mangan (2008) classify the species of fruit flies into four types, according to their ability to colonize host plants: the species that infest fruits of different families/orders of plants are polyphagous; those that develop in fruits of the same family are oligophagous; species that infest fruits of a single genus of plants are stenophagous, and finally, monophagous species of fruit flies colonize fruits of only a single species of plant.

The most species rich genera of frugivorous Tephritoidea in Brazil are *Anastrepha* Schiner (Tephritidae) and *Neosilba* McAlpine (Lon-

chaeidae), with 251 (Uramoto et al. 2008; Norrbom & Korytkowski 2009; Canal 2010; Uramoto & Zucchi 2010; Norrbom & Korytkowski 2011; Norrbom & Uchôa 2011), and 17 described species (Strikis & Prado 2005, 2009; Strikis & Lerena 2009), respectively.

No host plant is known for 51 of the 112 species of *Anastrepha* reported from Brazil, (Zucchi 2008; Garcia et al. 2008; Uramoto & Zucchi 2010; Uchôa & Nicácio 2010; Norrbom & Uchôa 2011). In the genus *Anastrepha*, some species are of economic importance in the American tropics and subtropics (Calkins & Malavasi 1995) and about half of the species of *Neosilba* have been associated with fruits and vegetables in the Neotropics.

Knowledge of trophic interactions between frugivorous Tephritoidea and their host plants is important to support strategies for integrated management of fruit fly pests (polyphagous or oligophagous), and for the conservation of stenophagous and monophagous species in their natural environments.

The aims of this study were (1) identify the diversity, abundance and frequency of species of frugivorous Tephritidae and Lonchaeidae (Tephritoidea) in the Pantanal and surrounding areas, (2) study the occurrence and larval viability of the species of fruit flies and lance flies in different naturally infested host fruits in the Pantanal and adjacent areas, and (3) quantify the mean period of pupation (from the exit of larva from the host fruit until adult emergence) for both males and females of the different species of Tephritidae and Lonchaeidae.

## MATERIALS AND METHODS

### Characterization of Climate, Relief and Vegetation

The climate in the state of Mato Grosso do Sul is basically tropical and influenced by cold fronts during the winter (Jun-Sep), when the environment is drier and rainfall vary from 30-60 mm / month. Monthly mean temperature vary from 20-34°C, and the mean annual precipitation ranges from 1300 to 1700 mm. The altitude ranges from 100 to 1000 m above sea level, and vegetation types include savanna, seasonal semideciduous, deciduous, and sub-mountains. In the plateaus near the foothills there are dense shrub-herbacous strata (1.5-2.0 m high), an intermediate continuous arboreal strata forming a canopy about 10 m above the ground with some trees of 15-25 m (Radam Brasil 1982; Galati et al. 2006).

The biome Pantanal (16-20°S/55-58°W, an environment that resembles the Florida Everglades), is the largest periodically flooded plain in the world, with an area of approximately 160,000 km<sup>2</sup> (140,000 km<sup>2</sup> in Brazilian territory, 15,000 km<sup>2</sup> in Bolivia and 5000 km<sup>2</sup> in Paraguay). It is recognized by the United Nations Educational,

Scientific and Cultural Organization (UNESCO) as a natural heritage of mankind, biological reserve of the biosphere, and included among the most fragile and threatened biomes of the world (Junk et al. 2006). The Pantanal is connected with the Serra de Maracajú and Cerrado.

The Serra de Maracajú is a plateau that divides the state of Mato Grosso do Sul into 2 distinct biomes: the Cerrado and the Pantanal. To the east of the capital (Campo Grande), Cerrado environments predominate, with soil composed mainly of sandstones, and to the west of Campo Grande, the Pantanal begins (Radam Brasil 1982).

The Cerrado biome, an environment that resembles an African savanna, is located mainly in Central Brazil and occupies approximately 2 million km<sup>2</sup> (about 25% of the Brazilian territory). Vegetation varies, but is characterized by its great diversity and high rates of endemism (about 2% of global diversity of plants). Among 26 global biodiversity-hotspots listed for preservation of habitat, it is listed as the sixth most important (Myers et al. 2000; Carvalho et al. 2009).

The original vegetation of the Cerrado biome occupied 1,783,200 km<sup>2</sup>, but currently only 356,630 km<sup>2</sup> remain natural, which represent 20% of the original area. Of this, only 22,000 km<sup>2</sup> (6.2%) are located in protected areas, such as National Parks or private reserves. About 10,000 plant species are cataloged in the Cerrado, but for animals only 4 groups of vertebrates are well known (mammals, birds, reptiles and amphibians: 27,298 species). The diversity of invertebrates, totaling more than 95% of living species of animals and represented mainly by insects, is poorly documented (Myers et al. 2000).

#### Sampling of Plants

A total of 184 trips was made to sample the native fruits of South Pantanal, Cerrado and Serra de Maracajú. Fruits of 92 plant species from 22 orders and 36 families were evaluated for the occurrence of frugivorous tephritoid larvae.

The samples of fruits were taken during the seasons of fruit maturation for angiosperms in the South Pantanal Region (Pott & Pott 1994). Fruits were harvested directly from trees, or occasionally fruits recently fallen to the soil were collected, between Apr 1998 and Aug 2000, in 11 municipalities in the 3 different environments (Pantanal, Cerrado, and Sierra de Maracajú) of the state of Mato Grosso do Sul. The fruits of *Ximena americana* L. (Olacaceae) also were collected in Oct 2003 and Oct 2004 in the Pantanal.

#### Sampled Environments

Pantanal: Miranda (20°20'36"S/56°23'49"W, altitude 121 m); Aquidauana: Fazenda Aguapé

(20°6'18"S/55°58'11"W, 144 m), Fazenda Rio Negro (19°34'6"S/56°14'44"W, 107 m) and Aquidauana City - Lagoa dos Padres (20°28'46"S/55°48'35"W, 141 m); Corumbá: Passo do Lontra (19°35'32"S/57°32'34"W, 89 m) and Fazenda São Domingos (19°31'24"S/57°2'22"W, 90 m).

Cerrado: Aquidauana (20°28'36"S/55°47'15"W, altitude 151 m); Anastácio (20°29'1"S/55°49'48"W, 148 m) and Fazenda Nossa Senhora Aparecida (20°33'2"S/55°52'45"W, 173 m), Dois Irmãos do Buriti (20°40'47"S/55°17'46"W, 318 m), Terenos (20°27'2"S/55°5'3"W, 263 m), Campo Grande (20°26'34"S/54°38'47"W, 581 m); Nioaque (21°8'7"S/55°49'48"W, 213 m) and Rio Negro (19°26'58"S/54°59'13"W, 261 m).

Serra de Maracajú: Aquidauana - Fazenda Rio Doce: (20°21'52"S/55°36'35"W, altitude 478 m) and Morro do Paxixi (20°28'1"S/55°39'40"W, 192 m), Rochedo (19°57'11"S/54°53'33"W, 257 m), Miranda (20°20'36"S/56°23'49"W, 121 m) and Bodoquena (20°5'19"S/56°46'54"W, 130 m).

#### Collection of Larvae of Frugivorous Flies

Fruit samples were transported to the Laboratório de Controle Biológico de Insetos, Departamento de Biociências, Universidade Federal de Mato Grosso do Sul (UFMS), Campus de Aquidauana, where fruits were counted and weighed, then held to obtain associated insects according to methodology by Uchôa & Zucchi (1999). Photoperiod was 12h:12h (L:D). The temperature and relative humidity ranged from 15 to 40°C and from 40 to 90%.

Voucher specimens of plants were deposited in the Central Herbarium of the Universidade Federal de Mato Grosso do Sul (UFMS) in Campo Grande-MS, and in the Herbarium of the Departamento de Botânica, Universidade de São Paulo (USP) in São Paulo-SP, Brazil.

Exiting third instar tephritoids (L3) were counted and separated in transparent acrylic containers (300 mL) with sterile sand moistened with distilled water until adult emergence. Each container was labeled to identify the host fruit species and sample date, place, and municipality of collection, fly family, and date of L3 leaving the fruits. The larvae of Lonchaeidae and Tephritidae were differentiated by the shape of the posterior spiracles, body color, and morphology of the mandibles. The posterior spiracles of tephritid larvae (*Anastrepha* and *Ceratitis capitata* (Wiedemann)) are yellowish, inconspicuous, and lacking a sclerotized peritreme. The cephalopharyngeal region is shorter, compared to that of lonchaeids. The Lonchaeidae larvae have the posterior spiracles blackish, with a sclerotized peritreme, and more noticeable than those of tephritids, and the body of the lonchaeids is more filiform in shape, whitish, with the cephalopharyngeal region more elongated. Furthermore, the mouth hooks of the

Lonchaeidae larvae are darker and more visible than those of tephritids.

The adult flies after emergence, were kept alive for 2 or 3 d to allow full development of color patterns of the body and of the wings of each species. After that, they were killed by exposure to ethyl acetate, and preserved in vials with 70% ethanol.

#### Identification of Host Plants and Frugivorous Tephritoidea

The plants were identified by the botanists Ubirazilda Maria Rezende from the Herbarium of the Universidade Federal de Mato Grosso do Sul (UFMS) at Campo Grande-MS, and José Rubens Pirani from the Herbarium of the Departamento de Botânica, Universidade de São Paulo (USP), São Paulo, Brazil.

The species of *Anastrepha* and *C. capitata* were identified in the Laboratório de Insetos Frugívoros, Faculdade de Ciências Biológicas e Ambientais (FCBA), Universidade Federal da Grande Dourados (UFGD), by M. A. Uchôa using keys and species description (Lima 1934; Stone 1942; Foote 1980; Norrbom & Korytkowski 2009).

The species of *Neosilba* were identified mainly based on the morphology of the male genitalia (McAlpine & Steyskal 1982) by Pedro Carlos Strikis, UNICAMP, Campinas-SP, Brazil. Voucher specimens of Tephritidae are deposited in the Entomological Collection of the Museu da Biodiversidade (MuBio), FCBA-UFGD, Dourados-MS, Brazil, and voucher specimens of *Neosilba* (Lonchaeidae) are in the Zoological Collection of Universidade Estadual de Campinas-UNICAMP, Campinas-SP, Brazil.

#### Definition of Variables, Statistical Analysis and Methods

Statistical analysis was based on 5 qualitative variables: species, orders and families of plants, species and environments of emerged frugivorous flies. Five quantitative variables were evaluated: number of emerged flies, pupal period of the species of fly, number of third instar larvae (L3) / the number of fruit and number of L3 / the mass of fruit (g).

The fruit infestation levels were measured by 2 indexes: average number of third instars (= pre-pupal larva or L3) emerged / fruit, and average number of L3 / mass (g) of fruit. The first index was categorized into 3 intervals of classes: (1) low infestation (<0.1 larvae / fruit); (2) mean infestation (0.1 to 1.0 larvae / fruit); and (3) high infestation (>1.0 larvae / fruit).

The pupal period is defined as the time between the exit of the pre-pupal larva (L3) from the fruit until the emergence of the adult. Four class intervals were established for the average of

pupal period: 1 (6-10 d); 2 (10-14 d); 3 (14-18 d); and 4, over 18 d. The averages of pupal period were compared for 13 species of *Anastrepha*, *C. capitata* and 6 species of *Neosilba*. The statistical analysis included only those species that occurred in at least 3 fruit samples.

The viability of the pre-pupal larva (L3) was calculated by the equation: %V = No. of EA/L3) × 100, where: %V = Percent of viability), No. of EA = number of emerged adults, and L3 = Total number of pre-pupal larva; and the quotient was multiplied by 100.

The tests used were chi-square of Pearson ( $\chi^2$ ) to test the hypothesis of independence between 2 variables (Dawson & Trapp 2003), and the Kruskal-Wallis Test to compare each 2 variables (Pestana & Gageiro 2008).

We considered  $\alpha < 1\%$  (highly significant difference),  $1\% < \alpha < 5\%$  (significant difference), and  $5\% < \alpha < 10\%$  (marginally significant difference).

Analysis of variance (ANOVA) was used to compare means when assumptions of homogeneity occurred (Levene's Test), and normality (Kolmogorov-Smirnov Test) for dependent variables (Maroco 2007).

#### RESULTS

From the total of 92 species of fruits sampled, 53 were infested by tephritoid larvae, from which 40 species had not been surveyed previously for Tephritoidea infestation (Uchôa et al. 2002; Zucchi 2007; Uramoto et al. 2008; Garcia et al. 2008; Uchôa & Nicácio 2010) (Table 1). A total of 89,593 fruit were collected weighting 1,141.55 kg, from which 28,714 third-instars (L3) exited.

In all the species of host fruit (except from *Duguetia furfuraceae* Saint Hilaire) only pulp feeding frugivorous flies were obtained. The Tephritidae comprised 22,505 pre-pupal larva (L3) and 13,443 adults, and the Lonchaeidae: 6,209 larvae (L3) and 3,770 adults (Table 1).

Thirty-nine species of plants (Aristolochiaceae [Aristolochiales], Bromeliaceae [Bromeliales], Cactaceae [Cactales]; Curcubitaceae [Curcubitales], Erythroxylaceae [Gentianales], Bommabaceae and Malvaceae [Malvales], Smilacaceae [Liliflorae], Meliaceae [Rutales], Sapindaceae [Sapindales], and Verbenaceae [Verbenales] were not infested by the tephritoid larvae (Uchôa & Nicácio 2010).

In this series of samples, 26 species of Neotropical Tephritoidea (16 species of *Anastrepha*, *C. capitata*, Tephritidae, and 9 species of Lonchaeidae) were reared from their host fruits (Table 2).

Tephritidae. The tephritids infested 30 species of fruits in 17 families and 13 orders of Angiospermae. Seventeen species emerged (16 *Anastrepha* and *C. capitata*), and a single species emerged from 5 hosts. The highest species richness of Te-

TABLE 1. HOST PLANTS (ANGIOSPERMÆ) AND INFESTATION INDICES BY FRUGIVOROUS LARVAE OF FRUIT FLIES AND LANCE FLIES (DIPTERA: TEPHRITOIDEA) IN THE SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004).

Order	Families	Sampled Plants	Obtained Tephritoidea						
			Fruit Tree Species			Larvae			
			Infested Fruit Tree Species	Not Infested Tree Species	Total of Sampled fruits	Total Biomass of Fruits (Kg)	Number of 3rd Instars (L3)	Number of L3 Larvae	Number of Adults
22	36	53	39	89,533	1,141.55	28,714	22,505	13,443	6,209
									3,770

phritidae occurred in the mountainous environment, where 10 species were recovered (Table 2).

The most ubiquitous species was *Anastrepha sororcula* Zucchi, which occurred in all 3 environments, followed by *Anastrepha zenildae* Zucchi in mountainous and cerrado areas. At the other extreme, *Anastrepha undosa* Stone was characterized as a monophagous species restricted to the swamp environment of the Pantanal (Table 2).

The host fruits *Terminalia catappa* L., *Psidium kennedyanum* Morong and *Ximenia americana* L. had the highest abundance of larvae. The most frequent species were *A. sororcula*, *Anastrepha striata* Schiner, and *A. zenildae*, which occurred in 26, 16, and 15 samples of fruits, respectively (Table 2).

The highest infestation rates (L3/fruit) occurred in *Andira cuyabensis* Bentham, followed by *Terminalia catappa* and *Ximenia americana*, with 9.59, 9.26, and 4.75 larvae per fruit, respectively. However, taking into account the rate of infestation number of pre-pupal larva by fruit mass (L3/g of fruit), the highest rates occurred in *T. catappa* (0.4 L/g), followed by *Andira cuyabensis* (0.33 L3 /g), and *Psidium kennedyanum* (0.31 L3/g) (Table 2).

The percentage of viability for the third instar (L3) was highest in the hosts *Sorocea sprucei saxicola* (Baillon) J. F. Macbride (95.83%), *Licania tomentosa* (94.29%), and *Andira cuyabensis* (94.0%) (Table 2).

The more generalist species of Tephritidae were *A. sororcula*, *C. capitata*, *Anastrepha obliqua* (Macquart), and *A. zenildae*, which infested 10, 10, 7, and 6 hosts, respectively (Table 2).

Lonchaeidae. Nine lonchaeid species (8 *Neosilba* spp. and 1 *Lonchaea* sp.) occurred in fruit of 48 species of plants from 24 families and 15 orders. From 2 hosts (*Syagrus flexuosa* (Martius) Beccari, and *Eugenia pitanga* (O. Berg) Kiaerskou, larvae exited but no adults emerged. Only species of *Neosilba* were obtained from 21 species of plants, and the highest species richness of this genus occurred in the Cerrado environment (S = 8) (Table 3).

The highest rates of fruit infestation by the species of *Neosilba* occurred in the hosts *Duguetia furfuracea* Saint Hilaire (10.78 L3/fruit and 0.22 L3/g of fruit), *Annona crassiflora* Martius (4.97 L3/fruit and 0.01 L3/g of fruit), and *Citrus sinensis* (L.) Osbeck (1.36 L3/fruit and 0.01 L3/g of fruit) (Table 3).

The highest viability (% of adult emergence from L3 larvae) for the Lonchaeidae occurred in *Andira cuyabensis* Bentham (100%), *Physalis angulata* L. (99.55%), *Licania tomentosa* (96.30%), and *Alibertia edulis* (Richard) A. Richard (93.75%) (Table 3).

The most abundant, frequent, and ubiquitous species of Lonchaeidae were *Neosilba zadolicha* McAlpine & Steyskal, *Neosilba pendula* (Bezzi),

TABLE 2. TAXONS OF PLANTS (ANGIOSPERMÆ), AND PATTERNS OF RELATIONSHIP WITH SPECIES OF FRUIT FLIES (DIPTERA: TEPHRITIDAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). ENVIRONMENT LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL, AND ORIGIN OF THE SPECIES OF PLANTS: N = NATIVE, E = EXOTIC.

PLANT TAXA	HOST ENVIRONMENTS	Nº OF FRUITS	MASS OF FRUITS (g)	LARVAE (L3)	EMERGED ADULTS	ASSOCIATED PARASITOIDS	ANASTREPHA spp. ♀♂	A. DISTINCATA Greene 1934	A. FRATERCULUS (Wied. 1830)	A. HASTATULA Stone 1942	A. LEPTOZONA Hendel 1914	A. MACRURTA Hendel 1914	A. OBLIQUEA (Macquart 1835)	A. NR. PICHELI Lima 1934	A. RHEDDETA Stone 1942	A. SERPENTINA (Wied. 1830)	A. SORORCULA Zucchi 1979	A. STRITTA Schiner 1868	A. TURPITTAE Stone 1942	A. UNDOSA Stone 1942	A. ZENILDAE Zucchi 1979	A. ZERNYI Lima 1934	C. CAPITATA ♂	C. CAPITATA ♀	C. CAPITATA ♂♂	INFESTATION (MEAN NO. OF L3 / FRUITS)	% VL3	INDICES / RATES	
ARECALES																													
Arecaceae																													
<i>Syagrus flexuosa</i> (Martius)	P-n	620	4,200	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Becari</i>																													
<i>Allogopiera leucoxylon</i> (Drude) Kuntze	C-n	264	2,350	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
CELASTRALES																													
Hippocrateaceae																													
<i>Cheiloclinium cognatum</i> (Miers)	C-n	161	1,471.4	131	31	—	6	—	—	25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23.66		
<i>Salacia elliptica</i> (Martius) G. Don	S-n	374	16,792.5	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
EBENALES																													
Ebenaceae																													
<i>Diospyros hispida</i> A. de Candolle	S/c-n	593	18,565.4	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
ERICALES																													
Sapotaceae																													

TABLE 2. (CONTINUED) TAXONS OF PLANTS (ANGIOSPERMÆ), AND PATTERNS OF RELATIONSHIP WITH SPECIES OF FRUIT FLIES (DIPTERA: TEPHRITIDAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). ENVIRONMENT LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL, AND ORIGIN OF THE SPECIES OF PLANTS: N = NATIVE, E = EXOTIC.

PLANT TAXA	HOST ENVIRONMENTS	Nº of fruits	Mass of fruits (g)	SAMPLES	SPECIES OF FRUIT FLIES		INDICES / RATES	
					Larvae (L3)	Emerged Adults	Associated Parasitoids	% VL3
<i>Chrysophyllum</i> <i>gonocarpum</i> (Martius & Eichler) Engler	s-n	521	22,821.9	6	5	—	—	83.33
<i>Chrysophyllum</i> <i>saboiifolium</i> Rizzini	c-n	1,578	14,650	0	0	—	—	—
<i>Pouteria</i> <i>glomerata</i> (Miquel) Radlkofler	c-n	752	17,552	1,070	825	389	—	77.10
<i>Pouteria ramiflora</i> (Martius) Radlkofler	p-n	1,111	21,954	694	156	1	64	—
<i>Pouteria torta</i> (Martius) Radlkofler	c/s-n	1,600	34,593.5	616	185	15	90	—
Fabales							64	—
Fabaeeae							16	—
<i>Andira</i> <i>cuyabensis</i> Bentham	s/c-n	66	1,915	633	595	335	—	—
Flacourtiaceae							5	—
<i>Banara arguta</i> Briquet	s-n	880	1,100	10	5	1	—	—
<i>Casuarina</i> <i>syphilitris</i> Swartz	c-n	2,009	1,970	6	1	—	—	—

TABLE 2. (CONTINUED) TAXONS OF PLANTS (ANGIOSPERMÆ), AND PATTERNS OF RELATIONSHIP WITH SPECIES OF FRUIT FLIES (DIPTERA: TEPHRITIDAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). ENVIRONMENT LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL, AND ORIGIN OF THE SPECIES OF PLANTS: N = NATIVE, E = EXOTIC.

PLANT TAXA	HOST ENVIRONMENTS	Nº OF FRUITS	MASS OF FRUITS (g)	LARVAE (L3)	SAMPLES		SPECIES OF FRUIT FLIES			INDICES / RATES									
					EMERGED ADULTS	ASSOCIATED PARASITOIDS	A. albovittata spp. ♀♂	A. distincta Greene 1934	A. fraterculus (Wied. 1830)	A. obliqua (Macquart 1835)	A. picea Lima 1934	A. rheeediae Stone 1942	A. serpentifera (Wied. 1830)	A. sororcula Zuccchi 1979	A. undosa Stone 1942	A. zernyi Lima 1934	C. capitata ♂	C. capitata ♀	INFESTATION (MEAN NO. OF L3 / MASS IN g)
Mimosaceae <i>Inga laurina</i> (Swartz) Willdenow	c/p/s-n	1,042	15,192	49	21	1	3	—	—	—	—	—	—	—	—	—	—	—	42.86
Gentianales Apocynaceae <i>Hancornia speciosa</i> Gomez	c-n	395	8,769.5	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Loganiaceae <i>Strychnos pseudoquina</i> Saint-Hilaire	c/s-n	1,335	17,160	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rubiaceae <i>Alibertia edulis</i> (A. Richard) A. Richard <i>Genipa americana</i> L. <i>Tocoyena formosa</i> (Chamisso & Schlechtendal) K. Schumann	c/p-n	304	19,306.5	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	c/p-n	741	82,773	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	c/p-n	162	4,670	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 2. (CONTINUED) TAXONS OF PLANTS (ANGIOSPERMÆ), AND PATTERNS OF RELATIONSHIP WITH SPECIES OF FRUIT FLIES (DIPTERA: TEPHRITIDAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). ENVIRONMENT LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL, AND ORIGIN OF THE SPECIES OF PLANTS: N = NATIVE, E = EXOTIC.

PLANT TAXA	HOST ENVIRONMENTS	Nº OF FRUITS	MASS OF FRUITS (g)	LARVAE (L3)	EMERGED ADULTS	ASSOCIATED PARASITOIDS	ANASTREPHA spp. ♀♂	A. ALBELLIDES Blanckhardt 1961	A. DISTINCTA Greene 1934	A. FRATERCULUS (Wied. 1830)	A. HASTATA Stone 1942	A. LEPTOZONA Hendel 1914	A. MACRURA Hendel 1914	A. OBLIQUA (Macquart 1835)	A. PHEDIA Stone 1942	A. SERPENTINA (Wied. 1830)	A. STRIATA Schiner 1868	A. TURPINA Stone 1942	A. UNDOSA Stone 1942	A. ZENILDAE Zucchi 1979	A. ZERNYI Lima 1934	A. ZOROCULA Zucchi 1979	A. ZUMBAELENI Schiner 1868	C. CAPITATA ♂	C. CAPITATA ♀	C. ZUMBAELENI Schiner 1868	INFESTATION (MEAN NO. OF L3 / FRUITS)	INFESTATION (MEAN NO. OF L3 / MASS IN g)	SPECIES OF FRUIT FLIES			INDICES / RATES		
Geraniales																																		
Euphorbiaceae																																		
<i>Manihot</i> sp. Miller	c-n	396	6,350	12	11	—	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.03	0	91.67						
Gutiferales																																		
Clusiaceae																																		
<i>Rheedia brasiliensis</i> Planchon & Triana	p-n	460	1,311.5	174	49	3	33	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—						
Magnoliales																																		
Annonaceae																																		
<i>Annona crassiflora</i> Martius	s-n	29	24,413.4	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—						
Dipteridae																																		
<i>Duguetia furfuracea</i> (Saint-Hilaire) Bentham	c-n	184	9,049	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—						
Lauraceae																																		
<i>Persica americana</i> Miller	c-e Mex.	31	21,100	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—						
Myrtales																																		
Combretaceae																																		

TABLE 2. (CONTINUED) TAXONS OF PLANTS (ANGIOSPERMAE), AND PATTERNS OF RELATIONSHIP WITH SPECIES OF FRUIT FLIES (DIPTERA: TEPHRITIDAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). ENVIRONMENT LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL, AND ORIGIN OF THE SPECIES OF PLANTS: N = NATIVE, E = EXOTIC.

TABLE 2. (CONTINUED) TAXONS OF PLANTS (ANGIOSPERMÆ), AND PATTERNS OF RELATIONSHIP WITH SPECIES OF FRUIT FLIES (DIPTERA: TEPHRITIDAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). ENVIRONMENT LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL, AND ORIGIN OF THE SPECIES OF PLANTS: N = NATIVE, E = EXOTIC.

PLANT TAXA	HOST ENVIRONMENTS	Nº OF FRUITS	MASS OF FRUITS (g)	LARVAE (L3)	SAMPLES		SPECIES OF FRUIT FLIES		INDICES / RATES	
					EMERGED ADULTS	ASSOCIATED PARASITOIDS	C. capitata ♀	C. capitata ♂	INFESTATION (MEAN NO. OF L3 / FRUITS)	% VL3
<i>Licania tomentosa</i> (Benth.) Frisch	c-n	916	36,899.7	210	198	—	8	—	—	94.29
Rutales Malpighiaceae										
<i>Byrsinima orbigniana</i> A. Jussieu	c/p-n	5,192	8,887	3	1	—	—	—	—	33.33
Rutaceae										
<i>Citrus jambhiri</i> Lush	c/p/s-n	79	11,113	0	0	—	—	—	—	—
<i>Citrus sinensis</i> (L.) Osbeck	c/p-n	33	4,411	0	0	—	—	—	—	—
Santalales										
Oleaceae										
<i>Schoepfia</i> sp.	s-n	1,601	3,715	15	8	—	1	—	—	0.01
<i>Ximenia americana</i> L.	p-n	646	14,761	3,069	1,396	465	428	503	—	53.33
Sapindales										
Anacardiaceae										45.49

TABLE 2. (CONTINUED) TAXONS OF PLANTS (ANGIOSPERMÆ), AND PATTERNS OF RELATIONSHIP WITH SPECIES OF FRUIT FLIES (DIPTERA: TEPHRITIDAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). ENVIRONMENT LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL, AND ORIGIN OF THE SPECIES OF PLANTS: N = NATIVE, E = EXOTIC.

PLANT TAXA	HOST ENVIRONMENTS	NO. OF FRUITS	MASS OF FRUITS (g)	LARVAE (L3)	SAMPLES		SPECIES OF FRUIT FLIES		INDICES / RATES	
					EMERGED ADULTS	ASSOCIATED PARASITOIDS	C. capitata ♀	C. capitata ♂	INFESTATION (% L3)	INFESTATION (MEAN NO. OF L3 / FRUITS)
<i>Anacardium humile</i> Saint-Hilarie	c-n	715	21,335.8	70	40	—	25	—	—	—
<i>Anacardium othonianum</i> Rizzini	c-n	157	9,000	29	11	—	5	—	—	57.14
<i>Mangifera indica</i> L.	c-n	111	23,060	320	188	—	66	—	—	37.93
<i>Spondias dulcis</i> Parkison	c-e (Ind)	246	21,159	0	0	—	—	—	—	—
<i>Spondias lutea</i> L.	c/s-n	120	1,024	260	165	6	72	—	—	58.75
<i>Spondias purpurea</i> L.	p-n	468	6,880.8	12	10	—	7	—	—	—
Tubiflorae									—	—
Convolvulaceae									—	—
<i>Operculina aitata</i> (Hamilton)	c-n	1,073	3,661.5	0	0	—	—	—	—	—
Solanaceae									—	—
<i>Physalis angulata</i> L.	c-n	7,254	5,302.7	1	1	—	—	—	—	—
<i>Solanum sisymbriifolium</i> Lamark	c-n	616	693.7	0	0	—	—	—	—	100.00
Urticales									—	—

TABLE 2. (CONTINUED) TAXONS OF PLANTS (ANGIOSPERMÆ), AND PATTERNS OF RELATIONSHIP WITH SPECIES OF FRUIT FLIES (DIPTERA: TEPHRITIDAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). ENVIRONMENT LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL, AND ORIGIN OF THE SPECIES OF PLANTS: N = NATIVE, E = EXOTIC.

PLANT TAXA	HOST ENVIRONMENTS	Nº of fruits	Mass of fruits (g)	Larvae (L3)	Emerged Adults	Associated Parasitoids	SPECIES OF FRUIT FLIES		INDICES / RATES		
							INFESTATION (Mean No. of L3 / mass in g)	% VL3			
Moraceae											
<i>Ficus insipida</i>	s-n	3,111	13,400	0	0	—	—	—	—	—	—
Willdenow	c/p-n	173	4,096.3	0	0	—	—	—	—	—	—
<i>Sorocca sprucei</i>	c-n	102	10,149	0	0	—	—	—	—	—	—
<i>saxicola</i> (Baillou)	s/p-n	1,752	4,580	3	2	—	—	—	—	—	—
Macbride	p-n	53,538	669,441	22,505	13,443	—	—	—	—	—	—
Violales											
Passifloraceae											
<i>Passiflora coccinea</i> Aublet	c/p-n	760	3,425,503	3	6	25	64	1	207	4	15
<i>Passiflora edulis</i> Sims	c-n	73	4	1	4	2	6	1	10	2	3
"Pindaiava vermelha"	p-n	13	1	1	1	1	1	2	1	1	6
Totals											
Abundance by fruit flies species											
Frequency by fruit flies species											
Nº of plant genera infested											
Nº of plant family infested											
Nº of hosts colonized											

TABLE 3. TAXA OF PLANTS (ANGIOSPERMÆ) AND PATTERNS OF RELATIONSHIP WITH SPECIES OF LANCE FLIES (DIPTERA: LONCHIADAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL; ORIGIN OF PLANTS: N = NATIVE, E = EXOTIC.

SAMPLES	PLANT TAXA	FRUGIVOROUS LONCHAEIDAE				INDICES / RATES														
		% environments	No. of fruits	Biomass of fruits (g)	Larvae (L3)	Emerged Adults	Associated Parasitoids	Lonchaea sp. (Fallén)	Nesotilla bifida Strikis & Prado	N. certra (Walker)	N. glaberrima (Wied.)	N. inesperrata Strikis & Prado	N. pendula (Bezzii)	N. pradai Strikis & Larena	N. zaddoitha MacAlpine & Steyskal	Nesotilla morphotype MSP1	Mean No. of L3/fruits	Mean No. of L3/m g	%V13	
	Arecaceae																			
	<i>Syagrus flexuosa</i> (Martius) Beccari	p-n	620	4,200	9	0	—	0	—	—	—	—	—	—	—	0.01	0.00	0.00		
	<i>Allogoptera leucocalyx</i> (Drude) Kunze	c-n	264	2,350	5	2	—	—	—	—	—	—	—	—	2	0.02	0.00	40.00		
	Celatrales																			
	Hippocrateaceae																			
	<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	c-n	161	1,471	0	0	—	—	—	—	—	—	—	—	—	0.00	0.00	0.00		
	<i>Salacia elliptica</i> (Martius) G.Don	s-n	374	16,793	7	4	—	—	2	—	—	—	—	—	2	0.02	0.00	57.14		
	Ebenales																			
	Ebenaceae															20	—	0.13	0.00	46.25
	<i>Diospyros hispida</i> A. de Candolle	s/c-n	593	18,565	80	37	—	17	—	—	—	—	—	—	—	—	—	—	—	
	Ericales																			
	Sapotaceae																			
	<i>Chrysophyllum gonocarpum</i> (Martius)	s-n	521	22,822	0	0	—	—	—	—	—	—	—	—	—	—	0.00	0.00	0.00	
	<i>Chrysophyllum sololiférum</i> Rizzini & Eichler Engler	c-n	1,578	14,650	8	1	—	—	—	—	—	—	—	—	—	—	0.01	0.00	12.50	
	<i>Pouteria glomerata</i> (Miquel) Radlkofler	c-n	752	17,552	55	7	—	—	2	—	1	—	—	—	4	—	0.07	0.00	12.73	
	<i>Pouteria ramiflora</i> (Martius) Radlkofler	p-n	1,111	21,954	816	340	—	—	163	—	1	1	8	—	167	—	0.73	0.04	41.67	
	<i>Pouteria torta</i> (Martius) Radlkofler	c/s-n	1,600	34,594	589	366	—	195	3	19	2	26	121	121	0.37	0.02	62.14			
Fabales																				
	Fabaceae																			
	<i>Andira cyathensis</i> Bentham	s/c-n	66	1,915	12	12	—	—	5	—	—	—	6	—	1	—	0.18	0.01	100.00	

\*Host plant with 2 Figitidae, *Lopheucoila anastrephae*, parasitizing larvae of *Neosilba* spp.

TABLE 3. (CONTINUED) TAXA OF PLANTS (ANGIOSPERMAE), AND PATTERNS OF RELATIONSHIP WITH SPECIES OF LANCE FLIES (DIPTERA: LONCHAEIDAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL; ORIGIN OF PLANTS: N = NATIVE, E = EXOTIC.

PLANT TAXA	SAMPLES		FRUGIVOROUS LONCHAEIDAE										INDICES / RATES	
	Nº of fruits	Biomass of fruits (g)	Larvae (L3)					Emerged Adults					%VII3	
Flacourtiaceae														
<i>Banara arguta</i> Briquet	S-n	880	1,100	4	2	—	—	1	—	—	—	—	0.00	0.00
<i>Caseraria sylvestris</i> Swartz	c-n	2,009	1,970	9	1	—	—	1	—	—	—	—	0.00	0.00
Mimosaceae														
* <i>Inga laurina</i> (Swartz) Wildenow	c/p/s-n	1,042	15,192	127	80	2	—	38	—	—	—	—	0.12	0.01
Gentianales														
Apocynaceae														
<i>Hancornia speciosa</i> Gomes	c-n	395	8,770	5	2	—	—	—	—	—	—	2	—	0.01
Loganiaceae														
<i>Strychnos pseudoquina</i> Saint-Hilaire	c/s-n	1,335	17,160	27	14	—	—	6	—	—	—	2	—	0.02
Rubiaceae														
<i>Alibertia edulis</i> (A. Richard) A. Richard	c/p-n	304	19,307	32	30	—	—	19	—	—	—	5	—	—
<i>Genipa americana</i> L.	c/p-n	741	82,773	13	8	—	—	4	—	—	—	1	—	—
<i>Tecomania formosa</i> (Chamisso & Schechtendal) K. Schumann	c/p-n	162	4,670	9	6	—	—	2	—	—	—	—	—	—
Geraniales														
Euphorbiaceae														
Manihot sp.	c-n	396	6,350	0	0	—	—	—	—	—	—	—	—	0.00
Guttiferales														
Clusiaceae														
<i>Rheedia brasiliensis</i> Planchon & Triana	p-n	460	1,312	0	0	—	—	—	—	—	—	—	—	0.00

\*Host plant with 2 Figitidae, *Lophostoma anastrophae*, parasitizing larvae of *Neosilba* spp.

TABLE 3. (CONTINUED) TAXA OF PLANTS (ANGIOSPERMAE), AND PATTERNS OF RELATIONSHIP WITH SPECIES OF LANCE FLIES (DIPTERA: LONCHAEIDAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL; ORIGIN OF PLANTS: N = NATIVE, E = EXOTIC.

PLANT TAXA	SAMPLES		FRUGIVOROUS LONCHAEIDAE										INDICES / RATES	
	Nº of fruits	Biomass of fruits (g)	Larvae (L3)					Emerged Adults					%VII <sup>a</sup>	
Magnoliales														
Annonaceae														
<i>Annona crassiflora</i> Martius	S-n	29	24,413	144	93	—	—	48	—	1	—	—	44	—
<i>Duguetia furfuracea</i> (Saint-Hilaire) Bentham	c-n	184	9,049	1983	1100	—	—	584	—	1	41	1	473	—
Lauraceae														
<i>Persea americana</i> Miller	c-e Mex.	31	21,100	60	49	—	—	27	—	—	—	—	22	—
Myrtales														
Combretaceae														
<i>Buchenavia</i> sp.	c-n	300	1,722	4	1	—	—	—	—	27	1	11	—	1
<i>Terminalia catappa</i> L.	c/p-e Mal.	987	23,121	386	181	—	—	93	—	—	27	—	22	—
Melastomataceae														
<i>Mouriri elliptica</i> Martius	c-n	378	5,697	20	5	—	—	4	—	—	—	—	—	1
Myrtaceae														
<i>Syzygium cumini</i> (L.) Skeels	c-n	6,651	16,607	29	14	—	—	11	—	—	—	3	—	—
<i>Syzygium jambos</i> (L.) Alston	c/p-n	1,030	4,034	106	72	—	—	41	—	1	8	—	—	22
<i>Eugenia pitanga</i> O.Berg	p-n	105	72	1	0	—	—	0	—	—	—	—	—	—
<i>Psidium cattleianum</i> Sabine	c-n	524	12,745	24	13	—	—	4	—	—	—	2	6	—
<i>Psidium guajava</i> L.	c/s-n	399	17,673	61	49	—	—	22	—	—	—	1	17	1
<i>Psidium kennedyanum</i> Morong	c/s-n	2,694	11,822	4	3	—	—	2	—	—	—	—	—	1
Rosales														
Chrysobalaceae														
<i>Licania tomentosa</i> (Bentham) Fritsch	c-n	916	36,900	6	10	—	—	8	—	—	—	—	—	2
														0.01
														96.30

\*Host plant with 2 Figitidae, *Lophostoma anastrephae*, parasitizing larvae of *Neosilba* spp.

TABLE 3. (CONTINUED) TAXA OF PLANTS (ANGIOSPERMAE), AND PATTERNS OF RELATIONSHIP WITH SPECIES OF LANCE FLIES (DIPTERA: LONCHAEIDAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL; ORIGIN OF PLANTS: N = NATIVE, E = EXOTIC.

PLANT TAXA	SAMPLES		FRUGIVOROUS LONCHAEIDAE												INDICES / RATES	
			Mean No. of L3/in g						Mean No. of L3/in g						%VII <sup>a</sup>	
Rutales																
Malpighiaceae																
<i>Byrsinima orbignyana</i> A. Jussieu	c/p-n	5,192	8,887	8	3	—	—	2	—	—	—	—	—	—	0.00	0.00
Rutaceae																37.50
<i>Citrus jamburii</i> Lush	c/p-s-n	79	11,113	20	14	—	—	5	—	—	1	4	—	4	0.25	0.00
<i>Citrus sinensis</i> (L.) Osbeck	c/p-n	33	4,411	45	36	—	—	20	1	1	3	—	—	11	1.36	0.01
Santalales																70.00
Olaceae																80.00
<i>Schoepfia</i> sp.	s-n	1,601	3,715	57	42	—	—	29	—	—	9	—	—	8	0.04	0.02
<i>Ximenia americana</i> L.	p-n	646	14,761	91	27	—	1	11	—	—	—	—	—	—	0.14	0.01
Sapindales																29.67
Anacardiaceae																
<i>Anacardium humile</i> Staint-Hilaire	c-n	715	21,336	35	10	—	—	4	—	—	—	—	—	5	—	0.05
<i>Anacardium obovatum</i> Rizzini	c-n	157	9,000	6	2	—	—	—	—	—	—	—	—	—	—	28.57
<i>Mangifera indica</i> L.	c-n	111	23,060	42	33	—	—	16	—	—	—	—	—	2	—	0.04
<i>Spondias dulcis</i> Parkison	c-e (Ind)	246	21,159	9	1	—	—	1	—	—	—	—	—	—	17	0.38
<i>Spondias purpurea</i> L.	p-n	468	6,881	17	8	—	—	4	—	—	1	—	—	1	—	0.04
<i>Spondias lutea</i> L.	c-s-n	120	1,024	0	0	—	—	—	—	—	—	—	—	2	—	0.04
Tubiflorae																47.06
Convolvulaceae																0.00
<i>Opercularia alata</i> (Hamilton) Urban	c-n	1,073	3,662	23	21	—	—	15	—	—	3	—	—	1	—	0.02
Solanaceae																91.30
<i>Physalis angulata</i> L.	c-n	7,254	5,303	893	889	—	—	484	—	—	16	—	—	387	—	1.12
															1	0.17
															1	95.55

<sup>a</sup>Host plant with 2 Figitidae, *Lopheucoila anastrophae*, parasitizing larvae of *Neosilba* spp.

TABLE 3. (CONTINUED) TAXA OF PLANTS (ANGIOSPERMAE), AND PATTERNS OF RELATIONSHIP WITH SPECIES OF LANCE FLIES (DIPTERA: LONCHAEIDAE) IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004). LEGEND: C = CERRADO, S = SIERRA, P = PANTANAL; ORIGIN OF PLANTS: N = NATIVE, E = EXOTIC.

PLANT TAXA	SAMPLES		FRUGIVOROUS LONCHAEIDAE										INDICES / RATES						
	Nº of fruits	Biomass of fruits (g)	Larvae (L3)	Emerged Adults	Associated Parasitoids	<i>Loechaea</i> sp. (Fallen)	<i>Neosilba</i> spp. (♂)	<i>Neosilba bifida</i> Strikis & Prado	<i>N. glaberrima</i> (Wied.)	<i>N. pendula</i> (Bezz.)	<i>N. tenebrata</i> Strikis & Prado	<i>N. zadolicha</i> McAuliffe & Steyskal	<i>Neosilba</i> morphotype MSP1	Mean No. of L3/in g	% VL3				
<i>Solanum sisymbriifolium</i> Lamark	c-n	616	693.7	38	22	—	—	15	—	—	7	—	—	—	0.06	0.05	57.89		
Urticales																			
Moraceae																			
<i>Ficus insipida</i> Willdenow	s-n	3,111	13,400	127	91	—	—	56	—	5	18	—	1	—	—	0.04	0.01	71.65	
<i>Sorocea sprucei saxicola</i> (Baillon)	s/p-n	497	1,787.6	9	2	—	—	1	1	—	—	—	—	—	0.02	0.01	22.22		
Violales																			
Passifloraceae																			
<i>Passiflora coccinea</i> Aubler	c/p-n	173	4,096.3	80	63	—	—	30	—	—	—	—	—	—	33	—	0.46	0.02	78.75
<i>Passiflora edulis</i> Sims	c-n	102	10,149	65	1	—	—	—	—	—	—	—	—	—	1	—	0.64	0.01	15.4
Family not identified "Pindaiava vermelha"	p-n	1,752	4,580	9	5	—	—	—	—	—	—	5	—	—	—	—	0.01	0.00	55.56
Totals	—	53,538	669,443.6	6,209	3,770	—	—	—	—	—	—	—	—	—	—	—	—	—	
Abundance by Species	—	—	—	—	2	1	1,992	2	59	103	443	127	1	1,038	4	—	—	—	
Frequency by Species	85	—	—	—	1	1	85	2	12	16	20	30	1	62	2	—	—	—	
Nº of Infested Genera of Plants	—	—	—	—	1	1	13	1	6	6	8	7	1	13	2	—	—	—	
Nº of Infested Family of Plants	24	—	—	—	1	23	1	8	6	10	9	1	21	2	—	—	—	—	

\*Host plant with 2 Figitidae, *Lopheucoila anastrephae*, parasitizing larvae of *Neosilba* spp.

and the recently described *Neosilba inesperata* Strikis & Prado (2009), which colonized 36, 18, and 14 hosts, respectively (Tables 3).

The infestation rate for the total of larvae (L3) in the 92 species of plants was 78.38% by tephritids and 21.62% by lonchaeids (Table 4).

**Larval Viability and Duration of Pupal Period.** The relative viability of the larvae from both families of Tephritoidea was 59.73% for the tephritids, and 60.72% for the lonchaeids (Table 4). The pupal period (on average) for *Anastrepha* species, *C. capitata* (including male and female), and *Neosilba* species were 15.85 d, 10.62 d, and 12.21 d, respectively (Table 5). Among *Anastrepha* species, *A. hastata* Stone had the longest pupal period (21.92 d), and *A. zenildae* (mean 13.61 d) the shortest among all species of *Anastrepha*. The females of *C. capitata* emerged after 11.03 d. Among the lonchaeids, *N. inesperata* had the longest pupal period (13.43 d), and *Neosilba glaberrima* (Wiedemann) the shortest, emerging at 11.48 d (Table 6).

## DISCUSSION

From the 53 species of fruits infested by frugivorous larvae of Tephritoidea, 25 were attacked by Tephritidae plus Lonchaeidae, 23 only by *Neosilba* species (Lonchaeidae), and 5 only by Tephritidae species. The plant species infested by the highest diversity of Tephritoidea species were *Psidium guajava* (8 spp., 5 of Tephritidae and 3 of Lonchaeidae), *Terminalia catappa* (8 spp., 3 of Tephritidae and 5 of Lonchaeidae), and *Pouteria ramiflora* (Martius) Radlkofer (7 spp., 3 of Tephritidae and 4 of Lonchaeidae) (Table 2).

The species *Ceratitis capitata*, *A. sororcula*, *A. zenildae*, and *Anastrepha alveatoides* Blanchard were the most numerically abundant. The species with the widest host ranges were *A. sororcula*, *C. capitata*, and *A. zenildae*. *Ceratitis capitata* and *A. sororcula* both infested 10 species of host fruits. *Ceratitis capitata* was exclusive in Chrysophyllum

*gonocarpum* and *Hancornia speciosa*. *Anastrepha sororcula* was the only species reared from fruits of *Casearia sylvestris* Swartz, *Physalis angulata*, and *Byrsonima orbigniana* A. Jussieu, and *A. obliqua* infested 7 species of host fruits (Table 2).

The highest general infestation rates by larvae occurred in *T. catappa* (0.41 L3/g of fruit), *A. cuyabensis* (0.34 L3/g of fruit) and *P. kennedyanum* (0.31 L3/g of fruit). The viability for all the larvae (Tephritidae plus Lonchaeidae) was 59.95%. The host fruits with highest viability rates were *Physalis angulata* (99.55%), *Licania tomentosa* (96.30%), and *Andira cuyabensis* (94.11%) (Table 2).

The host fruits with the highest rates of infestation (L3/g) were *Terminalia catappa* (Combretaceae, Afrotropical), *A. cuyabensis* (Fabaceae, Neotropical), and *Psidium kennedyanum* (Myrtaceae, Neotropical) (Table 2). Uramoto et al. (2008) also found high levels of infestation by Tephritidae in native Myrtaceae from the Atlantic Forest in the state of Espírito Santo, Brazil. Fruits of Neotropical species of Myrtaceae are known to keep a high diversity of Tephritoidea in natural environments (Uchôa et al. 2002; Uramoto et al. 2008), probably, because their fruits are nutritionally adequate, and some species (e.g., *Psidium* spp.), produce fruit more than a season during the year.

**Tephritidae.** The host fruits with highest Tephritidae diversity were *Psidium guajava*, and *P. kennedyanum* (Myrtaceae, Neotropical), with 5 spp. each, and *L. tomentosa* (Chrysobalanaceae, Neotropical), infested by 3 species (Table 2).

The species of Tephritidae were more abundant than those of Lonchaeidae for both number of larvae and adults. However, the Lonchaeidae larvae were more frequently collected. While Tephritidae were obtained on 73 fruit sampling expeditions (Table 2), Lonchaeidae were collected on 85 of 184 sampling trips (Table 3).

TABLE 4. INFESTATION RATES BY LARVAE (L3) OF FRUGIVOROUS TEPHRITOIDEA (DIPTERA), VIABILITY (%), AND RELATIVE ABUNDANCE (%) IN HOST FRUITS FROM SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004)

Families of Frugivorous Tephritoidea	3rd Instars				Emergence	
	No. of L3	Relative Abundance of Infestation (%)	Not emerged adults from L3 (%)	Viability of L3 (%)	No. of adults	Relative Abundance of adults (%)
Lonchaeidae	6,209	21.62	2,439 (39.28)	60.72	3,770	21.90
Tephritidae	22,505	78.38	9,062 (40.26)	59.73	13,443	78.10
Total	28,714	100	11,501 (40.05)	59.95	17,213	100

Larvae of Lonchaeidae Collected × Number of Adults of Lonchaeidae Emerged: ( $\chi^2_{(1)} = 15.29$ ;  $P < 0.01$ ).

Larvae of Tephritidae Collected × Number of Adults of Tephritidae Emerged: ( $\chi^2_{(1)} = 10.00$ ;  $P < 0.01$ ).

Total of Larvae of Collected Tephritoidea × Number Total of Adults Tephritoidea Emerged: ( $\chi^2_{(1)} = 37.41$ ;  $P < 0.01$ ).

TABLE 5. PUPAL PERIODS FOR GENERA OF FRUGIVOROUS FLIES (DIPTERA: TEPRHITOIDEA) IN HOST FRUITS SAMPLED IN 3 ENVIRONMENTS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004).

Genera of Tephritoidea	Descriptive			Comparison of the Means	Mean Pupal Period of Genus
	Mean (days)	Standard Deviation	n		
<i>Anastrepha</i> ♀ ♀	16.02	3.04	106	a	15.85
<i>Anastrepha</i> ♂ ♂	15.69	2.92	65	a	
<i>Neosilba</i> ♂ ♂	12.23	2.30	146	b	12.21
<i>Neosilba</i> ♀ ♀	12.20	2.05	81	b	
<i>Ceratitis capitata</i> ♀ ♀	11.03	2.25	16	c	10.62
<i>Ceratitis capitata</i> ♂ ♂	10.21	2.06	19	c	

Kruskal-Wallis Test ( $\chi^2_{(2)} = 188.26$ ;  $P < 0.001$ ), Mann-Whitney's Test  $\alpha = 1\%$ ; ( $P < 0.01$ ).

Means followed by the same letter are not significantly different at 1% of probability.

Lonchaeidae. The host fruits with highest diversity of *Neosilba* species were *Pouteria torta* (Martius) Radlkofer (5 spp.) and *T. catappa* (5 spp.). The most abundant species of Lonchaeidae were *Neosilba zadolicha* Steyskal & McAlpine, and *N. pendula* (Table 3). Although in a old paper, the species of *Neosilba* McAlpine, as *Silba* (Lonchaeidae), were considered as secondary fruit infesters that use the oviposition wounds made by tephritids to gain access to fruit tissue (Souza et al. 1983), results in other papers are in disagree with this information (Malavasi & Morgante 1980; Norrbom & McAlpine 1997; Uchôa & Zucchi 1999; Uchôa et al. 2002; Strikis & Lerena 2009; Uchôa & Nicácio 2010). In fact, in this study a large numbers of fruit/lonchaeid combinations that have no associated tephritids suggest that that generalization can be reconsidered. Of course, *Neosilba* species have a less sclerotized aculeus in comparation to that of *Anastrepha* and *Ceratitis* species (tephritids), but further studies are needed to clarify if the females of *Neosilba* species are able to use muscular power to insert their eggs inside the fruit pulp or if the newly-hatched larvae are able to bore the fruit peel to reach and feed inside the fruits.

The species of *Neosilba* were characterized as polyphagous (*sensu* Aluja & Mangan 2008). *Neosilba zadolicha*, *N. pendula*, and *N. inesperata* were the species with the highest number of host plants (36, 18, and 14 species, respectively). These results show the potential of the species of *Neosilba* as pests of fruits and vegetables in the Neotropical Region (Uchôa et al. 2002; Strikis & Prado 2005; Strikis & Prado 2009; Strikis & Lerena 2009).

The highest rates of infestation by Lonchaeidae (L3/g) occurred in *Duguetia furfuracea* (Annonaceae, Neotropical), *Physalis angulata* (Pantropical), and *Solanum sisymbriifolium* Lamarck (Solanaceae, Neotropical), respectively. *D. furfuracea* was the only host fruit in which a seed-feeding species, a wasp, *Bephratelloides* sp. (Eurytomidae, Hymenoptera), was obtained. Spe-

cies of *Bephratelloides* are common pests on *Annona* seeds in the Neotropics (Peña & Bennet 1995).

The general pattern for Lonchaeidae was that the females of all *Neosilba* species emerged earlier than the conspecific males and on average, the pupal period was 12.21 d, differing significantly from the pupal period of Tephritidae species (Table 4).

Tephritidae versus Lonchaeidae. In this study, *Neosilba* species (Lonchaeidae) were the only tephritoids infesting species of Annonaceae, Arecaceae, Lauraceae, Loganiaceae, Rubiaceae, Rutaceae, and Passifloraceae. On the other hand, the tephritids were exclusive only in Clusiaceae and Euphorbiaceae. However, this does not mean that the former plant taxa could not be infested by tephritids nor that Clusiaceae and Euphorbiaceae are never adequate host fruits for lonchaeids either. For example, different *Neosilba* species have been reared from fruits or apical and axillary buds of *Manihot esculenta* Crantz (Euphorbiaceae), *C. capitata* and *A. turpiniæ* were reared from fruits of *Citrus sinensis* (Rutaceae) (Uchôa et al. 2002), and *A. fraterculus* was reared from fruits of *Rollinia laurifolia* Schlechtendal (Annonaceae) (Uramoto et al. 2008).

In previous studies, a total of 35 plant species were evaluated for frugivorous insects in areas of Cerrado near the Pantanal, and frugivorous Tephritoidea were found in fruits of 29 species from 16 families. In that study 16 species of *Anastrepha*, *C. capitata* (Tephritidae), and 3 species of Lonchaeidae were recovered from their host fruits (Uchôa et al. 2002). Herein, in addition to the species found by Uchôa et al. (2002), 9 different species of Tephritidae were associated with their host plants (*Anastrepha alveatoides*, *A. distincta* Greene, *A. hastata*, *A. leptozona* Hendel, *A. macrura* Hendel, *A. rheediae* Stone, *A. serpentina* (Wiedemann), *A. undosa*, and *A. zernyi* Lima), and new association was found between *C. capitata* and *Hancornia speciosa* (Apocynaceae).

TABLE 6. NUMBER OF HOST FRUIT SAMPLES (ANGIOSPERMÆ) FROM THE SOUTH PANTANAL REGION AND NEIGHBORHOOD, BRAZIL, NUMBER AND RELATIVE PERCENT OF REARED FLIES BY GENERA AND SPECIES (TEPHRITOIDEA: DIPTERA), THEIR PUPATION PERIOD (MEAN IN DAYS), STANDARD DEVIATION, AND COMPARISON OF MEANS (APR 1998 TO AUG 2000, OCT 2003, AND OCT 2004).

Species of frugivorous Flies	N° of samples	N° of individuals	Relative occurrence for Genera (%)	(%) Relative occurrence for species	Mean period of pupation (days)	Standard Deviation	Comparison of the means
<i>Anastrepha hastata</i>	4	25	0.74	0.31	21.92	0.59	A
<i>A. zemnyi</i>	8	7	0.21	0.09	20.90	4.43	A
<i>A. fraterculus</i>	16	6	0.18	0.07	20.38	1.97	A
<i>A. rheediae</i>	5	15	0.44	0.19	19.50	278	A b
<i>A. undosa</i>	4	436	12.83	5.40	17.40	2.73	b c
<i>A. striata</i>	19	167	4.92	2.07	16.83	2.52	b c d
<i>A. turpiniae</i>	18	16	0.47	0.20	16.10	2.25	c d E
<i>A. leptozona</i>	6	64	1.88	0.79	16.07	1.89	c d E
<i>A. obliqua</i>	25	207	6.09	2.56	15.69	1.64	c d E f
<i>A. adveatooides</i>	2	503	14.81	6.22	15.36	0.35	c d E f
<i>A. sororcula</i>	43	1,301	38.3	16.10	14.84	2.64	c d E f g
<i>A. serpentina</i>	12	97	2.86	1.20	13.95	0.93	d E f g H
<i>A. zenilidae</i>	22	553	16.28	6.84	13.61	1.44	E f g H
<i>Neosilba inexpectata</i>	50	443	24.99	5.48	13.43	3.39	E f g H
<i>Neosilba MSP1</i>	3	4	0.23	0.05	13.39	1.25	E f g H
<i>Neosilba certa</i>	32	59	3.33	0.73	12.74	1.89	f g H
<i>Neosilba zadolichia</i>	130	1,037	58.49	12.83	12.06	2.21	g H
<i>Neosilba pendula</i>	58	127	7.16	1.57	11.85	1.59	g H
<i>Neosilba glaberrima</i>	45	103	5.81	1.27	11.48	1.42	H
<i>Ceratitis capitata</i> ♀	37	2,911	100	36.02	11.03	2.25	H
Total	177	8,080	—	100	—	—	—

ANOVA = 1%; Duncan's Test ( $P < 0.05$ ); Means followed by the same letter are not significantly different.

*Anastrepha* was the most abundant Tephritoidea genus reared from naturally infested host fruits in this study. A similar pattern was found by Malavasi et al. (1980) in a survey including 55 fruit species sampled in several states of Brazil. Herein, *A. sororcula* and *A. zenildae* were the most frequent (percentage of individual of a fly species in relation to the total number of individuals of all fruit fly species) and abundant (relationship of the number of individuals of each species of fruit fly by each species of host fruits) *Anastrepha* species.

The species of *Neosilba* were more generalists. They attacked more hosts (48) than the Tephritidae (30). Similar results were obtained in a previous survey in the Cerrado of Mato Grosso do Sul, Brazil (Uchôa et al. 2002).

Larval viability was lower for tephritids (59.73%) than for lonchaeids (60.72%) (Table 4). In this study the larval viability of the tephritids was higher than that reported by Malavasi & Morgante (1980) (10%). This suggests that the methodology herein employed is adequate for obtaining frugivorous insects.

The higher viability of the pre-pupal larva of Lonchaeidae species is probably due to the lower parasitism rates in this taxon than in Tephritidae species (M. A. Uchôa et al., unpublished data). No adult emerged from 40.05% of the pre-pupal larvae of Tephritoidea. Despite of the lower viability (59.73%) of *Anastrepha* spp. and *Ceratitis capitata* larvae, their relative abundance in fruit infestation was higher (78.1%), in comparison with Lonchaeidae species (21.9%, Table 4).

The genera of Tephritoidea showed a highly significant difference in their pupation period. The species of *Anastrepha* had the longest pupation period, followed by *Neosilba* spp., and *C. capitata*, respectively. The males of all Tephritidae species (16 *Anastrepha* spp. and *C. capitata*) emerged before their conspecifics females. Although mating systems of the Lonchaeidae must be more ancient in relation to that of tephritids, because the lonchaeids are among the most primitive Tephritoidea, the opposite pattern was found in the species of *Neosilba*. All females emerged earlier than the conspecifics males, although the difference was not statistically significant (Table 5).

The average pupation period for the 20 species of frugivorous flies evaluated in this study showed significant differences among 3 groups of species: (*Anastrepha hastata* Stone to *Anastrepha fraterculus* (Wiedemann)), (*Anastrepha rheediae* Stone to *Anastrepha striata* Schiner), and (*Neosilba certa* (Walker) to *Ceratitis capitata*), ranging from 21.92 d for *A. hastata* to 11.03 d for *C. capitata* (Table 6). In this analysis, *Anastrepha macrura* Hendel (22 d) (1♀), *Anastrepha* n. sp. aff. *pickeli* Lima (18.33 d) (4♀), *Anastrepha distincta* Greene (13 d) (3♀), *Lonchaea* sp. (7.0 d) (1♀), and

*Neosilba pradoi* Strikis & Lerena (16.80 d) (1♂), were not included, because each of them occurred in fewer than 3 fruit samples.

Facholi-Bendassoli & Uchôa (2006) studied the reproductive behavior of *Anastrepha sororcula* and found a marked protandry: males reached sexual maturity at an average of 11.75 d after emergence, and females became sexually mature, on average, 19 d after emergence. There are no reports on the sexual maturation of *Neosilba* species, but as evidenced in this study, it is probable that the females of *Neosilba* reached sexual maturity earlier than the conspecific males, a case of protogyny. However, a more specific study is necessary to answer this question satisfactorily. The asynchronous development between males and females of these insects may play an important evolutionary role. If males and females of the same progeny (offspring) reach sexual maturity at different times in nature, the chance of inbred mating decreases, which increases the genetic variability of the species (Futuyma 1992).

The average for the pupal period (interval between L3 exiting from fruits and emergence of adults) showed significant differences between the evaluated genera: *Anastrepha* (15.85 d), *Ceratitis* (10.62 d, mean between ♂♂ and ♀♀) (Tephritidae), and *Neosilba* (12.21 d, mean between ♂♂ and ♀♀ (Table 5)). However, when this period was compared between the species of the 3 genera, there is no standard pattern for each genus, because there are strong variations among the congeneric species (Table 6). We do not know if this difference were influenced by the differences in ambient conditions from the sites of fruits collections.

On average, the duration of the pupal period showed highly significant differences between *C. capitata* and the *Anastrepha* species. *Ceratitis capitata* emerged after 10.62 d and the *Anastrepha* species after 15.85 d. The Tephritidae with the highest mean for pupal period were *Anastrepha hastata* Stone (21.92 d) and *Anastrepha zernyi* Lima (20.90 d). *Ceratitis capitata* (♀♀) and *A. zenildae* had the shortest pupal periods of 11.03 and 13.61 d, respectively (Table 6). The pupal period for *C. capitata* obtained in this study (10.62 d) is similar to that found by Papadopoulos et al. (2002), 10 d under laboratory conditions (25°C 2 and 65% 5 RH (relative humidity).

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