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NATIVE LARVAL PARASITOIDS (HYMENOPTERA) OF FRUGIVOROUS TEPHRITOIDEA (DIPTERA) IN SOUTH PANTANAL REGION, BRAZIL

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Abstract

The frugivorous larvae of Tephritidae and Lonchaeidae are key pests of fruit trees and vegetable crops in Brazil and in many other South American countries. Their most important natural enemies are parasitoids of the families Braconidae and Figitidae (Hymenoptera). The aim of this study was to evaluate the incidence of parasitoids in larvae of fruit flies (Tephritidae) and frugivorous Lonchaeidae that infest several species of native and exotic fruit trees in the South Pantanal Region, Mato Grosso do Sul, Brazil. Ninety-two species of fruits from 36 families and 22 orders were sampled. From 11 species of host fruits, we obtained 11,197 larvae of Tephritoidea, and in some samples there occurred Braconidae, Figitidae or Pteromalidae parasitoids. The Braconidae totaled 99.45%, represented by 3 species: *Doryctobracon areolatus* (Szépligeti) 92.45%, *Utetes anastrephae* (Viereck) 6.17%, and *Opius bellus* (Gahan) with 0.82%. The Figitidae were represented by *Lopheucoila anastrephae* (Rohwer) (0.28%), and Pteromalidae by *Spalangia endius* (Walker) (0.28%). *Lopheucoila anastrephae* emerged from puparia of *Neosilba* spp. (Lonchaeidae) infesting pods of *Inga laurina* (Swartz) Willdenow. *Doryctobracon areolatus* was associated with 2 species of *Anastrepha*: *A. rheediae* Stone in *Rheedia brasilensis* Planchon & Triana and *A. zenildae* Zucchi in *Sorocea sprucei saxicola* (Hassler) C. C. Berg. In *Ximenia americana* L. 14% of the larvae of *Anastrepha* spp. were parasitized and *D. areolatus* reached more than 96% of total parasitism in this host fruit. The braconids were specific to Tephritidae, and the Figitidae species collected in this work were associated only with larvae of *Neosilba* spp. (Lonchaeidae).

Key Words: Braconidae, fruit flies, Figitidae, frugivory, Lonchaeidae, tritrophic interactions

Resumen

Las larvas frugívoras de Tephritidae y Lonchaeidae son las principales plagas de frutas y vegetales en Brasil y en muchos países de América del Sur. Sus enemigos naturales más importantes son los parasitoides Braconidae y Figitidae. El objetivo de este estudio es evaluar la incidencia de los parasitoides (Hymenoptera) sobre larvas de Tephritidae (moscas de la fruta) y los Lonchaeidae frugívoros, en varias especies frutiferas nativas y exóticas en el Pantanal sur, Mato Grosso do Sul, Brasil. Noventa y dos especies de frutas de 36 familias y 22 órdenes fueron evaluadas. En once especies de frutos hospederos se obtuvieron 11.197 larvas de Tephritoidea y de algunas muestras de frutos emergieron parasitoides (Braconidae, Figitidae o Pteromalidae). Los Braconidae ascendieron a 99,45% y estuvieron representados por *Doryctobracon areolatus* (Szépligeti) 92,45%, *Utetes anastrephae* (Viereck) 6,17% y *Opius bellus* (Gahan) (0,82%). Figitidae fue representado por *Lopheucoila anastrephae* (Rohwer) (0,28%), y Pteromalidae por *Spalangia endius* (Walker) (0,28%). *L. anastrephae* emergio de puparios de especies de *Neosilba* (Lonchaeidae) que infestan las vainas de *Inga laurina* (Swartz) Willdenow. *D. areolatus* se asoció con dos especies de *Anastrepha*: *A. rheediae* Stone en frutos de *Rheedia brasilensis* Planchon & Triana y *A. zenildae* Zucchi en frutos de *Sorocea sprucei saxicola* (Hassler) CC Berg. En frutos de *Ximenia americana* L., el 14% de las larvas de *Anastrepha* spp. fueron parasitadas, y *D. areolatus* ascendió a 96% del parasitismo total en este hospedero. Los Braconidae fueron específicos de Tephritidae y el Figitidae, *Lopheucoila anastrephae*, emergió de puparios de *Neosilba* spp. (Lonchaeidae).

Translation provided by the authors.

Several fruit fly species of the genus *Anastrepha* Schiner and the introduced *Ceratitis capitata* (Wiedemann) (Tephritidae) are among the most important frugivorous insects in edible fruit trees and vegetable crops in the Neotropics (Norrbom 2010). In South America some species of lance flies (Lonchaeidae) of the genera *Neosilba* McAlpine and *Dasiops* Rondani are the major agricultural pests in fruits and vegetables (Uchôa et al. 2002; Strikis & Prado 2005; Souza-Filho et al. 2009). A number of *Neosilba* species are recorded in Brazil including 8 species reported from Mato Grosso do Sul (Uchôa & Nicácio 2010).

Control of fruit flies and lance flies in orchards is still done mainly through application of chemical pesticide sprays. Worldwide, however, the widespread use of chemical pesticides to protect agricultural products against insects and other arthropod pests is of increasing concern (Cancino et al. 2009), especially because of inevitable environmental pollution and potential human health effects.

Biological control of frugivorous larvae with parasitoids is a promising component of integrated pest management programs, because it is environmentally friendly and works in synergy with the sterile insect technique (SIT) (Wong et al. 1992). Braconidae is the most abundant and species rich parasitoid family of fruit flies in Neotropics. Species of this group also serve as bioindicators of the presence and absence of populations of their host insects, and they have been associated with areas with more open canopy in the vegetation, even in the Atlantic Forest (Azevedo et al. 2002; Cirelli & Penteado-Dias 2003).

Parasitism of the frugivorous larvae of tephritoids is quite variable in natural environments. The rate of parasitism is affected by factors, such as the host larvae of the tephritoid species, traits of host fruit species, and the environment. Frugivorous larvae attacking a relatively small fruit, with a thin pericarp and mesocarp, have higher probabilities of being parasitized by parasitoids, in comparison to larvae colonizing fruit with a thicker epicarp and mesocarp (Sivinski et al. 1997; Uchôa et al. 2003; Costa et al. 2009).

Hymenopteran parasitoids are important natural enemies of pestiferous tephritoid larvae throughout both the Neotropical and Nearctic Regions. These entomophagous insects help reduce naturally, sometimes substantially, populations of Tephritidae and Lonchaeidae pests in the field (Uchôa et al. 2003; Ovruski et al. 2009). Mass-rearing and augmented releases of braconid parasitoids have been considered an important component of area-wide management programs for some species of fruit flies, including widespread *Anastrepha* species (Marinho et al. 2009; Palenchar et al. 2009).

Tritrophic interactions among wild tephritoids, their host plants and associated parasitoids, has been a largely neglected field of study in some regions and could suggest possible applications for native parasitoid species of local pests (Cancino et al. 2009). The autotonous parasitoids are particularly interesting, because of interations over extensive periods of time with their hosts (Williamson 1996), they can be effective in lowering pest populations in orchards (Cancino et al. 2009), keeping tephritoid outbreaks in check without diminishing local biodiversity, as may occur with the use of exotic natural enemies (Williamson 1996; Uchôa et al. 2003).

The aims of this study are to (1) evaluate species richness of hymenopteran parasitoids in frugivorous larvae of different species of Tephritoidea in 3 different environments from Brazil (Cerrado, Pantanal, and Serra de Maracajú), (2) determine parasitoid numbers and rates of parasitism, (3) examine seasonal patterns of parasitoid abundance and frequency, and (4) compare pupation durations in the various parasitoid species, including within-species host effects.

MATERIALS AND METHODS

Fruits from 3 different environments were sampled: Pantanal, Cerrado, and Serra de Maracajú. The sample area include 9 municipalities from the East and West Regions of the Mato Grosso do Sul, Brazil: Campo Grande (20°26'34" N, 54°38'47" W, 581 m), Terenos (20°27'2"S / 55°5' 3"W, 263 m), Dois Irmãos do Buriti (20°40'47"N, 55°17'46" W, 318 m), Anastácio (20°29'1"S / 55°49' 48"W, 148 m), Aquidauana (20°28'36"N, 55°47' 15"W, 151 m), north of the city of Nioaque (21°8'7"N, 55°49'48"W, 213 m), Miranda [2 localities: Passo do Lontra (19°35'32"S / 57°03'34"W, 89 m) and Fazenda São Domingos (19°31'24"S / 57°2' 22"W, 90 m)], Bodoquena (20°5'19"N, 56º46'54"W, 130 m), and south of Rio Negro (19º26'58"S / 54°59'13" W, 261 m).

The biome Pantanal (16-20°S/55-58°W, an environment that resembles the Everglades in Florida), is the largest periodically flooded plain in the world, with an area of approximately 160,000 km^2 (140,000 km^2 in Brazilian territory, 15,000 km^2 in Bolivia, and 5000 km^2 in Paraguay). It is recognized by 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, begins the Pantanal (Radam Brasil 1982).

The Cerrado biome, an environment that looks like the African savanna, is located mainly in Central Brazil, with approximately 2 million km^2 (about 25% of Brazilian territory) with varying vegetation (similar to savanna formations, rain and riparian forests). It contains a great diversity of plants and animals, with high rates of endemism (about 2% of global diversity of plants). It is the sixth diversity hotspot of the planet, among 26 listed in order of priority for conservation of habitat (Myers et al. 2000; Carvalho et al. 2009).

Fruits were collected in the trees at irregular intervals, following maturation of each species in the region (Pott & Pott 1994) and then transported to the Laboratório de Controle Biológico de Insetos, Departamento de Biociências (DBC), Universidade Federal de Mato Grosso do Sul (UFMS), Aquidauana Campus, MS, Brazil. In the laboratory they were weighed, counted, and kept in plastic trays containing water as a collection medium for the third instars (L3) that leave the fruits to pupate (Uchôa & Zucchi 1999). The L3 were quantified and the larvae of each family (Tephritidae or Lonchaeidae) were separated, placed in transparent acrylic cups, and labeled with data of fruit species, fruit weight, data of collection, and locality. The cups contained about 5 cm^3 of sterile sand, moistened with sterile water (to avoid fungus or bacteria), and were monitored until insect emergence. All biological material (fruits, immature and adult insects) were kept in a room with light of about 100 Lux. The photoperiod was 12:12 h (L:D), controlled by a timer. Temperature and air humidity inside the laboratory were not controlled and varied according to ambient conditions (temperature ranged from about 15 to 40°C and air relative humidity from about 40 to 90%).

Two or 3 d after emergence, when adults had acquired the characteristic pattern of color for the species, they were killed and stored in vials with 70% ethanol for species identification.

Host fruits 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 Universidade de São Paulo (USP, São Paulo, Brazil) from dried parts of plants (branches, flowers, and fruits) collected in the environments. Vouchers of hosts were deposited in collections of the institutions mentioned above, and the vouchers of Braconidae parasitoids were deposited in the Entomological Collection of the Universidade de São Paulo, at Piracicaba; the Figitidae in EMBRAPA Hortaliças, Brasília-DF, Brazil and the Pteromalidae in the Collection of Arthropods of Instituto Biológico, Campinas, SP, Brazil.

In this inventory, the L3 of frugivorous Lonchaeidae and Tephritidae were kept separate in different containers until adult emergence (Uchôa et al. 2003). Thus, it was established that the larvae of Tephritidae were parasitized by braconids while that of lonchaeids were parasitized by figitids.

Braconid parasitoids were identified by Claudia Fidelis Marinho (Departamento de Entomologia, USP, Piracicaba, São Paulo, Brazil) and Jorge Anderson Guimarães (EMBRAPA Hortaliças, Brasília-D, Brazil), who also identified Figitidae. Pteromalidae were identified by Valmir Antônio Costa (Instituto Biológico, Campinas, SP, Brazil). Species of fruit flies were identified by Uchôa, M. A., based on keys and original descriptions (Lima 1934; Stone 1942; Foote 1980; Korytkowski 2004). Voucher specimens are in the Coleção Entomológica do Museu da Biodiversidade (MuBio)-UFGD, Dourados, MS, Brazil. The Lonchaeidae were identified by Pedro Carlos Strikis (Universidade Estadual de Campinas-UNICAMP, Campinas-SP), and voucher specimens are in the Coleção Entomológica of UNICAMP, Campinas, SP, Brazil.

Climatic data from the collection sites (temperature, relative humidity, and rainfall) were recorded from Apr 1998 to Aug 2000 for all host fruits, except *Ximenia americana* L., whose fruits were sampled in Oct of 2003 and 2004.

The analyses considered the effect of climate upon adult flies or hymenopteran parasitoids in the field, particularly, when they oviposited into hosts. In order to do so, oviposition-time stimates were by subtracting approximate developmental times (~40 d for fly development) from adult emergence times (Uchôa, M. A., unpublished). Climatic conditions were determined and gathered by backdating that number of days from the time fruit were collected in the field.

Altitude was classified into 3 ranges: (1) 100 to 200 m; (2) 201 to 300 m, and (3) above 300 m height. Relative humidity (RH) was divided into 3 ranges: (1) 55% to 65% RH, (2) 65.1% to 75% RH, and (3) above 75% of RH, and rainfall into (1) 0 to 50 mm, (2) 51 to 100 mm, and (3) above 100 mm of accumulated precipitation per month.

Fruits were considered small, medium, or large, according to their average weight. Small fruits had an average weight between 0.1 and 10 g, medium fruits weighed from 10.1 to 50 g, and large 51 g or more. These criteria were applied to ensure that each category was evenly represented in terms of fruit weight for all surveyed fruits.

Levels of infestation was categorized into 3 classes: (1) low infestation was considered below 0.1 larvae per fruit, (2) intermediate infestation between 0.2 to 1 larvae per fruit, and (3) high infestation when there was more than 1 larva per fruit.

Mean pupal period were calculated from the times elapsed between obtaining mature larvae (L3) from fruit samples, until emergence of adult flies or parasitoids. Four classes were established:

(1) 6 to 10 d, (2) 10.1 to 14 d, (3) 14.1 to 18 d, and (4) more than 18 d.

The total percentage of parasitism was calculated by the equation: TP = N° RP × 100 / N° L3; in which TP = total parasitism (%); N° PR = Total number of Recovered Parasitoids / N°. of L3 = Total Number of Prepuparial Larvae (L3) (Uchôa et al. 2003).

The phorid *Megaselia scalaris* (Loew) is considered as saprophagous; an invader of insect rearing in laboratories (Disney 2008), so it was not considered among the parasitoids in the calculations in this study.

Data used in the different statistical analysis are listed (Table 1; Kruskal-Wallis's Test or Mann-Whitney's Test). The chi-square test was used to verify the dependence between the variables, and all samples were analyzed according to Maroco (2007). Calculations by the chi-square method were standardized to the level of significance ($P < 0.01$) ** ($0.01 < P < 0.05$), and * ($0.05 < P < 0.1$); T test ($\alpha = 0.05$); (1.76); Gl (28). Shannon index (*H'*) was used for analysis of species diversity.

To test the relationship between the species of parasitoid and the host plants of frugivorous larvae were used the randomization method suggested by Blüthgen et al. (2000). This method involves comparing real matrices of occurrence's frequency of the species observed in nature, with arrays generated at random. In these matrices the rows represent the parasitoid species, and columns represent the species of plants.

The species-specific association between fruit flies and parasitoids was established when only 1 species of fruit fly or parasitoid species emerged from a particular host (Wharton & Gilstrap 1983; Canal & Zucchi 2000).

Results

Five species of parasitoids were recovered from 11 of the 53 species of plants that were infested by frugivorous larvae of Tephritidae and Lonchaeidae, among the 92 sampled species (Uchôa, M. A. & Nicácio, J. N., unpublished). Three families of parasitoids were recovered: Braconidae (Opiinae), Figitidae (Eucoilinae) and Pteromalidae (Spalangiinae). All the parasitoids herein were koinobiont species (*sensu* Hoffmeister 1992), because females laid their eggs into the larvae of Tephritoidea, and even *Spalangia endius* (Walker) and the parasitoids emerged from their host pupae as adults (Table 1).

The opiines attacked larvae of species of *Anastrepha* and/or *Ceratitis capitata* (Tephritidae). *Lopheucoila anastrephae* (Rohwer) (Figitidae: Eucoilinae) parasitized larvae of *Neosilba* species (Lonchaeidae) infesting pods of *Inga laurina* (Swartz), and *Spalangia endius* (Walker) (Pteromalidae) were obtained from containers with L3 of Tephritidae from samples of *Ximenia americana* L. fruits (Santalales: Olacaceae) (Table 1).

The braconids *D. areolatus* and *Utetes anastrephae* (Viereck) occurred in all 3 environments, but were more abundant and frequent in the Pantanal, but *Opius bellus* (Gahan) emerged only from tephritids feeding in the fruits of *Ximenia americana* from Pantanal. *Lopheucoila anastrepha* occurred in the Serra de Maracajú and *Spalangia endius* only in the Pantanal (Table 1).

The phorid *Megaselia scalaris* was also found in some containers (more than 500 adults) in samples of *Ximenia americana*, *Psidium kennedyanum* and *Pouteria torta* fruits.

Doryctobracon areolatus emerged from 7.23% of the collected larvae. The rates of parasitism for the other 2 groups of parasitoids together (Eucoilinae and Spalangiinae) totaled only 0.56% (Fig. 2). The highest frequencies and rates of parasitism occurred in the Pantanal, followed by the Cerrado (Table 2).

The highest rates of parasitism were inflicted by the opiine on larvae of tephritids feeding in fruits of *Ximenia americana*, *Sorocea sprucei saxicola* (Hassler) C. C. Berg (Urticales: Moraceae), *Psidium kennedyanum* Morong (Myrtales: Myrtaceae), and *Mouriri elliptica* Martius (Myrtales: Melastomataceae), 14.00%, 11.11%, 6.01% and 4.38%, respectively (Table 3).

Parasitoids were recovered only from larvae feeding in fruits of native species ($\chi^2 = 66.73$, Gl (1), $P < 0.01$), and each parasitoid families were specific to a particular tephritoid family, so Braconidae was obtained only from Tephritidae, and Figitidae only from Lonchaeidae (Table 4). The opiines *Doryctobracon areolatus* emerged from larvae of *A. rheediae*, *A. leptozona*, *A. serpentina*, *A. zenildae*, and *C. capitata*, and *Utetes anestrephae* from *A. obliqua*, *A. sororcula*, *A. striata*, *A. turpiniae*, *A. zenildae*, and *C. capitata*. They were correlated with the presence of Tephritidae larvae [$\chi^2 = 19.62$, Gl (8), $p < 0.012$], with frequencies of 69.0% and 20.7%, respectively. In the environments *D. areolatus* presented strong relationship of dependence with the occurrence of species of *Anastrepha* and *C. capitata* (Table 4).

The occurrence of the opiine species was correlated with altitude ($\chi^2 = 15.025$, Gl (8), $P < 0.059$). Higher frequency of *D. areolatus* (69%) occurred in altitudes up to 200 m. On the other hand, *Utetes anastrephae* was more abundantly obtained (85.7%) in higher elevations (201 to 300 m), and 84.6% of opiines abundance occurred in altitudes up to 200 m ($\chi^2 = 11.41$, Gl (4), $P < 0.022$). The longest pupal period observed (from L3 off the host fruit until the emergence of parasitoid) was correlated with intermediate altitude (from 201 m up 300 m) ($\chi^2 = 13.43$, Gl (4), $P < 0.009$) (Table 5).

TABLE 1. NATIVE LARVAL PARASITOIDS (HYMENOPTERA) OF FRUGIVOROUS TEPHRITOIDS (DIPTERA) IN FRUITS FROM 3 ECOSYSTEMS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, APR 2003, AND APR 2004).

Species of Host Plants and Environments					Species of Frugivorous Tephritoidea and their Parasitoids	
Species	Sampling Period	Ecosystem	Altitude (m)	Locality	Species and ( ) Number of Adults	Species and ( ) Number of Adults
Anacardiaceae (Sapindales)						
Spondias lutea L.	Feb 2000	Pantanal	125	Pousada Aguapé, Aquidauana	*Anastrepha obliqua* (82) *A. striata* Schiner (5)	*Utetes anastrephae* (Viereck,1913) (6)
Clusiaceae (Guttiferales)						
Rheedia brasilensis Planchon & Triana	Feb 2000	Pantanal	125	Fazenda Baiazinha, Aquidauana	*A. rheediae* (46)	*Doryctobracon areolatus* (Szépligeti,1911) (3)
Fabaceae (Fabales)						
Andira cuyabensis Bentham	Dec 1999	Sierra	192	Morro do Paxixi, Aquidauana	*A. turpiniae* Stone (5) *A. zenildae* (24)	*U. anastrephae* (1)
Mimosaceae (Fabales)						
Inga laurina (Swartz) Willdenow	Mar 1999	Sierra	196	Distrito de Piraputanga (Aquidauana)	*N. pendula (Bezzi)* (11) *N. zadolicha* McAlpine & Steyskal (7) *N. pradoi* (1) *N. inesperata* Strikis & Prado (21)	*Lopheucoila anastrephae* (Rohwer 1919) (2)
Melastomataceae (Myrtales)						
Mouriri elliptica Martius	Dec 1998 Jan 1999	Cerrado	220	Chácara Estrela (Aquidauana)	*A. zenildae* (163) *Ceratitis capitata* (1)	*D. areolatus* (41)
Myrtaceae						
Psidium guajava L.	Jan 1999	Cerrado	163	Aquidauana	*Ceratitis capitata* (114) *A. obliqua* (4) *A. sororcula* (26) *A. striata* (2) *A. turpiniae* (2)	*U. anastrephae* (1)
Psidium kennedyanum Morong	Jun 1998 Apr 1999 May 1999 Jun 1999	Pantanal	151	Fazenda Baiazinha, Aquidauana	*A. fraterculus* (5) *A. obliqua* (2) *A. sororcula* (1,023) *A. striata* (151) *A. turpiniae* (1)	*D. areolatus* (191) *U. anastrephae* (29)

TABLE 1. (CONTINUED) NATIVE LARVAL PARASITOIDS (HYMENOPTERA) OF FRUGIVOROUS TEPHRITOIDS (DIPTERA) IN FRUITS FROM 3 ECOSYSTEMS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, APR 2003, AND APR 2004).

Species of Host Plants and Environments					Species of Frugivorous Tephritoidea and their Parasitoids	
Species	Sampling Period	Ecosystem	Altitude (m)	Locality	Species and ( ) Number of Adults	Species and ( ) Number of Adults
Moraceae (Urticales)						
Sorocea sprucei saxicola (Hassler) C. C. Berg	Oct 1998 Nov 1998	Sierra	222	Morro do Paxixi, Aquidauana	*A. zenildae* (29)	*D. areolatus* (8)
Olacaceae (Santalales)						
Ximenia americana L.	Oct 2003 Oct 2004	Pantanal	89	Passo do Lontra, Corumbá	*A. alveatoides* Blanchard (503)	*D. areolatus* (415) *U. anastrephae* (8) *Opius bellus* Gahan 1930 (6) *Spalangia endius* (Walker 1839) (2) (Pteromalidae)
Sapotaceae (Ebenales)						
Pouteria ramiflora (Martius) Radlkofer	Jan 2000	Sierra	195	Morro do Paxixi, Fazenda Santa Bárbara, Aquidauana	*A. leptozona* Hendel (81) *A. serpentina* (32)	*D. areolatus* (1)
Pouteria torta (Martius) Radlkofer	Oct 1998 Feb 1999 Nov1999	Sierra	317	Morro do Paxixi, Fazenda Santa Bárbara, Aquidauana	*A. leptozona* (64) *A. serpentina* (16)	*D. areolatus* (15)
Total: 11spp.	30 months	3	—	—	Tephritidae.= 11 spp. (2,385 adults) Lonchaeidae = 4 spp. (208 adults)	5 species (729 adults)

TABLE 2. NATIVE LARVAL PARASITOIDS (HYMENOPTERA) OF FRUGIVOROUS TEPHRITOIDS (DIPTERA), AND THEIR DATA OF BIOECOLOGY IN FRUITS FROM SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, APR 2003, AND APR 2004).

	Cerrado		Pantanal		Sierra		Total					Rate of Combined Parasitoidism	
Parasitoids	[1]N°	Host Plants	[1]N°	Host Plants	[1]N°	Host Plants	[1]N°	Host Plants	Pupal Period (days)	Relative Frequency of Parasitoidism (%)	N° of Larvae	Mortality (%)	General by Species
Doryctobracon areolatus	41	*Mouriri elliptica*	610	*Psidium kennedyanum, Rheedia brasilensis, Ximenia americana*	21	*Sorocea sprucei saxicola, Pouteria torta, Pouteria ramiflora*	685	7	15.4^{a}	93.97	6,205	7.23	6.02
Utetes anastrephae	1	*Psidium guajava*	45	*Psidium kennedyanum, Spondia lutea, Ximenia americana*	1	*Andira cuyabensis*	34	5	13.16^{b}	4.66	1,667	2.70	0.40
Opius bellus	—	—	6	*Ximenia americana*	—	—	6	1	15.0^{ns}	0.82	3,150	0.19	0.05
[2]*Lopheucoila anastrephae*	—	—	—	—	2	*Inga laurina*	2	1	31.5^{ns}	0.27	175	0.14	0.018
Spalangia endius	—	—	2	*Ximenia americana*	—	—	2	1	23.0^{ns}	0.27	—	0.06	0.018
Total	42	2	663	4	24	5	729	11	19.61	100	11,197	6.51	—

Anova $F_{?}$[(0.01) (1; 28) = 7.66]; Average Comparison Test.
NS = Not significant; a and b significantly different;
[1]N = Number of Parasitoids obtained;
[2]Parasitoids upon Larvae of Lonchaeidae.

TABLE 3. TRITROPHIC INTERACTIONS AMONG HOST FRUIT SPECIES, FRUGIVOROUS TEPHRITOIDEA (DIPTERA) AND THEIR NATIVE LARVAL PARASITOIDS (HYMENOPTERA) IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, APR 2003, AND APR 2004).

	Taxons of Frugivorous Larvae and N° of Adults				Species of Parasitoids						
Species of Plants	Larvae of Tephritidae	N° of Adults Tephritidae	Larvae of Lonchaeidae	N° Adults Lonchaeidae	*Doryctobracon areolatus*	*Opius bellus*	*Utetes anastrephae*	*Lopheucoila anastrephae*	*Spalangia endius*	N° of Parasitoids / Species of Plants	% Parasitoidism by Host Plant Species
Anacardiaceae											
Spondias lutea	[1]260	87	0	0	0	0	6	0	0	6	2.31
Clusiaceae											
Rheedia brasilensis	[1]174	46	0	0	3	0	0	0	0	3	1.72
Fabaceae											
Andira cuyabensis	[1]633	29	12	1	0	0	1	0	0	1	0.16
Melastomataceae											
Mouriri elliptica	[1]936	164	20	2	41	0	0	0	0	41	4.38
Mimosaceae											
Inga laurina	28	4	[1]174	40	0	0	0	2	0	2	1.15
Moraceae											
Sorocea sprucei saxicola	[1]72	29	9	1	8	0	0	0	0	8	11.11
Myrtaceae											
Psidium guajava	[1]774	148	61	15	0	0	1	0	0	1	0.13
Psidium kennedyanum	[1]3,659	1,182	0	0	191	0	29	0	0	220	6.01
Olacaceae											
Ximenia americana	[1]3,079	503	71	16	415	6	8	0	2	431	14.00
Sapotaceae											
Pouteria ramiflora	[1]448	113	287	4	1	0	0	0	0	1	0.22
Pouteria torta	[1]754	80	579	129	15	0	0	0	0	15	1.99
Total	10,817	2,385	1,572	208	674	6	45	2	2	729	
[2]F PSHP	85.47		14.53		92.45	0.82	6.17	0.28	0.28		

[1]Samples of larvae with occurrence of parasitoids.
[2]F PSHP = Frequency of parasitoid species in each host plant.

The parasitism rates were higher during the spring (Sep-Nov), followed by the autumn (Mar-May) (Fig. 1) with D. *areolatus* as the predominant species (Fig. 2). The rates of parasitism were highest in species of plants with small fruits, such as *Spondias lutea* and *Psidium kennedyanum* (Table 1). The cumulative curves of the sampling effort revealed little difference between the number of species sampled and the estimated number of species (Fig. 3). *Utetes anastrephae* was more abundant during the autumn (Fig. 4).

DISCUSSION

In this work fruits of *Ximenia americana* and *Psidium kennedyanum* had the highest abundance and species richness of parasitoids. Probably the small size of host fruits and the ovipositor length of the parasitoid species were responsable for this pattern, as pointed out by Sivinski et al. (1997, 2001). Only *Doryctobracon areolatus* was associated with 2 species of *Anastrepha*: *A. rheediae* in *Rheedia brasiliensis* Planchon & Triana (Clusiaceae: Guttiferales), and *A. zenildae* in *Sorocea sprucei saxicola* (Table 1).

TABLE 4. FACTORS INFLUENCING PARASITISM OF FRUGIVOROUS TEPHRITOIDEA (DIPTERA), BY HYMENOPTERAN PARASITOIDS IN THE SOUTH PANTANAL REGION OF BRAZIL (APR 1998 TO AUG 2000, APR 2003, AND APR 2004).

Variables subjected to Chi-square Pearson's Test	χ^2	*n*	$P(x > \chi^2) = \alpha$
Environment versus *Doryctobracon areolatus*	55.92	5	0.00[1]
Environment versus *Utetes anastrephae*	15.54	10	0.11[Ns]
Environment versus *Opius bellus*	86.99	2	0.00[1]
Environment versus *Lopheocoila anastrephae*	4.04	2	0.13[Ns]
Environment versus *Spalangia endius* (Pteromalidae)	3.62	2	0.16[Ns]
Species of Parasitoids versus Native and exotic plants	66.73	1	0.00[2]
Species of Parasitoids versus Urban and Rural Areas	0.87	3	0.83[Ns]
Species of Parasitoid versus Flies Family	19.62	8	0.01[1]
Species of Parasitoid versus Genera of Flies	15.68	6	0.02[2]
Species of Parasitoids versus Altitude	15.02	8	0.06[3]
Families of Parasitoids versus Altitude	11.41	4	0.02[2]
Environments versus Mean Pupal Period of Parasitoids	13.43	4	0.00[1]

[1]Highly significant ($P < 0.01$).
[2]Significant ($0.01 < P < 0.05$).
[3]Marginally significant ($0.05 < P < 0.10$).

The Opiinae (Braconidae) were the most abundant and frequent hymenopterans, and accounted for 6.60% mortality of tephritids in the 11 species fruit trees. This taxa of parasitism is certainly unreal, because the fruits picked up from the field possibly had some fruit fly eggs, and larvae of first and second instar. So, when these immature tephritoids left the field and come to the laboratory, they have no more chance to be parasitized (Van Driesche 1983).

Doryctobracon areolatus, *Utetes anastrephae*, and *Opius bellus* totaled 99.45% of parasitism, but *O. bellus* was obtained only from samples of *Ximenia americana* fruits from Pantanal. In a general way, *D. areolatus* was more abundant in bigger fruits, in relation to the braconid others of shorter ovipositor. In relatively smaller fruit in which *D. areolatus* and *U. anastrephae* had co-occurrence, *D. areolatus* was dominant (i.e., no overlap). Possibly because *D. areolatus* have an ovipositor about 43% bigger than that of *U. anastrephae*, the first 1 reached the larvae in deeper position in the fruits. Absence of overlapping is a trait frequent between these 2 species (Sivinski et al. 1997). According to Hoffmeister (1992), these variations in rates of parasitism, species compositions, and abundance may be influenced regionally, temporally, spatially, and between samples of fruits.

In this survey *D. areolatus* was the predominant species, constituting 93.97% of all parasitoids (Table 2). These results were similar to those obtained in Southeastern (Aguiar-Menezes & Menezes 2001), and other parts of Brazil (Uchôa et al. 2003) where *D. areolatus* reached more than 70% of parasitism on frugivorous larvae of Tephritidae. Elsewhere in the Neotropics, Argentina (Ovruski et al. 2008), Bolivia (Ovruski et al. 2009), and Mexico (Hernández-Ortiz et al. 2006), *D. areolatus* is one of most ubiquitous, abundant and frequent species of parasitoids attacking frugivorous larvae of Tephritids. In Mexico, the level of parasitism by braconids in fruit flies under natural condition was between 0.4 and 83.8% in 15 species of fruit crops (López et al. 1999). Hernández-Ortiz et al. (1994) found *D. areolatus* in higher abundance and frequency (59.20%) in relation with other species of parasitoids in natural environments.

The diversity found in this survey is lower in comparison that from other Neotropical countries, such as Bolivia (Ovruski et al. 2009) and Mexico (Hernández-Ortiz et al. 1994). Probably some impacts in our environments contributed for this low species richness. The Serra de Maracajú and the Cerrado in that period (1998 to 2000) had problems with fire on part of its vegetation, and Pantanal is annually disturbed by the natural flooding (Uchôa, M. A. & Nicácio, J. N. personal observations).

In *X. americana*, 14% of the larvae of *Anastrepha alveatoides* Blanchard were parasitized by braconids, mainly *Doryctobracon areolatus* (Szépligeti) (96.29%). In this host there was no overlap between *Doryctobracon areolatus* and *Utetes anastrephae* (Table 3).

The figitids represented 0.28% of the total of parasitoids, and were obtained exclusively from larvae of *Neosilba* spp. (Table 3). As in braconids, the parasitism by figitids in lonchaeids also was underestimated (Van Driesche 1983). These results are different from those in the Cerrado of Mato Grosso do Sul, where the eucoilines (Figitidae) totaled 53% of all recovered parasitoids (Uchôa et al. 2003). However, in that survey most of sampled fruits were species of *Citrus* infested mainly by larvae of *Neosilba* species (Lonchaeidae) which are major eucoiline hosts.

TABLE 5. COMPARISON OF PUPAL PERIOD (MEANS) BETWEEN THE SPECIES *DORYCTOBRACON AREOLATUS* AND *UTETES ANASTREPHAE* (HYMENOPTERA: BRACONIDAE) IN DIFFERENT SEASONS IN SOUTH PANTANAL REGION, BRAZIL (APR 1998 TO AUG 2000, APR 2003, AND APR 2004).

		Species of Parasitoids				
		Doryctobracon areolatus		*Utetes anastrephae*		
Variables	Seasons	Mean, SD.	SE, (*n*)	Mean, SD.	SE, (*n*)	Mann-Whitney's Test (*U*) *Z* (*P*)
Number of Parasitoids (Mean)	Oct to Feb (Hot Humid)	$43.00^{aB} \pm 88.23$	25.47, (12)	$5.00^{bA} \pm 36.00$	2.08 (3)	5.40 (0.02)
	Apr to Jul (Cold and Dry)	$17.45^{aA} \pm 18.36$	5.54, (11)	$7.5^{bA} \pm 9.40$	4.72 (4)	3.27 (0.07)
Duration of Pupal Period (days)	Oct to Feb (Hot Humid)	$15.26^{aA} \pm 1.96$	0.57, (12)	$13.22^{bA} \pm 1.35$	0.73 (3)	-1.91 (0.07)
	Apr to Jul (Cold and Dry)	$16.86^{aB} \pm 1.65$	0.50, (11)	$14.25^{bB} \pm 1.50$	0.75 (4)	-2.10 (0.04)

SD = Standard Deviation of the mean; SE = Standard Error of the mean, and (*n*) = Number of samples with the occurrence of a species of a parasitoid. Means in the same column with at least one capital letter equal are equivalents; Means in the same line with equal lowercase letters are equivalent. No. of parasitoids: T ($P < 0.10$)], and Pupal period: T ($P < 0.01$)].

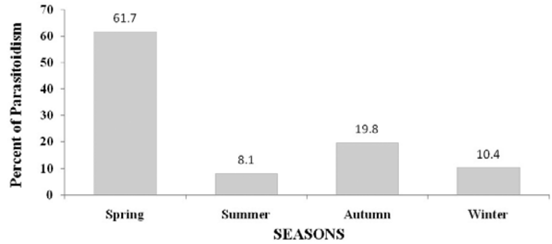

Fig. 1. Frequency (%) of parasitism of frugivorous fly (Tephritidae and Lonchaeidae) larvae during various seasons in Cerrado, Pantanal, and Sierra ecosystems, South Pantanal Region, Brazil (Apr 1998 to Aug 2000, Apr 2003, and Apr 2004).

The occurrence of the species of parasitoids presented dependence with the characteristics of the environments. This dependence was conditioned, probably, not only by the occurrence of the host species of flies, but also due to the peculiar characteristics of adaptability of the species of parasitoid to the climate of each environment, as suggested by the correlation test (Table 4).

In this paper, the overall rate of parasitism ranged from 0.13% to 14%. Similar rates, 0.07% to 14.37%, were observed by Uchôa et al. (2003) in 14 host plants in Cerrado environments. However, as pointed out by Van Driesche (1983), these percentages of parasitoidism were obtained from fruit sampled in the field and are usually underestimated. Due to the fact that, in general, the larvae of flies are removed from the environment before the guild of natural enemies can express its actions.

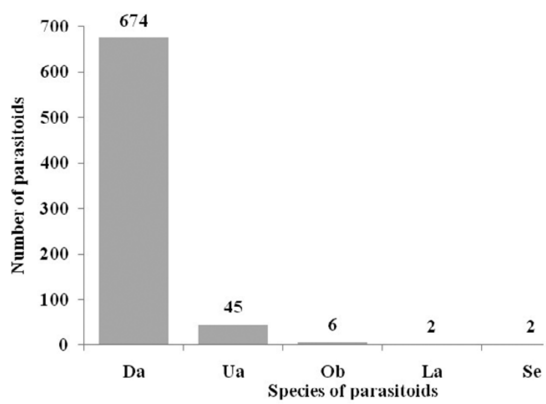

Fig. 2. Abundance of native parasitoids (Hymenoptera) obtained from larvae of frugivorous flies (Diptera: Tephritoidea) in Cerrado, Pantanal and Sierra ecosystems in South Pantanal Region, Brazil (Apr 1998 to Aug 2000, Apr 2003, and Apr 2004). Legend: Da = *Doryctobracon areolatus*; Ua = *Utetes anastrephae*; Ob = *Opius bellus*; La = *Lopheucoila anastrephae* and, Se = *Spalangia endius*.

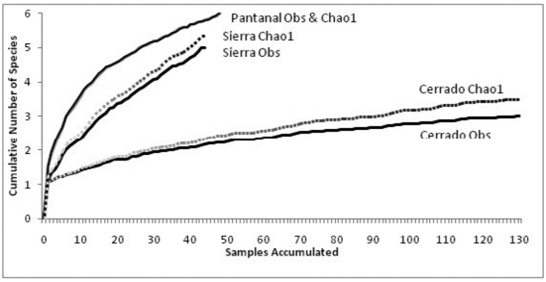

Fig. 3. Sampling effort in the survey of species of native parasitoids (Hymenoptera) of frugivorous larvae of Tephritoidea (Diptera) in ecosystems of Cerrado, Pantanal and Sierra in South Pantanal Region, Brazil (Apr 1998 to Aug 2000, Apr 2003, and Apr 2004).

The rate of parasitism by *D. areolatus* on larvae of fruit flies found in this study is similar to that reported in other studies in Brazil (Canal & Zucchi 2000; Uchôa et al. 2003), and abroad, like Guatemala (Jirón & Mexzon 1989), and Mexico (Hernández-Ortiz et al. 1994; López et al. 1999).

The predominance of *D. areolatus* is possibly related to its effectiveness in locating fruit fly host plants, to its long ovipositor, and to their ability to attacking host larvae in their initial instars, as have been pointed out by other researchers (Hernández-Ortiz et al. 1994; Sivinski et al. 1997, 2001; Costa et al. 2009).

The test of specificity (Blüthgen et al. 2000) among parasitoid taxa, plant species, and the host larvae of fruit flies found significant difference in the parasitoid specificity. This interaction is probably influenced for a biological factor. There was a marked variation in frequency between the parasitoid species in some species of plants (Table 4).

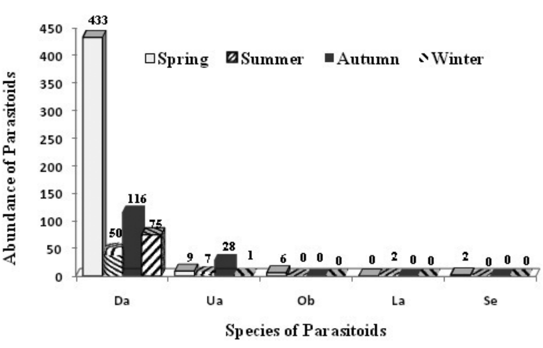

Fig. 4. Abundance of native parasitoids (Hymenoptera) upon frugivorous larvae of Tephritidae and Lonchaeidae (Diptera) during each season in Cerrado, Pantanal and Sierra ecosystems in South Pantanal Region, Brazil (Apr 1998 to Aug 2000, Apr 2003, and Apr 2004). Legend: Da = *Doryctobracon areolatus*; Ua = *Utetes anastrephae*; Ob = *Opius bellus*; La = *Lopheucoila anastrephae*, and Se = *Spalangia endius*.

In this survey *Utetes anastrephae* was the second most abundant species of parasitoid on larvae of *Anastrepha* species and was obtained from fruits of *P. kennedyanum*, *X. americana*, *Spondias lutea*, *P. guajava,* and *Andira cuyabensis*.

Utetes anastrephae was more abundant in the autumn and winter, and thus has the opposite pattern of seasonal abundance as *D. areolatus*. A similar pattern for these 2 species of parasitoids upon populations of fruit flies also was found in southern Brazil (Salles 1996), and in Mexico (Sivinski et al. 1997).

In terms of biological control, the integration of *D. areolatus* with *U. anastrephae* would allow year-long natural enemy suppression of pest populations. While *U. anastrephae* was relatively rare in our survey, it can be more abundant in other environments. As pointed out by Canal & Zucchi (2000), *U. anastrephae* is the prevalent opiine in some parts of southern Brazil. Because of its short ovipositor *U. anastrephae* is typically restricted to smaller host fruits, while *D. areolatus* with its longer ovipositor is able to reach larvae in a wider range of fruit species (Sivinski et al. 2001).

The parasitoid populations fluctuated with seasons, and their rates of parasitism were also related to altitude, peaking between 100 to 200 m, but not influenced by the climatic factors, relative humidity (RH) neither accumulated rainfall (Table 4).

The cumulative curves of the sampling effort in relation to the number of species revealed a small difference between observed (recovered) and the expected for the Pantanal and Serra de Maracajú, but this were more linear for the Cerrado. This mean that the number of samples taken in the Pantanal and in the Serra de Maracajú were not enough to represent the parasitoid estimated species richness. In the Serra de Maracajú the number of samples was yet smaller than that in Pantanal. In the Cerrado the observed number of samples was almost sufficient to express the estimated species richness (Fig. 3). So, we expect that there are more species in Pantanal and in the Serra de Maracajú than were recovered in this survey.

The species richness of parasitoids was higher in the Pantanal region, which has lower altitude gradient. Samples from the Serra de Maracajú and Cerrado environments had lower species richness. Probably both (Serra and Cerrado) were impacted by the burning of some host plants, reducing larvae populations of tephritoids to the parasitoid species in those environments.

Another mortality factor related to parasitoid attack that is not measured by percentage of parasitism is the damage caused by the scars left by the ovipositor of parasitoid; even when ovipositions failed, there was the possibility of subsequent infections by viruses, bacteria, fungi, protozoa and nematodes (Van Driesche 1983) on the frugivorous larvae of tephritoids. There are still no methodologies available, however, to unambiguously evaluate these causes of mortality to immature frugivorous flies, and this is an area that will require further research. In the future is important to look for oviposition scars by parasitoids upon the third instar larvae or puparium of dead tephritoids to establish if they are correlated or not to death of flies.

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