Indigenous parasitoids (Hymenoptera) attacking *Anastrepha fraterculus* and *Ceratitis capitata* (Diptera: Tephritidae) in native and exotic host plants in Northwestern Argentina

Sergio M. Ovruski,[a,*] Pablo Schliserman,[a] and Martín Aluja[b]

[a] *Instituto Superior de Entomología-FCNeIML-UNT, CONICET, Fundación Miguel Lillo-CIRPON, Miguel Lillo 251, (T4000JFE)-San Miguel de Tucumán, Tucumán, Argentina*
[b] *Instituto de Ecología A.C., Apartado Postal 63, Xalapa, Veracruz 91000, Mexico*

Abstract

We collected 16 species of wild and cultivated fruit fly (Diptera: Tephritidae) host plants over a 5-year period (1991–1995) in the province of Tucumán, Northwestern Argentina, with the aim of determining: (1) relative abundance and variations in native parasitoid abundance over time, (2) parasitoid associations with *C. capitata*/*A. fraterculus* host plants, and (3) parasitoid guild composition in native and exotic hosts. The fruit species surveyed included the following native (3) and exotic (13) plants: *Juglans australis* Grisebach (Juglandaceae), *Eugenia uniflora* L., and *Myrcianthes pungens* (Berg) Legrand (Myrtaceae) (all native species); *Annona cherimola* Miller (Annonaceae), *Citrus aurantium* L., *C. paradisi* Macfadyen, *C. reticulata* Blanco, *C. sinensis* (L.) Osbeck (Rutaceae), *Prunus armeniaca* L., *P. domestica* L., *P. persica* (L.) Batsch, *Eriobotrya japonica* (Thunb.) Lindl. (Rosaceae), *Diospyros kaki* L. (Ebenaceae), *Ficus carica* L. (Moraceae), *Mangifera indica* L. (Anacardiaceae), and *Psidium guajava* L. (Myrtaceae) (all exotic fruits). Of these, only *J. australis*, *P. persica*, *P. armeniaca*, *P. domestica*, *E. uniflora*, *M. pungens*, and *P. guajava* harbored parasitoids. A total of 13,926 native larval–pupal parasitoids representing five species in two families were obtained. *Doryctobracon areolatus* (Szépligeti) (Braconidae: Opiinae) and *Aganaspis pelleranoi* (Brèthes) (Figitidae: Eucoilinae) represented 61.5 and 27.9%, respectively, of all recovered parasitoids. The other three species, *Doryctobracon brasiliensis* (Szépligeti), *Utetes anastrephae* (Viereck), and *Opius bellus* Gahan (all Braconidae: Opiinae), represented 9.2, 1.2, and 0.3%, respectively, of the total parasitoid number. Of the latter five parasitoid species, only *D. areolatus* and *A. pellenaroi* exhibited diapause. *A. pelleranoi* was significantly more abundant in guava and peach samples gathered from the ground than in samples collected from the trees. The fly species recovered were *Anastrepha fraterculus*, *Ceratitis capitata*, and *Anastrepha* sp. representing 76.3, 23.2, and 0.5%, respectively, of all emerged adults. Parasitization levels varied according to fruit type and year and ranged between 3.1 and 19.2%. Highest parasitism rates were recorded in "feral" *P. guajava* and *P. persica* (both exotic) and the native *E. uniflora*, which was one of the smallest fruits sampled. In exotic fruits such as *M. indica* L., *A. cherimola*, and *Citrus* spp. (all over 150 g) and *E. japonica*, *F. carica*, and *D. kaki* (all less than 89 g) not a single parasitoid was obtained over the 5-year study period. We discuss our findings in light of their biological relevance (e.g., lack of *C. capitata* parasitism by native braconid parasitoids) and their practical implications.
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Keywords: Tephritidae; *Ceratitis capitata*; *Anastrepha fraterculus*; Native parasitoids; Braconidae; Figitidae; Biological control; Argentina

1. Introduction

Tephritid fruit flies are some of the most important pests affecting commercial fruit production in Argentina. Fruit infestation levels vary between 15 and 20%, which can represent a reduction of up to US$ 90 million per year in profit margins countrywide (Aruani et al., 1996). These insects also represent an impediment to

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* Corresponding author. Present address: Instituto de Ecologia, A.C., Division de Ecologia, c/o Martin Aluja, Km 2.5, Antigua carretera a Coatepec No. 351, 91070, Xalapa, Veracruz, Mexico. Fax: +54-381-4346940/228-812-1897.
E-mail address: ovruski@infovia.com.ar (S.M. Ovruski).

fruit crop diversification plans by local governments and severely limit fresh fruit exports due to quarantine restrictions imposed by importing countries such as the USA and Japan. There are two economically important fruit fly species in Argentina: the introduced Mediterranean fruit fly (Medfly), *Ceratitis capitata* (Wiedemann), and the native South American fruit fly, *Anastrepha fraterculus* (Wiedemann). *Ceratitis capitata* was introduced to Argentina, probably via Buenos Aires, where it was found infesting peaches in 1905 (Turica and Mallo, 1960; Vergani, 1952) or did so naturally from Brazil (González, 1978). It is currently found throughout all fruit-growing regions of the country. *Anastrepha fraterculus* is basically restricted to NE and NW Argentina, but can be occasionally found in other parts of the country as a result of sporadic introductions via infested fruit.

Historically, *C. capitata* and *A. fraterculus* control in Argentina was attempted almost exclusively through insecticidal bait-spray applications (hydrolyzed protein and malathion) and cultural practices (Turica et al., 1971). More recently, the sterile insect technique (SIT) has been applied against the Medfly in the Province of Mendoza (Gómez Riera et al., 2000). There were also some isolated efforts throughout the last century to implement biological control programs. During the 1930s and early 1940s, native parasitoids such as *Aganaspis pelleranoi* (Brèthes) and *Doryctobracon areolatus* (Szépligeti) (reported as *Eucoila pelleranoi* Brèthes and *Diachasmoides*, or *Opius tucumanus* Turica and Mallo, respectively) were collected in wild vegetation and released in commercial fruit orchards (Hayward, 1940a,b; Ogloblin, 1937). Later, in the 1960s and 1970s, classical biological control was attempted through the introduction of *Fopius arisanus* Sonan (reported as *Opius oophilus* Fullaway), *Tetrastichus giffardianus* Silvestri, *Doryctobracon crawfordi* (Viereck), *Diachasmimorpha longicaudata* (Ashmead) (reported as *Opius longicaudatus*), *Aceratoneuromyia indica* (Silvestri) (reported as *Syntomosphyrum indicum*), and *Pachycrepoideus vindemmiae* (Rondani) (Ovruski and Fidalgo, 1994). From these species, *A. indica* and *D. longicaudata* were released in limited numbers in Tucumán (Ovruski et al., 1999). Unfortunately, the effectiveness of all these efforts in reducing fly populations to an economically significant level was never ascertained because of a total lack of follow-up studies (Ovruski et al., 1999).

There are two regions within Argentina in which fruit fly parasitoids are common: the Tucumán, Salta, and Jujuy provinces in the Northwest and the Misiones province in the Northeast. The original native vegetation in both regions was a subtropical rain forest, locally known as "Yungas" or "Selva Tucumano-Boliviana" in the Northwest and "Selva Paranaense" in the Northeast (Cabrera, 1976). In the remaining stands of pristine forest and in perturbed areas adjacent to commercial

orchards, one can find numerous native and exotic fruit fly host plants. Preliminary surveys by Fernández de Araoz and Nasca (1984), Hayward (1940b), Loiácono (1981), Nasca (1973), Ogloblin (1937), Ovruski (1995), and Turica and Mallo (1961), revealed that hymenopterous parasitoids commonly attack *A. fraterculus* larvae infesting these hosts. According to Ovruski et al. (2000), the following nine native fruit fly parasitoid species have been recorded in Argentina: *Doryctobracon brasiliensis* (Szépligeti), *D. areolatus*, *Opius bellus* Gahan, *Utetes anastrephae* (Viereck) (larval–pupal braconid), *A. pelleranoi*, *Lopheucoila anastrephae* (Rohwer), *Dicerataspis grenadensis* Ashmead (larval–pupal figitid), *Trichopria anastrephae* Costa Lima, and *Coptera haywardi* (Ogloblin) (both diapriids attacking pupae). However, little is known about their relative abundance, biology and ecology.

Based on the above and concerned by the fact that native vegetation is rapidly disappearing in north Argentina, we carried out a 5-year study aimed at determining: (1) relative abundance and variations in parasitoid numbers over time, (2) parasitoid associations with *C. capitata*/*A. fraterculus* host plants, and (3) parasitoid guild composition in native and exotic hosts. Similar studies in neighboring Brazil (Aguiar-Menezes and Menezes, 1996; Canal Daza et al., 1994; Canal et al., 1995; Canal and Zucchi, 2000; Carvalho et al., 2000; Guimarães et al., 1999, 2000; Leonel, 1991; Leonel et al., 1995; Salles, 1996), Venezuela (Katiyar et al., 1995), Colombia (Yépes and Vélez, 1989; Carrejo and González, 1999), Costa Rica (Wharton et al., 1981; Jirón and Mexzon, 1989), El Salvador (Ovruski et al., 1996), Guatemala (Eskafi, 1990), México (Aluja et al., 1990; Hernández-Ortiz et al., 1994; López et al., 1999; Sivinski et al., 1997, 2000, 2001a), and the United States of America (Florida) (Baranowski et al., 1993) have revealed the existence of a large guild of native larval–pupal and pupal parasitoids.

2. Materials and methods

2.1. Study areas

We collected fruit in 10 different sites with different environmental conditions in the Tucumán province (NW Argentina) (Table 1). La Rinconada, La Reducción, Lules, Tafí Viejo, San Miguel de Tucumán, and Sauce Guascho are located in the central lowlands of Tucumán locally known as "Llanura Principal" (Alderete, 1998), which is close to the eastern side of the "Sierras Centrales." In this area, the climate is characterized as temperate-warm humid (Cwa). Taruca Pampa is located in the northeastern lowlands of Tucumán near the "Sierras del Noreste" (Alderete, 1998). The climate is also characterized as "Cwa." Valles de San Javier and

Table 1
General description of collection localities in Tucumán, Argentina

Collection localities	Description	Altitude (m)	Southern latitude	Western longitude	Mean annual rainfall (mm)	Mean annual temperature (°C)
El Siambón	Rural area with small citrus and peach orchards and backyard gardens surrounded by native vegetation (rural area)	1185	26°43′	65°27′	700	19.0
La Reducción	Base of mountain range covered with native vegetation (Yungas Forest) and exotic fruit trees (rural area)	550	26°58′	65°22′	945	25.3
La Rinconada	Fruit orchards and backyard gardens surrounded by sugar cane plantation and urban houses devoid of fruit trees (urban area)	510	26°51′	65°19′	945	25.3
Quebrada de Lules	Base of mountain range covered with native vegetation (Yungas Forest) and exotic fruit trees (rural area)	545	26°56′	65°21′	945	25.3
San Javier	Rural area with small citrus and peach orchards and backyard gardens surrounded by native vegetation (rural area)	950	26°47′	65°24′	700	19.0
San Miguel de Tucumán	Botanical garden of the Tucumán National University with native and exotic vegetation (urban area)	426	26°50′	65°13′	945	25.3
San Pedro de Colalao	Small fruit orchards and backyard gardens with exotic fruit species in the middle of the city (urban area)	1080	26°14′	65°30′	569	16.0
Sauce Guascho	Large citus groves and family gardens and backyard gardens surrounded by sugar cane plantations (rural area)	500	26°59′	65°27′	945	25.3
Tafí Viejo	Protected area known as "Parque Sierra de San Javier" (Tucumán National University), covered with unperturbed and perturbed native vegetation (Yungas forest) (rural area)	609	26°44′	65°16′	945	25.3
Taruca Pampa	Citrus groves and family gardens and backyard gardens surrounded by soybean plantations (rural area)	548	26°35′	64°50′	945	25.3

El Siambón are located in the northern highlands of Tucumán's "Sierras Centrales." The climate is defined as temperate-humid (Cwb) (Sesma et al., 1998). San Pedro de Colalao is located in northern Tucumán, and the climate is characterized as steppe-dry (BSkwb) (Villecco, 1991). The rainy season in all the above-mentioned sites is during the summer months of December–March (Sesma et al., 1998). Further details on site coordinates, altitude, mean annual temperature, and rainfall are provided in Table 1. Insecticides were not regularly applied in any of the collection sites.

2.2. Sample collection and processing procedures

From January 1991 to December 1995, ripe fruits (100–300 fruits per month) were randomly collected from the canopy of trees and the ground below when available. Canopy and ground samples were always handled separately to determine if there were differences in parasitoid species found at each level. The fruit tree species surveyed follow, and information on the total number of trees and sample size [expressed as proportion of the total number of fruit collected in entire study] is provided in parenthesis: *Annona cherimola* Miller (cherimoya) (24, 0.2%) (Annonaceae), *Citrus aurantium* L. (sour orange) (112, 2.6%), *C. paradisi* Macfadyen (grapefruit) (80, 1.4%), *C. reticulata* Blanco (mandarin orange) (105, 1.6%), *C. sinensis* (L.) Osbeck (sweet orange) (178, 2.0%) (Rutaceae), *Diospyros kaki* L. (japanese persimmon) (33, 0.6%) (Ebenaceae), *Eriobotrya japonica* (Thunb.) Lindl. (loquat) (159, 5.3%) (Rosaceae), *Ficus carica* L. (fig) (100, 1.5%) (Moraceae),

Table 2
Fruit flies and hymenopterous parasitoid species recovered from seven host plants in Tucumán, Argentina, between 1991 and 1995

Host plant species	No. of fruit sampled	Weight (kg) of fruit	No. of pupae	Fruit flies			Parasitoid			% Parasitism per collecting year				
				Species	Total number	% in sample	Species	Total number	% in sample	1991	1992	1993	1994	1995
Small fruit (<30 g)														
E. uniflora	9450	44.9	3065	A. fraterculus	1010	65.1	D. areolatus	134	7.7	8.9	15.8	17.1	18.2	4.1
				C. capitata	483	20.8	U. anastrephae	77	4.4					
							A. pelleranoi	34	1.9					
							O. bellus	1	0.1					
M. pungens	3418	39.9	2379	A. fraterculus	274	63.6	D. areolatus	67	15.5	9.3	9.5	7.3	9.7	8.1
				C. capitata	16	3.7	U. anastrephae	49	11.4					
							A. pelleranoi	25	5.8					
Medium fruit (30–100 g)														
J. australis	893	29.8	1950	A. fraterculus	449	41.5	A. pelleranoi	50	4.6	4.1	5.1	5.2	8.6	11.9
				A. sp.	376	34.8	D. areolatus	18	1.7					
				C. capitata	179	16.5	D. brasiliensis	9	0.8					
P. armeniaca	1761	50.3	2854	A. fraterculus	1239	66.9	D. areolatus	57	3.2	3.1	5.2	5.8	4.4	4.2
				C. capitata	534	28.6	A. pelleranoi	15	0.8					
							D. brasiliensis	10	0.5					
P. domestica	2103	124.9	5771	A. fraterculus	2298	68.0	D. areolatus	236	6.9	7.4	7.1	11.4	15.1	9.5
				C. capitata	792	22.0	A. pelleranoi	75	2.2					
							D. brasiliensis	31	0.9					
P. persica	19,839	559.2	66,218	A. fraterculus	21,457	63.0	D. areolatus	3349	9.6	17.3	19.2	14.2	14.1	14.3
				C. capitata	7830	21.2	A. pelleranoi	1601	4.7					
							D. brasiliensis	557	1.5					
							U. anastrephae	4	0.01					
							O. bellus	3	0.01					
P. guajava	9220	419.1	78,986	A. fraterculus	31,996	71.9	D. areolatus	4728	10.8	6.9	11.6	15.1	22.2	15.4
				C. capitata	4967	11.1	A. pelleranoi	2072	4.6					
				A. sp.	19	0.03	D. brasiliensis	646	1.4					
							U. anastrephae	41	0.09					
							O. bellus	35	0.08					

Mangifera indica L. (mango) (46, 0.5%) (Anacardiaceae), *Prunus armeniaca* L. (apricot) (56, 3.2%), *P. domestica* L. (cultivated plum) (70, 3.8%), *P. persica* (L.) Batsch (peach) (310, 35.8%) (Rosaceae), *Psidium guajava.* (common guava) (220, 16.6%) (Myrtaceae) (all exotic species), *Eugenia uniflora* L. (Surinam cherry) (60, 17.1%) (Myrtaceae), *Juglans australis* Grisebach (wild walnut) (32, 1.6%) (Juglandaceae), and *Myrcianthes pungens* (Berg) Legrand (mato) (47, 6.2%) (Myrtaceae) (all native species).

Fruits were mainly collected in forest patches and backyard gardens located in close proximity to citrus groves and in patches of disturbed wild vegetation adjacent to agricultural areas in all collection sites, except in San Miguel de Tucumán and its surroundings. In the latter case, fruits such as Surinam cherry, guava, peach, orange, and wild walnut were collected in the botanical garden of the Facultad de Agronomía y Zootecnia, National University of Tucumán, located within the urban area of the city of Tucumán. Collections were also made on the grounds of the "Parque Sierra de San Javier," a protected area of native vegetation belonging to the National University of Tucumán, which is located in "Tafí Viejo" and "Yerba Buena" (20 min drive from the city of San Miguel de Tucumán).

In the laboratory, a separate sub-sample of each fruit species was individually weighed ($n = 30$) each time fruits were sampled. Based on fruit weight, samples were divided into the following categories: small (<30 g), medium (30–100 g), and large (101–500 g). Small and medium-sized fruit samples were placed in styrofoam containers ($20 \times 20 \times 30$ cm) while large fruit samples were placed in wooden crates ($65 \times 45 \times 35$ cm) containing damp sand in the bottom as a pupation medium for fly larvae. All fruits were placed over a metal screen (10 mm mesh) about 10 cm from the bottom of each styrofoam or wooden container. During 4 weeks, fruit samples were kept inside a room at $25 \pm 1\,^\circ$C, $65 \pm 10\%$ relative humidity and a photoperiod of 14:10 (L:D) h, and sand sifted weekly to collect pupae. Afterwards, fruits were dissected to determine the presence of larvae or pupae in the pulp. Live larvae were allowed to pupate and were then added to the other pupae collected from the same sample.

All pupae were counted and transferred to plastic petri dishes containing sterilized damp sand, which was re-moistened every two-three days until all samples had been processed. Each petri dish was then placed inside a sealed wooden box ($22 \times 18 \times 25$ cm), which had three glass tubes in the anterior side. Emerging flies or parasitoids flew towards the light and entered the glass tubes. Once a week, all insects were counted and transferred into vials containing 70% alcohol. The box was also opened to collect any live or dead insects that had not entered the glass tubes. After 6 months all remaining pupae were counted and a sub-sample dissected

to ascertain if there were any live diapausing individuals. If some dissected individuals were still alive, then the remaining pupae were held until adults emerged.

2.3. Parasitoid and fly identification

Parasitoid species were identified by one of us (SO) using the taxonomic keys of Wharton and Marsh (1978) and Wharton and Gilstrap (1983). The taxonomic descriptions by Blanchard (1966), Brèthes (1924), and Wharton et al. (1998) were also used. Selected specimens were compared with type specimens housed at the Museo de Ciencias Naturales de La Plata, Argentina (MLP) and Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (MACN). Nomenclature used follows Ronquist (1995), Wharton (1997), and Wharton et al. (1998). Fruit flies were identified using taxonomic keys of Blanchard (1961), Steyskal (1977), and Zucchi (2000). Identifications were confirmed by the expert Diptera taxonomist Keiko Uramoto (Universidade de São Paulo, Brazil). Parasitoid and fly specimens were placed in the entomological collections of the Instituto Fundación Miguel Lillo (IFML) (San Miguel de Tucumán, Argentina) and Instituto de Biociências—USP (Brazil).

2.4. Plant identification

All plant samples were compared to herbarium specimens at the IFML, and identified by the expert plant taxonomists Hugo Ayarde (IFML) and Alejandra Roldán (Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán). Nomenclature employed for native plant identification was based on Morales et al. (1995) and for exotic plant species on Boelcke (1992).

2.5. Data analysis

To test for significant differences in the number of parasitoids recovered from fallen fruits versus those collected in the tree canopy, we used a non-parametric Wilcoxon Signed Rank Test (Zolman, 1993). Only guava and peach samples were considered in this analysis because these fruit yielded by far the highest number of parasitoids during the entire study period. Data were pooled by year independent of collection site (i.e., five separate analyses were performed for each fruit type).

We calculated parasitization rates by dividing the total number of parasitoids that emerged by the sum of the number of parasitoids and flies that emerged. Even though this measure of parasitism underestimates the mortality inflicted by parasitoids (some fly larvae die after being stung and are therefore not considered when calculating percent parasitism; Van Driesche, 1983), it allows for comparisons between fruit fly hosts and is an

indirect measure of parasitoid foraging preferences (Sivinski, 1991; Sivinski et al., 1996). Parasitoid diversity was measured by calculating the Shannon–Weaver Index (Southwood and Henderson, 2000) for each fruit species.

3. Results

We only recovered three fruit fly species: *A. fraterculus*, *C. capitata*, and *Anastrepha* sp. (representing 76.3, 23.2, and 0.5%, respectively, of the 77,600 adult flies recovered). The unidentified *Anastrepha* species stemmed from guava and wild walnut (Table 2).

Of the 13,926 parasitoids we recovered in the five-year study, braconid species represented 72.2% of all emerged parasitoid adults. Considering all parasitoids recovered, 61.5% were *D. areolatus* (Szépligeti) (Braconidae: Opiinae), 27.8% *A. pelleranoi* (Brèthes) (Figitidae: Eucoilinae), 9.2% *D. brasiliensis* (Szépligeti), 1.2% *U. anastrephae* (Viereck), and 0.3% *Opius bellus* Gahan (all Braconidae: Opiinae). All these species are koinobiont larval–pupal endoparasitoids. Only two species (*A. pelleranoi* and *D. areolatus*) exhibited diapause and when such was the case, diapausing individuals originated from only three localities. For example, 9.6, 11.5, and 14.8% of all *A. pelleranoi* individuals, and 11.6, 10.6, and 8.4% of all *D. areolatus* individuals collected during 1995 in San Miguel de Tucumán, La Reducción and Tafí Viejo, respectively, emerged 6–8 months after pupation.

Parasitism levels varied over time and differed among fruit fly hosts (Table 2). For example, in *Prunus persica*, *P. armeniaca* L., and *M. pungens* parasitism rates were very similar from year to year, whereas in *E. uniflora*, *Psidium guajava*, *J. australis*, and *Prunus domestica*, we detected 4.5-, 3.2-, 3.0-, and 2.1-fold differences in parasitization of fruit fly larvae when comparing years 1994/1995, 1991/1994, 1991/1995, and 1992/1994, respectively (Table 2). The highest parasitism levels were recorded in *P. guajava* and *Prunus persica* (both exotic species), and in the native *E. uniflora*, which was one of the smallest fruit sampled (Table 2). The latter three plant species and *J. australis* harbored the largest number of parasitoid species (Fig. 1).

Doryctobracon areolatus was the most abundant parasitoid species in all fruit species we sampled, with the exception of *J. australis* (all years) (Table 2). This braconid species accounted for more than 60% of all parasitoids recovered from guava, peach, apricot, and cultivated plum. *A. pelleranoi*, the second most common parasitoid species, was always the most abundant species in the native *J. australis*, which was only sampled at ground level. This eucoilid was also recovered from six other fruit fly host plants (Table 2). *D. brasiliensis* was the third most abundant parasitoid species, and it was
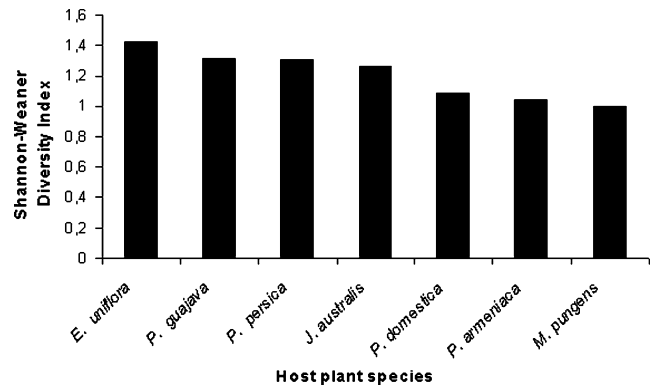

Fig. 1. Parasitoid species diversity as measured by the Shannon–Weaner Diversity Index in seven fruit fly host plants collected in Tucumán, Argentina.

recovered from five plant species (Table 2). *Opius bellus*, representing less than 1.5% of all emerged parasitoids, was recovered from four fruit species. Finally, *U. anastrephae* was mainly recovered from Myrtaceae, but it occasionally attacked fruit fly larvae in peaches (Table 2). *D. areolatus* and *A. pelleranoi* were not only the most abundant parasitoid species in terms of total numbers, but were also the most widely distributed (Table 3). Interestingly, in nine exotic fruit species not a single parasitoid was recovered (Table 4).

We found statistically significant differences in rates of parasitization by *A. pelleranoi* when comparing guava and peach samples collected in the tree canopy versus the ground. In contrast, no significant differences were found in the case of *D. areolatus* and the other braconid parasitoid species identified in the study (Tables 5 and 6).

Of the 13,926 parasitoids recovered during this study, 89.4% were registered in sites with perturbed and unperturbed native vegetation such as La Reducción, Quebrada de Lules, Tafí Viejo, San Miguel de Tucumán, and El Siambón. The remaining 1478 (10.6%) specimens were recovered in sites characterized by the existence of large citrus groves and backyard gardens with exotic fruit species surrounded by soybean and sugarcane plantations, such as La Rinconada, Sauce Guascho, Taruca Pampa, and San Pedro de Colalao. Furthermore, in sites with perturbed and unperturbed native vegetation we recovered up to five species of parasitoids, while in areas heavily modified for extensive agriculture, only three species were present (*Opius bellus* and *U. anastrephae* were missing).

4. Discussion

Parasitization in exotic fruit fly hosts followed two contrasting patterns. On the one hand, in medium-sized species such as *P. guajava* and *Prunus* spp., we recorded

Table 3
Larval–pupal parasitoid abundance in 10 localities in Tucumán, Argentina, between 1991 and 1995

Collection sites	Parasitoid species	Total number	Proportion (%) of total	Percent parasitism
Tafí Viejo	D. areolatus	3521	60.82	13.14
	A. pelleranoi	1430	24.61	5.33
	D. brasiliensis	759	13.11	2.84
	U. anastrephae	58	1.01	0.21
	O. bellus	27	0.45	0.10
	All species	5790	100.00	21.62
La Rinconada	D. areolatus	470	72.64	4.16
	A. pelleranoi	150	23.18	13.05
	D. brasiliensis	27	4.17	0.75
	All species	647	100.00	17.97
San Miguel de Tucumán	D. areolatus	1462	58.93	9.53
	A. pelleranoi	933	37.61	6.08
	U. anastrephae	60	2.41	0.39
	D. brasiliensis	25	1.01	0.16
	O. bellus	1	0.04	0.01
	All species	2481	100.00	16.17
San Pedro de Colalao	D. areolatus	215	58.26	9.16
	A. pelleranoi	149	40.38	6.70
	D. brasiliensis	5	1.36	0.23
	All species	369	100.00	16.09
La Reducción	D. areolatus	1836	69.27	10.76
	A. pelleranoi	485	18.40	2.86
	D. brasiliensis	301	11.43	1.78
	U. anastrephae	13	0.49	0.08
	O. bellus	11	0.41	0.06
	All species	2646	100.00	15.54
San Javier	A. pelleranoi	45	71.43	3.89
	D. areolatus	11	17.46	8.32
	U. anastrephae	7	11.11	1.31
	All species	73	100.00	13.52
Quebrada de Lules	A. pelleranoi	448	47.26	5.68
	D. areolatus	410	43.25	5.19
	D. brasiliensis	88	9.28	0.61
	U. anastrephae	2	0.21	0.03
	All species	948	100.00	11.51
El Siambón	D. areolatus	346	67.07	5.78
	A. pelleranoi	121	23.48	2.02
	D. brasiliensis	48	9.45	0.88
	All species	516	100.00	8.68
Sauce Guascho	D. areolatus	227	65.79	5.56
	A. pelleranoi	112	32.46	2.84
	D. brasiliensis	6	1.75	0.13
	All species	345	100.00	**8.53**
Taruca Pampa	D. areolatus	85	72.61	5.28
	A. pelleranoi	32	27.39	1.98
	All species	117	100.00	7.26

the highest rates in the entire study (Table 2). On the other, in small-sized species such as *E. japonica* and *F. carica*, in the medium-sized *C. reticulata* and *D. kaki*, and in the large-sized *M. indica*, *A. cherimola*, and *Citrus* spp., we did not recover a single parasitoid during the entire five-year study. A plausible explanation for this pattern, which is unrelated to fruit characteristics such as size (see Sivinski, 1991 and Sivinski et al., 1997) or

type of volatiles emitted (see Leyva et al., 1991 and Eben et al., 2000), is the type of fly species infesting a particular fruit. For example, *F. carica*, *C. reticulata*, *C. sinensis* and *C. aurantium* only yielded *C. capitata* adults, and *E. japonica*, *C. paradisi*, *D. kaki*, *A. cherimola*, and *M. indica* yielded a significantly higher proportion of them (Table 4). This could imply that native parasitoids are unable to attack *C. capitata* larvae or when doing so,

Table 4
Fruit fly host plants surveyed during study that did not yield parasitoids

Host plant species	No. of fruit sampled	Total weight (kg) of fruit sampled	No. of pupae	Fruit flies		
				Species	Total number	% in sample
Small fruit (<30 g)						
E. japonica	2936	24.7	604	C. capitata	340	74.1
				A. fraterculus	119	25.9
F. carica	828	15.2	129	C. capitata	67	100.0
Medium fruit (30–100 g)						
C. reticulata	891	68.6	205	C. capitata	123	100.0
D. kaki	320	28.4	299	C. capitata	153	83.2
				A. fraterculus	31	16.8
Large fruit (101–500 g)						
A. cherimola	81	13.6	286	A. fraterculus	145	78.4
				C. capitata	40	21.6
C. paradisi	787	185.5	2101	C. capitata	861	66.2
				A. fraterculus	440	33.8
C. aurantium	1440	213.1	3795	C. capitata	1740	100.0
C. sinensis	1131	144.3	3401	C. capitata	1504	100.0
M. indica	259	94.5	2147	C. capitata	807	63.3
				A. fraterculus	467	36.7

face severe hurdles to complete development. Because *C. capitata* was introduced to the American Continent at the beginning of last century (Gallo et al., 1970) there is no evolutionary relationship between this fly species and parasitoids native to the neotropics or between these parasitoids and the introduced host plants of *C. capitata*.

The apparent inability of native parasitoids to attack *C. capitata* has been previously documented in Argentina (Ovruski, 1995), Brazil (Canal and Zucchi, 2000; Leonel, 1991; Leonel et al., 1995, 1996), Venezuela (Katiyar et al., 1995), Colombia (Yépes and Vélez, 1989), Costa Rica (Jirón and Mexzon, 1989; Wharton et al., 1981), El Salvador (Ovruski et al., 1996), and Guatemala (Eskafi, 1990). All these authors report low levels of parasitism or lack of it in fruit species in which *C. capitata* was the dominant fly species. For example, Leonel (1991) working in Brazil reported the lack of parasitism in *D. kaki* and *C. reticulata*, two fruit species mainly infested by *C. capitata* larvae. The latter coincides with the information provided in Table 4. In our case, even small sized fruit such as *F. carica* and *E. japonica* with apparently ideal conditions for parasitoid boring activity (e.g., thin epicarp and soft pulp) yielded no parasitoids. However, the braconids *D. areolatus* (Fernández de Araoz and Nasca, 1984; Katiyar et al., 1995; Leonel et al., 1996), *D. crawfordi* (Eskafi, 1990), *Opius hirtus* Fischer (Wharton, 1983), *O. bellus* (Guagliumi, 1963; Leonel et al., 1995), and *U. anastrephae* (Nasca, 1973), have been supposedly reared from *C. capitata* larvae. Because none of these records provide sufficient evidence to unequivocally conclude that the larvae were indeed *C. capitata* and not some of the various *Anastrepha* species present in the study areas, we recommend confirmatory studies. In our case, we have recently collected close to 20,000 *C. capitata* puparia from various fruit species in NW Argentina. From these, we have been only able to obtain small numbers of the figitid *A. pelleranoi*. This information, added to previously published records (De Santis, 1965; Ovruski, 1995; Wharton et al., 1998), suggest that *A. pelleranoi* is better adapted to *C. capitata* larvae than any of the native braconid parasitoids common in Latin America. Two other figitids (Eucoilinae), *Odontosema anastrephae* Borgmeier and *Aganaspis nordlanderi* Wharton, have also been reared, albeit in small numbers, from *C. capitata* puparia in Costa Rica (Wharton et al., 1998). To us, the most plausible explanation has to do with an apparent lack of development of native braconid parasitoid larvae in *C. capitata*. Two possible mechanisms would be encapsulation or antibiosis, but unless experimentally tested, these scenarios will remain hypothetical.

As reported previously by Aluja et al. (1998), we also found that the most abundant native parasitoid species in our study, *A. pelleranoi*, and *D. areolatus*, exhibited diapause. Despite the fact that this phenomenon needs to be more thoroughly studied in this part of the world, we believe that it is a mechanism that allows parasitoid adults to overcome periods of pronounced host scarcity given that guava is the last widely available host before the winter season begins in June. Aluja et al. (1998), working in tropical sub-deciduous and deciduous forests and backyard gardens in Central Veracruz, México, found that one local species of native parasitoid (*D. crawfordi*) did not exhibit diapause. In our case, neither *D. brasiliensis*, *O. bellus*, nor *U. anastrephae* diapaused so. The case of *U. anastrephae* is interesting because

Table 5
Comparison of the number of larval–pupal parasitoids from guavas collected in tree canopy or from ground below

Year	Fruit origin	No. of fruits	No. of samples	Specimen number of each parasitoid species[a]				
				A. pelleranoi Mean ± SEM (total no.)	D. areolatus Mean ± SEM (total no.)	D. brasiliensis Mean ± SEM (total no.)	U. anastrephae Mean ± SEM (total no.)	O. bellus Mean ± SEM (total no.)
1991	Tree	316	14	1.5 ± 0.4a (7)	11.8 ± 1.3a (47)	0.2 ± 0.2a (3)	0	0
	Ground	296	14	11.2 ± 2.1b (45)	8.0 ± 2.4a (41)	0.1 ± 0.1a (1)	0	0
				$W = 91.0, P = 0.002$	$W = 47.0, P = 0.064$	$W = -1.0, P = 1.000$		
1992	Tree	739	10	4.5 ± 1.4a (37)	15.9 ± 5.4a (143)	1.5 ± 0.8a (17)	0.0 ± 0.0a (0)	0.0 ± 0.0a (0)
	Ground	679	10	34.6 ± 10.5b (307)	21.8 ± 6.1a (206)	1.1 ± 0.4a (12)	0.6 ± 0.6a (8)	0.3 ± 0.3a (4)
				$W = 91.0, P = 0.002$	$W = 15.0, P = 0.492$	$W = -5.0, P = 0.625$	$W = 1.0, P = 1.000$	$W = 1.0, P = 1.000$
1993	Tree	947	10	6.8 ± 1.6a (46)	39.1 ± 17.4a (345)	8.4 ± 4.7a (89)	0.4 ± 0.4a (4)	0
	Ground	1080	10	40.8 ± 8.9b (357)	100.1 ± 60.8a (943)	10.9 ± 6.0a (102)	0.2 ± 0.2a (2)	0
				$W = 55.0, P = 0.002$	$W = 25.0, P = 0.232$	$W = 19.0, P = 0.195$	$W = 1.0, P = 1.000$	
1994	Tree	1206	10	18.5 ± 15.2a (182)	109.6 ± 70.0a (1026)	13.2 ± 10.3a (125)	1.5 ± 1.1a (15)	1.2 ± 0.7a (14)
	Ground	1246	10	81.1 ± 42.5b (729)	127.7 ± 77.3a (1224)	18.0 ± 14.1a (188)	0.6 ± 0.6a (6)	0.5 ± 0.5a (5)
				$W = 55.0, P = 0.002$	$W = 24.0, P = 0.109$	$W = 16.0, P = 0.219$	$W = -3.0, P = 0.500$	$W = -6.0, P = 1.250$
1995	Tree	1315	11	5.6 ± 1.5a (36)	60.1 ± 12.3a (397)	5.4 ± 1.6a (45)	0	0.9 ± 0.7a (10)
	Ground	1416	11	35.2 ± 6.7b (328)	53.5 ± 14.4a (356)	6.0 ± 1.8a (44)	0	0.2 ± 0.2a (2)
				$W = 66.0, P < 0.001$	$W = 42.0, P = 0.067$	$W = 13.0, P = 0.557$		$W = -3.0, P = 0.500$

Data pooled over 5-year study period and all collection sites in Tucumán, Argentina.
[a] Means in the same column followed by the same letter are not significantly different (Wilcoxon Signed Rank Test, $P = 0.05$).

Table 6
Comparison of the number of larval–pupal parasitoids from peaches collected in tree canopy or from ground below

Year	Fruit origin	No. of fruits	No. of samples	Specimen number of each parasitoid species[a]				
				A. pelleranoi Mean ± SEM (total no.)	D. areolatus Mean ± SEM (total no.)	D. brasiliensis Mean ± SEM (total no.)	U. anastrephae Mean ± SEM (total no.)	O. bellus Mean ± SEM (total no.)
1991	Tree	2177	13	$8.6 \pm 4.8a$ (112)	$47.8 \pm 25.8a$ (621)	$13.8 \pm 9.7a$ (180)	0	$0.1 \pm 0.1a$ (1)
	Ground	2516	13	$19.3 \pm 7.3b$ (251)	$40.3 \pm 20.1a$ (524)	$14.2 \pm 11.0a$ (184)	0	$0.2 \pm 0.2a$ (2)
				$W = 78.0, P < 0.001$	$W = 53.0, P = 0.068$	$W = 3.0, P = 0.500$		$W = 1.0, P = 1.000$
1992	Tree	1650	11	$5.6 \pm 2.7a$ (62)	$24.6 \pm 12.5a$ (271)	$2.9 \pm 2.2a$ (32)	0	0
	Ground	1808	11	$29.1 \pm 14.4b$ (320)	$22.8 \pm 10.4a$ (249)	$1.9 \pm 0.7a$ (21)	0	0
				$W = 66.0, P < 0.001$	$W = 10.0, P = 0.625$	$W = 2.0, P = 0.813$		
1993	Tree	1996	12	$9.1 \pm 2.4b$ (109)	$34.6 \pm 11.1a$ (415)	$1.3 \pm 1.1a$ (15)	$0.1 \pm 0.1a$ (2)	0
	Ground	2512	12	$17.8 \pm 3.5b$ (214)	$26.7 \pm 8.9a$ (320)	$2.3 \pm 1.2a$ (28)	$0.1 \pm 0.1a$ (2)	0
				$W = 58.0, P = 0.002$	$W = 11.0, P = 0.625$	$W = 4.0, P = 0.625$	$W = 1.0, P = 1.000$	
1994	Tree	2060	11	$3.7 \pm 1.3b$ (41)	$23.5 \pm 4.4a$ (260)	$3.1 \pm 1.1a$ (34)	0	0
	Ground	1638	11	$21.5 \pm 3.9b$ (237)	$21.2 \pm 7.8a$ (245)	$1.5 \pm 0.7a$ (16)	0	0
				$W = 63.0, P = 0.002$	$W = 33.0, P = 0.105$	$W = 15.0, P = 0.156$		
1995	Tree	1715	10	$4.1 \pm 2.6b$ (37)	$18.5 \pm 4.2a$ (185)	$1.9 \pm 1.2a$ (19)	0	0
	Ground	1497	10	$19.8 \pm 7.8b$ (218)	$18.0 \pm 7.4a$ (182)	$1.2 \pm 0.9a$ (12)	0	0
				$W = 55.0, P = 0.002$	$W = 3.0, P = 0.910$	$W = -2.0, P = 0.750$		

Data pooled over 5-year study period and all collection sites in Tucumán, Argentina.
[a] Means in the same column followed by the same letter are not significantly different (Wilcoxon Signed Rank Test, $P = 0.05$).

Aluja et al. (1998) reported that diapause in this species is common and that it can last up to 11 months.

We were able to confirm previous reports by Sivinski et al. (1997) indicating that there are differences in the foraging patterns of figitid and braconid parasitoid species. For example, in our study there is a clear indication that *A. pelleranoi* (Figitidae) preferentially attacks larvae in fallen fruit (Tables 5 and 6). Out of 2084 *A. pelleranoi* adults recovered from guava and peach during the five-year study period, 308 (14.8%) stemmed from fruit collected in the tree canopy, and 1776 (85.2%) from fruit collected from the ground. *A. pelleranoi* females are able to penetrate fruit in search of larvae through previously existing holes or by biting their way through the skin (Aluja et al., 2001; Ovruski, 1994). In the cases of *D. areolatus*, *D. brasiliensis*, *U. anastrephae*, and *O. bellus* (all braconids) the tree/ground figures were 46.3 and 53.6, 48.0 and 52.0, 53.8 and 46.1, and 65.8 and 34.2%, respectively. Larvae in fallen fruit were most likely already parasitized by females of the above listed species in the tree canopy. But there is an indication that there is some foraging activity on the ground. In the case of *O. bellus*, total numbers were very low ($n = 38$), and no definitive conclusions can be reached at this stage. Based on these results, we plan to conduct a series of experiments with artificially infested fruit (unparasitized larvae), hung from branches or placed at ground level to unequivocally ascertain if females of native braconids do indeed forage at ground level. Such a phenomenon has been clearly documented by Purcell et al. (1994) and López et al. (1999) in the case of the exotic *D. longicaudata*.

We note that the eucoilines *L. anastrephae* and *Dicerataspis grenadensis* were not found during the present study. Both native species were previously registered in Tucumán by Wharton et al. (1998) supposedly in association with *Anastrepha* spp. in guava. However, the same authors indicated that drosophilids and lonchaeids appear to be the normal hosts of *D. grenadensis* and *L. anastrephae*, respectively. Based on the latter and on our results here, parasitism of flies in the genus *Anastrepha* by species of *Lopheucoila* and *Diceraspis* needs to be addressed in future studies.

None of the exotic larval-parasitoid species released in Tucumán were recovered during our study. *Diachasmimorpha longicaudata* had apparently disappeared from the region. In contrast, *D. longicaudata* was recovered immediately following releases and accounted for 36% of the fruit fly parasitism in the northeastern provinces of Entre Rios and Misiones (Turica, 1968). In Misiones, the permanent establishment of *D. longicaudata* was recently confirmed (P. Schliserman, unpublished data). *Aceratoneuromyia indica* was only recovered immediately following releases in Tucumán between 1966 and 1967. Even though Nasca (1973) considered it established, nobody has been able to collect it in more than 25 years.

The apparent inability of native parasitoids to attack *C. capitata* larvae, added to our finding indicating that native parasitoids are unable to attack *A. fraterculus/C. capitata* larvae in the various citrus species grown in Tucumán and neighboring regions have important practical implications. Because we also found that native parasitoids are common in all native fruit species and in some small exotic fruits, two possible scenarios for the implementation of fruit fly biological control in the region emerge. First, and as suggested by Headrick and Goeden (1996) for California, classical biological control of *C. capitata* through the importation of afro-tropical parasitoid species, seem particularly suited in NW Argentina. For example, species such as *Fopius ceratitivorus* Wharton and *F. caudatus* (Szépligeti), which are natural enemies of *C. capitata* in its center of origin (Wharton et al., 2000), are potential agents for biological control of Medfly in Guatemala (Sivinski et al., 2001c). Furthermore, the employment of Indo-Pacific parasitoid species, such as *F. arisanus* and *D. longicaudata*, for augmentative biological control against *C. capitata* should also be considered (Purcell, 1998). For example, the egg-parasitoid *F. arisanus* can be mass-reared (Bautista et al., 1999), and it can suppress *C. capitata* populations in coffee plantations in Hawaii (Vargas et al., 2001) and Guatemala (Sivinski et al., 2001b). For NW Argentina, we recommend that mass releases of *F. arisanus* should be targeted to areas where known alternative *C. capitata* hosts are abundant. Given that *D. longicaudata* is a particularly common in large, exotic commercial fruits, such as citrus and mango, in Veracruz, México (López et al., 1999), and that mass releases of *D. longicaudata* effectively suppressed *A. suspensa* populations in Florida, USA (Burns et al., 1996; Sivinski et al., 1996) and *A. ludens* populations in Chiapas, México (Montoya et al., 2000), we believe that mass releases of *D. longicaudata* in abandoned citrus groves could also possibly suppress *C. capitata* populations in NW Argentina. However, the apparent inability of *D. longicaudata* and *A. indica* to get established in Tucumán (discussed before), underscore the need of previous studies on bioclimatic requirements by exotic biocontrol agents, and of post-release monitoring and evaluation of parasitoid efficacy.

Furthermore, conservation biological control (Barbosa, 1998) of *A. fraterculus* could be achieved in areas where native vegetation is still dominant such as the Yungas forest or in patches with mixed stands of native and introduced fruit species adjacent to commercial groves. It is in these areas where *A. fraterculus* populations increase and from which individuals move to attack commercially grown fruit. Instead of removing native hosts, we recommend enhancing natural parasitoid reservoirs such as *E. uniflora*, *J. australis*, and *M. pungens*. Given the close association found in other parts of the world between native vegetation and the

presence of *Anastrepha* parasitoids (Aluja, 1999; López et al., 1999), we believe that widespread habitat destruction and replacement of native vegetation by commercial groves and annual crops in Tucumán could drastically reduce fruit fly parasitoid abundance and diversity in this NW province of Argentina. As noted by Aluja (1999), native vegetation can be managed to conserve and multiply native fruit fly parasitoids in rural areas in which farmers cannot afford expensive pest control and management procedures, we believe that it would be wise to at least think about the possibility of maintaining areas with native vegetation interspersed in regions of large-scale agricultural production. Such measures could be combined with timed massive releases of species such as *D. areolatus* and *A. pelleranoi* (Aluja, 1996). Moreover, pupal parasitoids such as the diapriid *Coptera haywardi* could also be released to attack the particularly susceptible pupal stage (Aluja, 1999). *Coptera haywardi* was originally recorded in NW Argentina attacking *A. fraterculus* and *A. shultzi* (Loiácono, 1981), and it has recently been cited as a viable fruit fly biocontrol agent by Sivinski et al. (1998). Up to nine native larval–pupal and pupal parasitoids (including *D. areolatus*, *A. pelleranoi*, and *C. haywardi*) are being currently reared under laboratory conditions by one of us (M. Aluja, unpublished data), and it opens up the possibility of implementing a mass-release program in Tucumán.

Acknowledgments

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