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Hymenopterous Larval–Pupal and Pupal Parasitoids of *Anastrepha* Flies (Diptera: Tephritidae) in Mexico

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We surveyed 15 wild and cultivated plant species in search of fruit fly (Diptera: Tephritidae) parasitoids during 4 years (1993–1996) in the state of Veracruz, Mexico. The following species were infested by *Anastrepha* larvae: *Spondias purpurea* L., *S. mombin* L., *Tapirira mexicana* Marchand, *Mangifera indica* L. (all Anacardiaceae), *Ximenia americana* L. (Olacaceae), *Citrus sinensis* L. and *Casimiroa edulis* Llave & Lex. (Rutaceae), *Psidium guajava* L., *P. sartorianum* (Berg.), *P. guineense* Sw., *Syzygium jambos* L., *Myrciaria floribunda* (West) O. Berg. (all Myrtaceae), *Chrysophyllum mexicanum* (Brandegce) ex. Standley and *Calocarpum mammosum* L. (Sapotaceae), and *Passiflora foetida* L. (Passifloraceae). Of these, only *C. mexicanum*, *C. edulis*, and *P. foetida* did not harbor parasitoids. We identified 10 native and exotic larval–pupal parasitoid species (all Hymenoptera): *Doryctobracon areolatus* (Szépligeti), *D. crawfordi* (Viereck), *Utetes* (*Bracanastrepha*) *anastrephae* (Viereck), and *Opius hirtus* (Fisher) (all Braconidae), *Aganaspis pellenaroi* (Brethes) and *Odontosema anastrephae* Borgmeier (Eucoilidae) (all native species), and *Diachasmimorpha longicaudata* (Ashmead) and *Aceratoneuromyia indica* (Silvestri) (Braconidae and Eulophidae, respectively; both exotic species). We also identified two pupal parasitoids: *Coptera haywardi* (Ogloblin) (Diapriidae; native) and *Pachycrepoideus vindemiae* (Rondani) (Pteromalidae; exotic). Parasitization levels ranged between 0.4 and 83.8%. Native, wild plants harbored significantly more parasitoids per fruit than cultivated ones. Interestingly, in *P. guajava* 2 fly species and 5 parasitoid species were once identified in a single fruit. We found a negative correlation between fruit size and number of parasitoids/fruit. We rank parasitoids based on host breadth (fruit fly species attacked) and number of plant species visited. We discuss some general ecological and practical implications of our findings (e.g., effect of fruit size on parasitism, mass-rearing, and augmentative releases of native vs exotic parasitoids) and compare our findings with previous surveys carried out in Mexico and in Central and South America. We also discuss the need to protect native vegetation because of the important role such vegetation plays as reservoirs of fruit fly parasitoids.

Key Words: Anastrepha; **Tephritidae; parasitoids;** ***Doryctobracon; Utetes; Opius; Aganaspis; Odontosema; Coptera; Diachasmimorpha; Aceratoneuromyia; Pachycrepoideus.***

INTRODUCTION

Flies in the genus *Anastrepha* Schiner are found from the southern United States to northern Argentina (Hernández-Ortíz and Aluja, 1993). Of the 187 reported species, 7 stand out because of their status as important pests: *Anastrepha fraterculus* (Wiedemann), *Anastrepha grandis* (Macquart), *Anastrepha ludens* (Loew), *Anastrepha obliqua* (Macquart), *Anastrepha serpentina* (Wiedemann), *Anastrepha striata* (Schiner), and *Anastrepha suspensa* (Loew) (Aluja, 1994). Historically, there has been heavy reliance on insecticidal bait sprays to control these flies (Aluja, 1993, 1996). Nevertheless, some attempts to also apply classical or augmentative biological control strategies have been made (Wharton, 1989; Sivinski, 1996). The most common approach has been to release exotic egg, larval–pupal, or pupal parasitoids. For example, in Mexico *Fopius arisanus* Sonan (reported as *Opius oophilus* Fullaway), *Opius novocaledonicus* Fullaway, *Opius formosanus* Fullaway, *Opius taiensis* Fullaway, *Opius vandenboschi* Fullaway, *Diachasmimorpha longicaudata* (Ashmead) (reported as *Opius compensans* Silvestri), *Aceratoneuromyia indica* (Silvestri) (Eulophidae) (reported as *Syntomosphyrum*), *Dirhinus giffardi* Silvestri, and *Pachycrepoideus vindemiae* (Rondani) (Pteromalidae) were repeatedly released in the late 1950's and early 1960's (Jiménez-Jiménez, 1956, 1958, 1967). Strikingly, in these classical biological control programs, little attention was paid to native parasitoids. More recently, exotic parasitoids were mass-released in an attempt to

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suppress *Anastrepha* populations on an area-wide basis. This is illustrated by a recent study in Key Biscayne and Clewiston, Florida, using the braconid larval–pupal parasitoid *D. longicaudata* (Sivinski *et al.*, 1996).

The study of native *Anastrepha* parasitoids has a long history and began in Mexico. De la Barrera (cited by Herrera, 1905), McPhail and Bliss (1933), Darby and Knapp (1934), and Stone *et al.* (1965), collecting natural enemies in various regions of Mexico, identified *Doryctobracon* (=*Opius*) *crawfordi* (Viereck), *Coptera* sp. (=*Galesus* sp.), *Aganaspis* sp. (=*Eucoila*), and the bombylid fly *Anthrax scylla* Oster Sacken. *Doryctobracon crawfordi* (reported as *Diachasma crawfordi*) was also reported in Costa Rica by Picado (1920). More recently, systematic surveys on native *Anastrepha* parasitoids were carried out in the United States (Florida) (Baranowski *et al.*, 1993), Mexico (Nuevo León, Veracruz, Chiapas) (González-Hernández and Tejada, 1979; Aluja *et al.*, 1990; Piedra *et al.*, 1993; Hernández-Ortíz *et al.*, 1994), Guatemala (Eskafi, 1990), Costa Rica (Wharton *et al.*, 1981; Jirón and Mexzon, 1989), Colombia (Yépes and Vélez, 1989), Venezuela (Katiyar *et al.*, 1995), Brasil (Costa Lima, 1937; Nascimento *et al.*, 1979; De Santis, 1980; Arrigoni, 1984; Aguiar *et al.*, 1992; Canal *et al.*, 1994, 1995; Leonel *et al.*, 1995; Araujo *et al.*, 1996), and Argentina (Turica and Mallo, 1961; Nasca, 1973; Fernández-de-Araoz and Nasca, 1984; Díaz, 1986; Ovruski, 1995). Several points relevant to the work described here stand out from these studies: (1) *Doryctobracon areolatus* (Szépligeti) is by far the most abundant and widespread native parasitoid of *Anastrepha* (its range extends from central Florida to northern Argentina). (2) There is no report of a native *Anastrepha* egg parasitoid. (3) Pupal parasitoids are poorly represented in samples probably because of the collection techniques used. (4) Most parasitoid species are generalists (i.e., they attack many *Anastrepha* species). (5) Many native species are found preferentially parasitizing *Anastrepha* larvae in native, wild fruit species.

Our aim here was to systematically survey native and exotic plants in crop fields and large and small patches of native vegetation adjacent to crops and to identify all larval–pupal and pupal fruit fly parasitoids present in a region where fruit growing is an important agricultural activity. Detailed information on the distribution of parasitoids within tree canopies and effect of microclimate on the latter and on parasitoid diapause schedules is reported elsewhere (Sivinski *et al.*, 1997; Aluja *et al.*, 1998).

METHODS

Study sites. Collections were made in the following sites: Apazapan, Llano Grande, Tejería, and Monte Blanco, all in central Veracruz, Mexico. Apazapan (19°19′ N, 96°42′ W) is at an elevation of 347 m. Climate is defined as Aw_1(w″) (i′)g (intermediate warm-subhumid) (García, 1973), with a mean annual temperature of 25°C and 1250 mm rainfall, mostly during the summer to early autumn rainy season. Occasional light rains also fall during winter months. Llano Grande (19°22′ N, 96°53′ W, elevation 950 m) has a climate defined as (A)C(m)aig (semi-warm, humid) (García, 1973), with mean annual temperature of 25°C and 1250 mm rainfall and with a summer rainy season. Tejería (19°22′ N, 96°56′ W) is at an elevation of 1000 m. Climate is defined as (A)C(fm)a (semi-warm, humid) (García, 1973), with a mean annual temperature of 21°C and 1600 mm rainfall. There is no distinct rainy season. Monte Blanco (19°23′ N, 96°56′ W) is at an elevation of 1050 m. Climate is defined as (A)C(m)(w″)big (semi-warm, humid) (García, 1973), with mean annual temperature of 20°C and 1750 mm rainfall and with a summer rainy season. All material collected in the field was processed in Xalapa, Veracruz. Xalapa (19°31′ N, 96°54′ W) is at an elevation of 1440 m.

Parasitoid collection and processing. We surveyed parasitoids (1) in tree canopies and (2) at ground level.

Survey of parasitoids in tree canopies. The fruit tree species surveyed are summarized in Table 1. Only fruit that was about to fall from the tree was harvested. This allowed larvae to complete development and gave fruit fly parasitoids the opportunity to parasitize larvae throughout their development. To collect fruit, we used a ladder or climbed the tree. A plastic basket attached to a wooden pole (to reach all fruit) was placed beneath the fruit and the branch gently shaken. In this manner only fruit that abscised naturally after the branch shaking procedure were collected. With the exception of *Syzygium jambos* L., *Psidium guineense* Sw., *Myrciaria floribunda* (West) O. Berg. (Myrtaceae), *Calocarpum mammosum* L., *Chrysophyllum mexicanum* (Brandegce) ex. Standley (Sapotaceae), *Casimiroa edulis* Llave & Lex. (Rutaceae), and *Passiflora foetida* L. (Passifloraceae), which were in very short supply, all fruit were placed individually in plastic containers into which vermiculite or a mixture of sand and soil had been previously added (pupation medium for larvae). A hole was cut in the middle of the lid of each plastic container and then covered with organdy for ventilation. If, during harvest, a fruit fell to the ground, it was discarded. Any fruits lying on the ground were not considered for data analysis. We note that no insecticides were applied in any of the collection sites.

Survey of parasitoids at ground level. To ascertain if certain parasitoid species preferred to forage and parasitize larvae in fruit that had fallen from the tree canopy and to detect pupal parasitoids, we placed the following types of samples under the canopy of fruit trees in Apazapan (*Spondias purpurea* L.), Llano Grande (*Spondias mombin* L. and *Mangifera indica* L.) (all Anacardiaceae), and Tejería (*Psidium guajava* L.)

TABLE 1

Anastrepha Host Plants Surveyed during This Study

Local common name	Scientific name	No. of trees sampled	Family	Status
Guayaba	*Psidium guajava* L.	3	Myrtaceae	Native
Guayaba Tejón	*Psidium sartorianum* (Berg.) Ndzu.	2	Myrtaceae	Native
Guayabilla	*Myrciaria floribunda* (West) O. Berg	1	Myrtaceae	Native
Pomarrosa	*Syzygium jambos* L.	1	Myrtaceae	Native
Guayabe ćida	*Psidium guineense* Sw.	1	Myrtaceae	Native
Mango	*Mangifera indica* L.	2	Anacardiaceae	Exotic
Jobo	*Spondias mombin* L.	2	Anacardiaceae	Native
Ciruelo	*Spondias purpurea* L.	2	Anacardiaceae	Native
Cacao	*Tapirira mexicana* Marchand	1	Anacardiaceae	Native
Naranja dulce	*Citrus sinensis* (L.) Osbeck	2	Rutaceae	Exotic
Zapote Blanco	*Casimiroa edulis* Llave & Lex.	1	Rutaceae	Native
Zapote Mamey	*Calocarpum mammosum* L.	1	Sapotaceae	Native
Zapote Niño	*Chrysophyllum mexicanum* (Brandegee) ex. Standley	1	Sapotaceae	Native
Ciruela de monte or Ciruela ácida	*Ximenia americana* L.	2	Olacaceae	Native
Granada roja	*Passiflora foetida* L.	1	Passifloreaceae	Native

(Myrtaceae) and (*Citrus sinensis* L.) (Rutaceae): (1) infested fruit collected in the same site (and thus exposed to parasitism in the tree canopy); (2) fruit that was infested in the laboratory (and thus harboring unparasitized larvae); (3) unparasitized pupae obtained from laboratory fly colonies exposed in conjunction with uninfested fruit (pupae were mixed with soil and fruit placed on top of soil); and (4) unparasitized pupae obtained from laboratory fly colonies exposed alone (no fruit). In all cases, a plastic basket was used to hold infested and uninfested fruit. This basket was, in turn, placed over a plastic washbowl containing a pupation medium. In the case of pupae brought from the laboratory, these were directly placed in the pupating medium. Exposure units were protected from rain by means of plastic sheets placed over the washbowls ("roof" at ca. 50 cm from washbowl) and from ants by means of an adhesive (Insect Tangletrap Coating, Tanglefoot; Tanglefoot Co., Grand Rapids, MI) applied around the exterior part of the washbowls.

On occasion, when we encountered fruit of a species of fruit not included in our formal sampling scheme on the ground, we also collected it. This was the case with *C. mammosum*, *C. edulis*, *P. foetida*, *M. floribunda*, *C. mexicanum*, and *S. jambos*.

Sample processing. All sampled fruit was transported to the laboratory daily. Plastic containers were grouped on shelves (lumped by date of harvest). Then, every second day, they were inspected to ascertain if the vermiculite needed to be moistened or if the fruit was starting to rot. If a fruit was totally covered by mold or had disintegrated (due to rotting), it was removed from the container and dissected to determine if any live or dead larvae remained in the pulp. The vermiculite was also sifted to count the number of pupae. In each case, the number of live or dead larvae and the number of pupae were recorded. All live larvae and pupae were left in the container until either a fruit fly or a parasitoid emerged. During this time, vermiculite was moistened regularly. Fly or parasitoid emergence was checked every third day. At the end, we also counted the dead puparia. All parasitism values reported here are based on the number of emerging adult flies and wasps. We acknowledge that this estimate of parasitism places limitations on predicting the impact of the parasitoid on host population levels.

Parasitoid and fly identification. Parasitoids were identified by Robert Wharton at Texas A&M University (College Station, TX) and Lubomir Masner (Canada Bureau for Agriculture, Ontario, Canada). Flies were identified by Vicente Hernández-Ortíz at the Instituto de Ecología, A.C. (Xalapa, Veracruz). Voucher specimens were placed in the TAMU (Texas A&M University) and IXAL (Instituto de Ecología, A.C.) permanent insect collections.

RESULTS

We identified a total of 10 *Anastrepha* larval–pupal and pupal hymenopterous parasitoid species: *D. areolatus, D. crawfordi, Utetes anastrephae* (Viereck), *D. longicaudata*, *Opius hirtus* (Fisher), (Braconidae), *Aganaspis pellenaroi* (Brethes), *Odontosema anastrephae* Borgmeier (Eucoilidae), *A. indica* (Eulophidae) (all larval–pupal parasitoids), and *Coptera haywardi* (Oglobin) (Diapriidae) and *P. vindemiae* (Pteromalidae) (both pupal parasitoids). Of these, only *D. longicaudata*, *A. indica*, and *P. vindemiae* are not indigenous.

The degree of parasitization in fruit sampled in the tree canopies varied from year to year and especially between tree species. For example, in *S. purpurea* and *Tapirira mexicana* Marchand, (Anacardiaceae), there were 20- and 60-fold differences in parasitization of

TABLE 2

Anastrepha Parasitoids Identified in Central Veracruz, Mexico, during a 4-Year Study (1993–1996)

(A) Parasitoids Emerging from Fly-Infested Fruit Collected from Tree Canopies

Plant species	Parasitoid species[a] and proportion in sample[b]		*Anastrepha* species[c] and proportion in sample		No. and mean individual weight (g) of fruit sampled: No.	Mean weight	% Infested fruit (fly larvae)	% Pupae yielding a parasitoid or fly: % P	% F	N
Spondias purpurea										
1993	*D. a.*	1.8	*A. o.*	98.1	6095	24.08 ± 0.09	10.9	1.9	98.1	827
	U. a.	0.1								
1994	*D. a.*	41.3	*A. o.*	57.1	1823	18.09 ± 0.12	39.9	42.9	57.1	823
	U. a.	1.6								
Spondias mombin										
1993	*D. a.*	67.5	*A. o.*	22.8	1432	3.73 ± 0.03	90.0	77.2	22.8	1545
	U. a.	9.3								
	D. l.	0.3								
1994										
Tree 1	*D. a.*	37.2	*A. o.*	24.5	292	4.69 ± 0.07	91.8	75.5	24.5	713
	U. a.	38.3								
1994										
Tree 2	*U. a.*	44.8	*A. o.*	16.2	2115	7.93 ± 0.03	56.7	83.8	16.2	1599
	D. a.	38.8								
	D. l.	0.3								
1995	*D. a.*	32.2	*A. o.*	31.6	3811	5.13 ± 0.03	86.7	68.3	31.7	5881
	U. a.	36.2								
1996	*D. a.*	27.5	*A. o.*	21.7	2418	5.61 ± 0.03	79.9	78.3	21.7	3272
	U. a.	50.8								
Psidium guajava										
1993										
Tree 1	*D. l.*	14.2	*A. s.*	67.6	468	20.81 ± 0.36	94.2	24.6	75.4	2664
	A. p.	4.2	*A. f.*	7.8						
	D. c.	3.4								
	D. a.	2.9								
	U. a.	0.1								
1994	*D. l.*	1.4	*A. f.*	97.6	781	25.97 ± 0.36	80.4	1.9	98.1	1845
	A. p.	0.5	*A. s.*	0.5						
	D. a.	0.2								
	D. c.	0.1								
1995	*D. l.*	7.6	*A. s.*	43.1	413	24.61 ± 0.55	75.5	18.1	81.9	1131
	A. p.	6.1	*A. f.*	38.8						
	D. c.	1.8								
	D. a.	1.7								
	O. a.	1.0								
1996	*D. l.*	1.8	*A. s.*	9.3	1378	28.15 ± 0.25	85.1	18.6	81.4	7621
	A. p.	14.9	*A. f.*	72.1						
	D. c.	0.7								
	D. a.	1.0								
	O. a.	0.1								
	U. a.	0.1								
Psidium guineense										
1996	*D. l.*	3.0	*A. s.*	20.0	—	3.82 ± 0.31	—	8.5	91.5	434
	A. p.	3.0	*A. f.*	71.5						
	D. c.	0.7								
	D. a.	0.9								
	O. a.	0.5								
	U. a.	0.2								
	A. i.	0.2								
Citrus sinenis var. "corriente"										
1993	*D. l.*	9.1	*A. l.*	80.9	149	159.96 ± 2.65	87.25	19.1	80.9	1015
	D. c.	7.4								
	D. a.	2.3								
	A. i.	0.3								
	A. p.	0.1								

TABLE 2—*Continued*

Anastrepha Parasitoids Identified in Central Veracruz, Mexico, during a 4-Year Study (1993–1996)

(A) Parasitoids Emerging from Fly-Infested Fruit Collected from Tree Canopies

Plant species	Parasitoid species[a] and proportion in sample[b]		*Anastrepha* species[c] and proportion in sample		No. and mean individual weight (g) of fruit sampled: No.	Mean weight	% Infested fruit (fly larvae)	% Pupae yielding a parasitoid or fly: % P	% F	N
1994	D. l.	4.2	A. l.	72.2	348	138.44 ± 1.56	75.86	27.8	72.2	1670
	D. c.	22.6								
	D. a.	0.9								
	A. p.	0.2								
1996	*D. l.*	5.1	*A. l.*	79.7	204	145.58 ± 2.24	80.40	20.3	79.7	897
	D. c.	15.2								
Citrus sinensis var. navel										
1993	*D. c.*	0.6	*A. l.*	99.1	147	228.80 ± 4.17	74.2	0.9	99.1	694
	D. l.	0.3								
1994	*D. c.*	9.7	*A. l.*	88.1	111	290.93 ± 6.58	26.1	12.0	88.0	226
	D. l.	2.2								
Ximenia americana										
1993	*D. a.*	41.2	*A. a.*	58.8	67	5.55 ± 0.16	23.9	41.2	58.8	17
1995	*D. a.*	16.1	*A. a.*	77.2	1287	4.89 ± 0.05	11.1	22.8	77.2	162
	U. a.	6.8								
1996										
Tree 1	*D. a.*	49.5	*A. a.*	42.9	970	4.58 ± 0.03	40.9	57.1	42.9	630
	U. a.	7.6								
1996										
Tree 2	*D. a.*	64.4	*A. a.*	26.3	929	—	66.1	73.7	26.3	1199
	U. a.	6.3								
	O. h.	3.0								
Mangifera indica var. "criollo"										
1993	*D. a.*	0.4	*A. o.*	83.6	210	136.97 ± 2.52	44.3	0.4	99.6	274
			A. l.	16.0						
Mangifera indica var. "Kent"										
1994	*D. l.*	4.5	*A. l.*	93.3	58	816.82 ± 32.31	87.9	4.7	95.3	762
	A. p.	0.3	*A. o.*	2.0						
Tapirira mexicana										
1993	*D. a.*	36.8	*A. o.*	30.9	924	3.06 ± 0.04	36.0	69.0	31.0	155
	U. a.	21.3								
	D. l.	9.7								
	D. c.	1.3								
1995	—		*A. o.*	100.0	1500	4.87 ± 0.04	22.7	—	100.0	219
Psidium sartorianum										
1995	*U. a.*	10.6	*A. f.*	70.5	—	2.43 ± 0.03	—	21.5	78.5	750
	D. l.	4.8	*A. s.*	8.0						
	D. a.	3.1								
	A. p.	3.0								
1996	*U. a.*	4.0	*A. f.*	29.0	748	1.81 ± 0.02	54.3	11.0	89.0	100
	D. a.	4.0	*A. s.*	60.0						
	D. c.	3.0								
Myrciaria floribunda										
1994	*D. a.*	41.2	*A. b.*	58.8	—	3.68 ± 0.28	—	41.2	58.8	198
			A. f.							
			A. o.							
Passiflora foetida										
1992	—		*A. c.*	7.7	3	20.71 ± 3.02	—	—	100.0	13
			BF	92.3						
Syzygium jambos L.										
1995	*D. l.*	50.0	*A. f.*	50.0	11	20.75 ± 2.52	—	50.0	50.0	12
Casimiroa edulis										
1996	—		*A. l.*	100.0	—	150.12 ± 10.5	—	—	100.0	68
Calocarpum mammosum										
1996	*P. v.*	8.2	*A. se.*	91.8	—	363.96 ± 25.6	—	8.2	91.8	195
Chrysophyllum mexicanum										
1995	—		*A. h.*	100.0	—	36.02 ± 6.52	—	—	100.0	—

TABLE 2—*Continued*

(B) Parasitoids Emerging from Fly-Infested Fruit and Fly Pupae Placed at Ground Level

Plant species	Type of setup	Parasitoid species	Percentage parasitism	*Anastrepha* species
Citrus sinensis	Field-infested fruit	*D. longicaudata*	34.0	*A. ludens*
		C. haywardi	7.4	
		D. crawfordi	9.0	
		A. pellenaroi	0.8	
	Field cage or lab.-infested fruit	*D. longicaudata*	9.3	*A. ludens*
	Pupae from lab. with uninfested fruit	*C. haywardi*	22.5	*A. ludens*
	Pupae from lab. with no fruit	—	0	*A. ludens*
Psidium guajava	Field-infested fruit	*A. pellenaroi*	6.1	*A. fraterculus*
		D. longicaudata	1.2	
		C. haywardi	6.1	
	Field cage or lab.-infested fruit	*A. pellenaroi*	9.6	*A. striata*
		D. longicaudata	5.3	*A. fraterculus*
	Pupae from lab. with uninfested fruit	*C. haywardi*	15.0	*A. striata*
	Pupae from lab. with no fruit	—	0	*A. striata*
Spondias mombin	Field-infested fruit	*D. areolatus*	13.3	*A. obliqua*
		U. anastrephae	66.7	
	Field cage or lab.-infested fruit (none available)			
	Pupae from lab. with uninfested fruit	—	0	*A. obliqua*
	Pupae from lab. with no fruit	—	0	*A. obliqua*
Mangifera indica	Field-infested fruit	*D. longicaudata*	18.2	*A. obliqua*
				A. ludens
	Field cage or lab.-infested fruit	*D. longicaudata*	16.3	*A. obliqua*
	Pupae from lab. with uninfested fruit	—	0	*A. obliqua*
	Pupae from lab. with no fruit	—	0	*A. obliqua*
Spondias purpurea	Field-infested fruit	*D. areolatus*	51.3	*A. obliqua*
	Field cage or lab.-infested fruit	—	0	*A. obliqua*
	Pupae from lab. with uninfested fruit	—	0	*A. obliqua*
	Pupae from lab. with no fruit	—	0	*A. obliqua*

[a] *D. a., Doryctobracon areolatus; U. a., Utetes anastrephae; D. l., Diachasmimorpha longicaudata; D. c., Doryctobracon crawfordi; O. a., Odontosema anastrephae; A. p., Aganaspis pelleranoi; O. h., Opius hirtus; A. i., Aceratoneuromyia indica; P. v., Pachycrepoideus vindemiae.*

[b] Proportion in sample considering all individuals that emerged (both parasitoids and fruit flies). See next column (values add to 100%, adding proportion of parasitoids and fruit flies).

[c] *A. o., Anastrepha obliqua; A. l., Anastrepha ludens; A. s., Anastrepha striata; A. f., Anastrepha fraterculus; A. se., Anastrepha serpentina; A. c., Anastrepha chiclayae; A. h., Anastrepha hamata; A. b., Anastrepha bahiensis; A. a., Anastrepha alveata;* BF, unidentified black fly.

Anastrepha larvae when comparing years 1993/1994 and 1993/1995, respectively (Table 2A). In sharp contrast to this, in *S. mombin* the degree of larval parasitization remained quite stable over a period of 4 years (1993–1996). Marked yearly variations were also observed in *P. guajava.* In the case of *X. americana,* differences in degree of larval parasitization were observed not only in different years, but also in different trees sampled in a single year (Table 2A).

Anastrepha in mango seedlings (ungrafted "criollo" cultivar) and citrus (navel orange) had the lowest parasitism rates. These two fruit species (both exotic) had the heaviest fruit of all species we sampled (Table 2A). Highest levels of parasitism were recorded in the native species *S. mombin,* which is one of the smallest fruit sampled (Table 2A). Overall (i.e., considering all fruit sampled), there was a significant negative correlation between fruit size and degree of parasitization (Fig. 1).

D. areolatus, A. pellenaroi, U. anastrephae, and *D.*

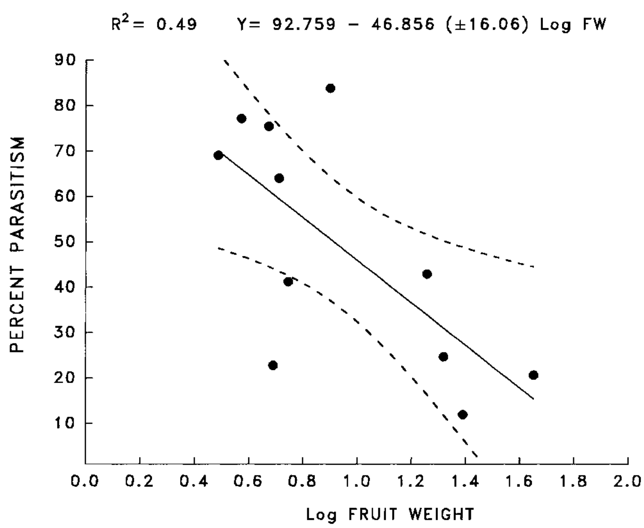

FIG. 1. Effect of fruit size on rate of parasitism by parasitoids attacking *Anastrepha* spp. larvae. Dotted lines represent 95% confidence limits.

longicaudata parasitize larvae in fallen fruit. These species were the only ones that parasitized larvae in fruit that had been artificially infested in the laboratory and then placed under the canopy of a fruit tree (Table 2B). Interestingly, *C. haywardi* parasitized only pupae that were placed together with fruit (Table 2B).

D. areolatus was the most abundant parasitoid species and also the one with the widest host breadth (Table 3). Of the 15,066 parasitoids collected, 43.7% were *D. areolatus* (Table 4). This species attacked larvae of six *Anastrepha* species (*Anastrepha alveata* Stone, *Anastrepha bahiensis* Costa Lima, *A. fraterculus*, *A. ludens*, *A. obliqua*, and *A. striata*) in 10 plant species among four families (Anacardiaceae, Myrtaceae, Olacaceae, and Rutaceae). *D. crawfordi* was most abundant in citrus fruit in which it attacked larvae of *A. ludens* but occasionally parasitized larvae in guavas, whereas *A. pellenaroi* and *O. anastrephae* were found almost exclusively in guavas (*P. guajava*, *P. sartorianum*, and *P. guineense*) in larvae of *A. striata* and *A. fraterculus*. *O. hirtus* was only found attacking *A. alveata* larvae in *X. americana* (Table 2A). Thus, all larval–pupal parasitoids identified in this study, with the exception of *O. hirtus*, can be considered general-

TABLE 3

Rank of Parasitoid Species Based on Host Breadth

Parasitoid species	Rank	Plant species visited	Fly species attacked
Doryctobracon areolatus	1	*Spondias purpurea*	*Anastrepha alveata*
		Spondias mombin	*A. bahiensis*
		Ximenia americana	*A. fraterculus*
		Tapirira mexicana	*A. ludens*
		Psidium guajava	*A. obliqua*
		Psidium sartorianum	*A. striata*
		Psidium guineense	
		Citrus sinensis	
		Myrciaria floribunda	
		Mangifera indica	
Diachasmimorpha longicaudata	2	*Syzygium jambos*	*A. ludens*
		Spondias mombin	*A. obliqua*
		Tapirira mexicana	*A. striata*
		Psidium guajava	*A. fraterculus*
		Psidium sartorianum	
		Psidium guineense	
		Citrus sinensis	
		Mangifera indica	
Utetes anastrephae	3	*Spondias purpurea*	*A. alveata*
		Spondias mombin	*A. fraterculus*
		Ximenia americana	*A. obliqua*
		Tapirira mexicana	*A. striata*
		Psidium guajava	
		Psidium sartorianum	
		Psidium guineense	
Doryctobracon crawfordi	4	*Psidium guajava*	*A. ludens*
		Psidium sartorianum	*A. obliqua*
		Psidium guineense	*A. striata*
		Citrus sinensis	*A. fraterculus*
		Tapirira mexicana	
Aganaspis pellenaroi	5	*Psidium guajava*	*A. ludens*
		Psidium sartorianum	*A. obliqua*
		Psidium guineense	*A. striata*
		Citrus sinensis	*A. fraterculus*
		Mangifera indica	
Odontosema anastrephae	6	*Psidium guajava*	*A. striata*
		Psidium guineense	*A. fraterculus*
Aceratoneuromyia indica	7	*Psidium guineense*	*A. ludens*
		Citrus sinensis	*A. striata*
			A. fraterculus
Coptera haywardi	8	*Psidium guajava*	*A. striata*
		Citrus sinensis	*A. fraterculus*
			A. ludens
Opius hirtus	9	*Ximenia americana*	*A. alveata*
Pachycrepoideus vindemiae	10	*Calocarpum mammosum*	*A. serpentina*

ists. They attacked not only larvae of various *Anastrepha* species, but also searched for these larvae in different fruit species (Table 2A, Table 5).

Fruits of *S. mombin* yielded the highest mean number of parasitoids per kg/fruit (206.7) and *M. indica* cultivar "Kent" the smallest number (0.75). With respect to the diversity of parasitoids harbored per fruit or fruit species, guavas (*P. guajava* and *P. guineense*) yielded the highest values. During 1993, a single fruit of *P. guajava* (collected from the tree crown) harbored two fruit fly species (*A. fraterculus* and *A. striata*) and five parasitoid species (*A. pellenaroi*, *D. areolatus*, *D. crawfordi*, *D. longicaudata*, and *U. anastrephae*).

Pachycrepoideus vindemiae was not abundant in our study sites. The few parasitized pupae we collected stemmed from *C. mammosum*. Larvae pupated inside the fruit and, through this fortuitous event, we were able to obtain the parasitoids when we brought the fruit to the laboratory.

The site where the most species of larval–pupal parasitoids were identified was Tejería (Table 6). Interestingly, in this site *D. areolatus* was less abundant than in all other sites. In Apazapan, only *D. areolatus* and *U. anastrephae* were identified (Table 6).

DISCUSSION

Five findings of the present survey are particularly noteworthy: (1) the high diversity of native *Anastrepha* parasitoids, (2) the relative abundance of *D. areolatus*, (3) the commonness of a native parasitoid (*D. crawfordi*) in an exotic fruit fly host plant (*C. sinensis*), (4) the wide host breadth exhibited by most larval–pupal parasitoids reported here (expressed both in terms of species of *Anastrepha* larvae attacked and *Anastrepha* host plant species visited), and (5) the important role that native host plants play as reservoirs of *Anastrepha* parasitoids.

The number of parasitoid species in our study sites was high compared to other similar studies in Mexico. This may be the result of a highly heterogeneous environment that offered parasitoids the opportunity to parasitize larvae or pupae in many types of wild and cultivated fruit throughout most of the year. It is significant that this pattern was maintained even in a very small area. For example, in Tejeria four species of plants harbored over five species of larval–pupal parasitoids (six, five, seven, and five for *P. guajava*, *P. sartorianum*, *P. guineense* (native), and *C. sinensis* (exotic), respectively). We also found two species of pupal parasitoids there.

Of all the parasitoids collected in the four study sites, ca. 44% were *D. areolatus*. This pattern of abundance was reported previously by Hernández-Ortíz *et al.* (1994) collecting in a tropical rainforest in southern

TABLE 5

Parasitoid Abundance (Percentage of Total Collected) in Most Representative Fruit Fly Host Plants

Fruit fly host plant	Parasitoid species	Total number	Percentage of total by plant host
Psidium guajava	*Aganaspis pelleranoi*	1326	57.53
	Diachasmimorpha longicaudata	621	26.94
	Doryctobracon areolatus	173	7.50
	Doryctobracon crawfordi	161	6.98
	Odontosema anastrephae	18	0.78
	Utetes anastrephae	6	0.27
Citrus sinensis	*Doryctobracon crawfordi*	588	69.92
	Diachasmimorpha longicaudata	208	24.73
	Doryctobracon areolatus	38	4.52
	Aganaspis pelleranoi	4	0.47
	Aceratoneuromyia indica	3	0.36
Tapirira mexicana	*Doryctobracon areolatus*	57	53.27
	Utetes anastrephae	33	30.84
	Diachasmimorpha longicaudata	15	14.02
	Doryctobracon crawfordi	2	1.87
Spondias mombin	*Utetes anastrephae*	4922	51.00
	Doryctobracon areolatus	4719	48.90
	Diachasmimorpha longicaudata	9	0.09
Ximenia americana	*Doryctobracon areolatus*	1117	86.79
	Utetes anastrephae	134	10.41
	Opius hirtus	36	2.80
Mangifera indica	*Diachasmimorpha longicaudata*	34	91.89
	Aganaspis pelleranoi	2	5.41
	Doryctobracon areolatus	1	2.70
Spondias purpurea	*Doryctobracon areolatus*	355	96.20
	Utetes anastrephae	14	3.80
Citrus sinensis (Wash.)	*Doryctobracon crawfordi*	26	78.78
	Diachasmimorpha longicaudata	7	21.21

TABLE 4

Overall Abundance (Percentage of Total Collected) of Larval–Pupal and Pupal Parasitoids (All Study Sites Considered)

Parasitoid species	Total number	Percentage of total
Doryctobracon areolatus	6579	43.67
Utetes anastrephae	5200	34.51
Aganaspis pellenaroi	1387	9.21
Diachasmimorpha longicaudata	946	6.28
Doryctobracon crawfordi	788	5.22
Coptera haywardi	90	0.60
Opius hirtus	36	0.24
Odontosema anastrephae	20	0.13
Pachycrepoideus vindemiae	16	0.11
Aceratoneuromyia indica	4	0.03

TABLE 6

Parasitoid Abundance (Percentage of Total Collected) in Each of Four Study Sites

Study site	Parasitoid species	Total number	Percentage of total	Percentage of total global (15,066)
Llano Grande	*Doryctobracon areolatus*	5864	52.60	38.92
	Utetes anastrephae	5140	46.11	34.12
	Diachasmimorpha longicaudata	78	0.70	0.52
	Opius hirtus	36	0.32	0.24
	Aganaspis pelleranoi	22	0.20	0.15
	Doryctobracon crawfordi	7	0.03	0.05
	Total	11,147	100.00	74.00
Tejeria	*Aganaspis pelleranoi*	1356	40.61	9.00
	Diachasmimorpha longicaudata	862	25.81	5.72
	Doryctobracon crawfordi	781	23.40	5.18
	Doryctobracon areolatus	218	6.53	1.44
	Coptera haywardi	90	2.70	0.60
	Odontosema anastrephae	20	0.59	0.13
	Utetes anastrephae	8	0.24	0.05
	Aceratoneuromyia indica	4	0.12	0.03
	Total	3339	100.00	22.15
Apazapan	*Doryctobracon areolatus*	437	96.90	2.90
	Utetes anastrephae	14	3.10	0.09
	Total	451	100.00	2.99
Monte Blanco	*Doryctobracon areolatus*	57	44.19	0.37
	Utetes anastrephae	33	25.58	0.22
	Diachasmimorpha longicaudata	21	16.28	0.14
	Pachycrepoideus vindemiae	16	12.40	0.12
	Doryctobracon crawfordi	2	1.55	0.01
	Total	129	100.00	0.86

Veracruz, by Canal *et al.* (1995) and Leonel *et al.* (1995) collecting in various parts of Brazil, and by Katiyar *et al.* (1995) collecting in Venezuela. *D. areolatus* has also been reported in studies in Guatemala (Eskafi, 1990), Costa Rica (Jirón and Mexzon, 1989), Colombia (Yépes and Vélez, 1989), and Argentina (Ovruski, 1995). It is thus a widely distributed species that exhibits a broad host range.

The most common parasitoid in oranges (an exotic fruit fly host plant introduced to the region during the Spanish conquest) was the native species *D. crawfordi*. This species far outnumbered the exotic species *D. longicaudata* in our study sites. The only other fruit that yielded *D. crawfordi*, albeit in small numbers, were guavas and *T. mexicana*. Two interesting hypotheses emerged from these discoveries: (1) Since *D. longicaudata* was introduced to the region only 30 years ago (Jiménez-Jiménez, 1956), it is likely that there is an ongoing process of niche partitioning between these two fruit fly parasitoid species. Sivinski *et al.* (1997) found evidence of competition between *D. crawfordi* and *D. longicaudata* in the same study region. This is in contrast to an apparently less competitive interaction between two native parasitoids in a native host plant (*D. areolatus* vs *U. anastrephae* in *S. mombin*). The two native species have interacted over a long period, and as a result their niches have diverged. (2) Of all the native parasitoid species identified here, *D. crawfordi* has the longest ovipositor. This, we believe, has allowed this species to exploit a larval resource occurring at greater depth in the fruit pulp (an orange is 6–12 and 40 times larger than a guava and a *S. mombin* fruit, respectively). Given the close association of *D. crawfordi* and citrus fruit, we wonder in what trees this parasitoid foraged before citrus were introduced ca. 400 years ago, and if the introduction of citrus allowed *D. crawfordi* to escape competition through expansion of its niche.

As reported previously (Sivinski, 1991; Hernández-Ortíz *et al.*, 1994) we found that cultivated fruit harbored significantly fewer parasitoids than wild fruit. Furthermore, we were able to confirm the observation by Sivinski (1991) that there is a negative correlation between size of fruit and percentage parasitism (Fig. 1). This has interesting evolutionary and ecological implications. Fruit flies are able to escape parasitism if they infest large, exotic, fruit. For example, in this study parasitism in mango and navel oranges was very low. These fruits are 10 to 270 times larger than *S. mombin* or *T. mexicana* fruit (both native species). A switch from a native plant to an introduced one that allows fruit flies to escape parasitism has been documented and discussed by Monteith (1971) and Gut and Brunner (1994). These authors showed that the apple maggot (*Rhagoletis pomonella* [Walsh]) is parasitized when it infests its native host (*Crataegus* spp.), but is not when infesting the larger fruits of an exotic host, apple. Another implication of low parasitism in introduced fruits is that, by replacing native fruit trees with exotic ones, there is a chance of causing the local disappearance of an entire guild of native fruit fly parasitoids.

Two practical implications can be drawn from our study: (1) the need to protect parasitoid reservoirs and (2) the possibility of using native parasitoid species in fruit fly control programs. It becomes obvious from this and similar studies (e.g., Hernández-Ortíz *et al.*, 1994; Canal *et al.*, 1995; Leonel *et al.*, 1995) that wild plants play an important role as parasitoid reservoirs. For example, in our study *S. mombin*, *P. guajava*, *P. sartorianum*, *P. guineense*, and *X. americana* yielded significant numbers of parasitoids. These reservoirs are disappearing at a rapid rate due to clearing of land for agriculture. We are therefore currently trying to develop schemes through which parasitoid reservoirs can be managed to naturally augment parasitoid numbers and to sustain parasitoid populations in areas of native vegetation. The case of *X. americana* is particularly interesting because it is infested by a fruit fly of no economic importance (*A. alveata;* Piedra *et al.*, 1993). Because it also harbors large populations of *D. areolatus* and smaller numbers of *U. anastrephae* and *O. hirtus*, it could be used to supplement parasitoid numbers without the danger of increasing the populations of pestiferous fruit flies.

The present survey suggests that there may be advantages to mass-rearing and augmenting native parasitoids. The biological control of *Anastrepha* has been attempted by introducing a large number of exotic egg, larval–pupal, and pupal parasitoids (Jiménez-Jiménez, 1956, 1967). This study and work elsewhere (e.g., Leonel *et al.*, 1995; Canal *et al.*, 1995) clearly show that native parasitoids are abundant and widespread. Furthermore, we show that many of the larval–pupal and pupal parasitoids reported here are notorious generalists. They visit many species of *Anastrepha* host plants and at the same time attack many species of *Anastrepha* larvae. At present, the exotic larval–pupal parasitoid *D. longicaudata* has been mass-reared and released in Florida (Sivinski *et al.*, 1996), Mexico (Jesús Reyes, personal communication), and Guatemala (J. Sivinski, unpublished data). However, this species may not be well adapted to all environmental conditions. The diversity of native species may allow the choice of one or more species adapted to a particular place and time. For example, *D. areolatus* has proven to be the most widespread species. *D. crawfordi* appears to do well in citrus. *A. pellenaroi* and *O. anastrephae* are two species that can be effective in guava plantations. *O. hirtus* seems to be very effective at low fly densities (J. Sivinski and M. Aluja, unpublished data). Furthermore, it may be beneficial to release a larval–pupal and a pupal parasitoid at the same time. Thus, a broader range of potential hosts can be targeted. In the past, this was attempted only with two parasitoids exotic to the New World: *D. longicaudata* and *P. vindemiae* (Sivinski, 1996). *Coptera haywardi* is a potentially ideal candidate to substitute for *P. vindemiae* since it is an endoparasitoid highly specific to fruit flies (Sivinski *et al.*, 1998). In contrast, *P. vindemiae* is a generalist that can attack beneficial Diptera and that loses effectiveness as the targeted pest becomes increasingly rare.

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